Forecasting Future Invasion Potential and Suitable Habitat Range Shift for Lantana camara in Uganda Under Changing Climate Scenarios

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Abstract

Background

Lantana camara, which originated from tropical America, is one of the top 10 invasive plant species globally, and among the top contributors to biodiversity and habitat losses in tropical Africa. Worst of all, its impacts and invasion potential tend to be compounded by climate change driven by ever-rising greenhouse gas (GHG) emissions. Numerous studies have revealed that climate change will continue to change habitats and increase its invasion risk. The findings from the study focused on assessing habitat suitability of *Lantana camara* in Uganda under both current and future environmental conditions. This will help to address the knowledge gap on their future invasion potential, and habitat shift in Uganda with the changing climate conditions. Our study was intended to evaluate the current invasion potential of *Lantana camara* within Uganda across various climatic conditions and predict their future distributions. We used the Maximum Entropy model with 1,001 cleaned species occurrence points retrieved from GBIF databases and nine climate uncorrelated variables for the model.

Results

The study showed that 47.2% (113,992 km^2) of Uganda's land is currently not suitable for *Lantana camara* invasion, while 6.8% (16,423 km^2) is highly suitable for its invasion. The results revealed substantial increase in highly suitable areas for invasion by 225.0% (36,960 km^2) in the future year 2070s' under SSP5-8.5. However, it is predicted that the unsuitable area will shrink to 32.8% (79,228 km^2) by 2070 under SSPs5-8.5 climate scenario. These results imply that *Lantana camara* will spread significantly as future climate change creates condition more favorable to its growth while rendering the environment less suitable to native flora.

Conclusions

The findings of this study could serve as an evidence-based tools for early identification of areas prone to future invasion, thereby guiding policymakers to come out with possible mitigation strategies.

Background

Invasive alien plant species (IAPS) impose significant risk on global ecosystem, ecological integrity, and biodiversity, especially in regions with vulnerable ecosystems and limited management policy, as they are listed as the main factor for biodiversity loss [1, 2]. Invasive plants are potentially capable of negatively affecting all biodiversity components within ecosystems. Even just about 10% of invasive plants can alter the nature, environment, plant cover, or species interaction within ecosystems in a short period of time [3].

One of the IAPS, *L. camara*, which was predominantly brought to the African continent by the early 19th century [4], originated from tropical America, and has emerged among the most aggressive invasive plants [5]. *Lantana camara*, a shrubby species, also ranked among the 10 most invasive plants globally, and among the 100 most aggressive alien invasive plants worldwide by the IUCN [5, 6].

In Africa, *L. camara* was initially brought as an ornamental plant and live fence uses by the British in the 19th century [7, 8]. It has since expanded widely over the continent, occupying different habitats and posing a severe threat to the ecosystem, biodiversity, agriculture, and land use systems [7]. Its ability to coppice, flower, and produce fruits throughout the year, and poisonous leaves are just a few of the many morphological attributes that have contributed to its widespread throughout the African continent at a high rate [9].

Most notably, the species have the ability to produce allelopathic chemicals that inhibit and suppress the germination and growth of nearby plant species. This is one of its outstanding attributes to avoid competition over natural resources and result in formation of invasive monotypic stands [10]. Unfortunately, climate change aggravated the invasive nature of *L. camara*, which is predicted to shift distribution and increase their suitable habitats and spread into previously uncolonized areas [11].

In Uganda, *L. camara* is spreading quickly throughout the country and is a common invasive species, especially in Kibale National Park. Its unique competitive advantage for natural resources prevents other native plant species from regenerating [12, 13]. Despite *L. camara* being regarded as the worst invasive plant globally [10], its current and future potential distribution within Uganda is yet less understood. It is very important to understand its distribution across Uganda landscapes, to predict how they will be spatially distributed in different ecological zones of Uganda and their impacts on difference native plants.

This will help in formulating Uganda specific strategy for managing their spreads, which is very key in informing timely and spatially targeted management interventions. In Uganda, *L. camara* has caused over 25% declined in crop production and has also resulted into over 50% loss of rangeland in pastoralists areas due to encroachment. This is attributed to their aggressive potential of invading large area of land within a short period [5, 7].

The continuous global rise in temperature and reduction of precipitation is expected to trigger further biological invasion and their impacts in Uganda. Regional studies on climate change, such as temperature rise for Africa also in agreement with what has been found for Uganda [14]. Therefore, it is logical to carefully study on a global, regional, and national level how *L. camara* distribution will be impacted by climate change over time [4, 5].

We used MaxEnt (Maximum Entropy modeling) as one of the species distribution models (SDMs) for species habitat suitability shift projection with different environmental conditions and climatic conditions [15]. Several studies within East Africa, especially in Ethiopia, have applied MaxEnt to predict the invasive species spatial distribution. Nonetheless, most of these studies have been conducted at a broad regional East Africa scale, and in some nations such as Ethiopia, yet very few have focused specifically on Uganda. A site-specific study is lacking in Uganda in order to guide policy and decision makers in IAS eradication. Integrating climate projections from global climate models (GCMs) under different climate scenarios can provide an insight into how *L. camara* habitat may shift over the coming decades [16].

This study aimed to analyze the present distribution of *L. camara* and forecast its potential habitat shift within the Ugandan landscape in the future. It also addressed the following specific objectives: (1) map the current suitable habitats, (2) project potential shifts in its habitat range, and (3) spot out vulnerable areas for surveillance and policy and strategic intervention. By modeling future *L. camara* invasion potential in Uganda, this study will support conservation authorities and policymakers in designing a proactive mitigation approach. Thus, eradicating its environmental and socio-economic impacts. Moreover, forecasting potential distributions of invasive plants such as *L. camara* is very crucial for proper management of their spread [11].

Methods

Study Area

This study was done in Uganda, which is situated at the heart of East Africa (Fig. 1). It covers more than 241,000 km^2 and is located between 1.5° and 4° latitude and longitude 29.5° to 35°. It is a landlocked country and bordered by Kenya, Tanzania, the DRC Congo, and South Sudan to the East, South, West, and North, respectively [17]. The country is renowned for its rich ecological zones and varied geography, which range from tropical rainforests and montane ecosystems. This is an important part of the biodiversity-rich Albertine Rift because of the variety of habitats supported by its environment [18]. Its Altitude ranges from 620 m.a.s.l. around the Albert Nile Basin to the highest 5,100 m.a.s.l. at Africa's third-highest mountain, Mount Rwenzori (Fig. 1).

Uganda has a tropical climate, with bimodal rainfall where the first season starts from March to May, and the second season starts from September to November. Uganda experiences total mean temperatures ranging from 16°C to 30°C per year [19]. Such conditions, together with anthropogenic pressures, have created an ideal condition for invasive plant species. *Lantana camara* has invaded over 66 km^2 of the two most protected and important National game parks in Uganda, such as Queen Elizabeth and Bwindi Impenetrable National Park, and this shows their aggressive potential in the country regardless of protected area [20].

Species Descriptions

Lantana camara is a woody, aromatic, perennial shrub form plant originates from tropical America [21]. It was primarily brought to the African continent in the early 19th century by the British during their time of colonization for two main purposes (to be used as a life fence and compound decoration/ornamental)

[8]. The species is a multi-stemmed, deciduous plant that reaches up to 2m in average height of growth [22]. The species also typically possess a wide variety of morphological traits, such as woody stems with recurved prickles, coarse leaves with fine hairs, and clusters of fragrant flowers which flower [23].

Most notably, the species' ability to produce allelopathic chemicals, serves as a defense mechanism, which contributes to its ability to rapidly invade new areas and become the dominant plant within a relatively short period [24]. *Lantana camara* invasion is more common and sever in areas that have been disturbed, riverbank, forest edge, roadsides, and degraded areas. It reduces biodiversity and ecological functioning within the ecosystem by outcompeting native plants through allelopathy, canopy shade, and nutrient competition [25, 26]. In Uganda, it is widely distributed across central, eastern, and south-western regions, especially in protected areas and agricultural landscapes [27].

Collection of Species Occurrent Data

The *Lantana camara* species occurrence data were retrieved from the Global Biodiversity Information Facility database (GBIF). It's accessed from the website (www.gbif.org), which were obtained on 01 July 2025 using the link https://doi.org/10.15468/dl.jyb7u9. A total of 1,036 *L. camara* occurrence data were initially downloaded. In Addition, occurrence data were supplemented with field survey records and locality data extracted from literature reviewed from the previous studies conducted in Uganda to ensure comprehensive spatial coverage.

According to previous studies conducted in Uganda, *L. camara's* localities were reported to currently abundant and widespread in the areas around Lake Victoria, Queen Elizabeth National Park, Kibale National Park. It's also reported in the districts such as Masindi, Nakasongola and Nakaseke in central part of Uganda in the district [3, 7, 13]. After cleaning and removal of duplicates, 1,001 occurrence coordinate points (Fig. 1) for *L. camara* were eventually used for the model construction. To minimize spatial autocorrelation and sampling bias, species occurrence locality points were spatially filtered using a minimum distance threshold of 1 km between locality in ArcGIS version 10.8. Particularly, SDM Toolbox in ArcGIS which reduces clustering effects hence improving model robustness was used.

Predictor variables

Using the Worldclim database, 19 bioclimatic variables were also retrieved from their website (www.worldclim.org) [28], which was accessed on 01 July 2025 with a spatial resolution of 2.5 minutes [29]. To avoid the correlated variables, we used the Pearson correlation coefficient to analyze the strong relationship among the 19 bioclimatic variables downloaded. Based on the Pearson correlation result, nine variables with a correlation coefficient value below the cutoff limit were included for the model analysis. The correlation coefficient value of 0.75 was used as a cutoff point to include bioclimatic variables (Table 1).

At the end, variables were reduced to a subset of less correlated and more significant variables [30], which includes: Bio1, Bio2, Bio4, Bio12, Bio15, Bio17, and Bio19, with a correlation coefficient below 0.75, were chosen. Additionally, land use, elevation, NDVI, and soil types were regarded as one of the key important variables in this study, and also incorporated into the analysis as a conservative variable (Table 1).

Soil pH and soil texture were extracted from ISRIC SoilGrids [31] using Google Earth Engine (GEE). Elevation data were sourced from the Shuttle Radar Topography Mission (SRTM) [32] via Google Earth Engine. Lastly, Vegetation indices (NDVI minimum and maximum) were derived from MODIS Collection 6 [33] using Google Earth Engine.

Table 1
Important selected variables used for predicting the distribution of *L. camara* in Uganda.

Variable	Variable Name/Description	Unit	Source
Bio1	Annual Mean Temperature	Millimeters (mm)	WorldClim
Bio2	Diurnal Range (Mean of Monthly (Max temp.-min temp.))	Degree Celsius (^{0}C)	WorldClim
Bio4	Temperature Seasonality	Degree Celsius (^{0}C)	WorldClim
Bio12	Annual Precipitation	Millimeters (mm)	WorldClim
Bio15	Precipitation Seasonality (coefficient of variable)	Percentage (%)	WorldClim
Bio17	Precipitation of the Driest Quarter	Millimeters (mm)	WorldClim
Bio19	Precipitation of Coldest Quarter	Millimeters (mm)	WorldClim
Elevation	Altitude above sea level	Meter (m)	SRTM
Land use	Land cover classification (e.g., forest, agriculture, urban)	Categorical	GEE (MODIS)
Soil pH	Soil acidity/alkalinity	Unitless	ISRIC SoilGrids
Soil texture	Soil particle composition (e.g., sandy, loamy, clayey	Categorical	ISRIC SoilGrids
NDVI Min	Minimum normalized difference vegetation index	Unitless	GEE (MODIS)
NDVI Max	Maximum normalized difference vegetation index	Unitless	GEE (MODIS)

Future Climate Projections

Three Global Climate Models (GCMs) from Coupled Model Intercomparison Project-Phase 6 (CMIP6), were selected for this model to project the future potential range shift of *L. camara's* habitat in Uganda under climate change. Those three GMs were, MIROC6, ACCESS-CM2, and MPI-ESM1 2 HR. These models were selected based on their previous demonstrated used in simulating East African climate drivers, which are critical for ecological modeling in Uganda.

The MPI-ESM1-2-HR provides high-resolution simulations of rainfall and temperature variability, and representation of the bimodal rainfall pattern and was recently employed in one of the studies in East Africa, Ethiopia with SDMs [34]. ACCESS-CM2 incorporates advanced ocean–atmosphere coupling and aerosol schemes, making it very effective in capturing large-scale circulation patterns such as the Indian Ocean Dipole, which strongly influences Uganda's rainfall seasonality. Moreover it has been used in species distribution projection in East Africa, Ethiopia [35]. The MIROC6 offers balanced climate sensitivity and improved representation of ENSO variability. This makes it an importance driver of interannual rainfall fluctuations across East Africa, thereby enhancing reliability of invasive species projections in Uganda. By using these three GCMs, the model captures a wide range of uncertainty in precipitation and temperature projections, while reducing regional bias through diverse institutional origins (Europe, Australia, and Asia).

This ensemble approach ensures that suitable habitat modeling of *L. camara* in Uganda is based on climate scenarios that reflect both local and global rainfall pattern. Such robustness is crucial for predicting the species' potential distribution under future climate conditions and for prior informing conservation and management strategies in Uganda. Most importantly, all the three selected CMIP6 GCMs have all been applied in previous East African climate studies [35]. Importantly, they have demonstrated skill in simulating rainfall pattern, ENSO variability, and Indian Ocean Dipole influences that are critical for Uganda's ecosystem.

The application of three GCMs made our study less reliance on the structure of a single model, which is crucial for ensemble forecasting and improves the projections' resilience and accuracy. To comprehend potential climate change effects without exaggerating or underestimating, we examined the average forecast raster produced by the three GCM models under three Shared Socio-economic Pathways (SSPs): SSP1-2.6, SSP2-4.5, and SSP5-8.5. Projected year, 2050 (average for 2041–2060) and 2070 (average for 2061–2080) (2070s) were selected among the three Shared Socio-economic Pathways (SSPs) for assessment [29, 36].

To ensure robust simulation of *L. camara* distribution under climate change in Uganda, we selected three CMIP6 Shared Socioeconomic Pathways (SSP126, SSP245, and SSP585). These scenarios captured low, intermediate, and high greenhouse gas emission trajectories. Among the SSPs, SSP126 scenario is the most aggressive in terms of Greenhouse gas (GHG) emissions reductions [37]. It represents a sustainability-oriented pathway with strong mitigation, aligning with conservation-focused projections of invasive species spread [7, 34]. We included SSP245 as a "middle-of-the-road" scenario to represent moderate greenhouse gas emissions and socioeconomic development, consistent with recent ecological niche modeling of *L. camara* in Ethiopia [38]. SSP585 depicts a fossil-fueled development pathway with very high emissions, serving as a worst-case scenario to stress-test species vulnerability, consistent with recent modeling of *L. camara* range shifts under climate change in Ethiopia [38].

By including these three SSPs, our modeling framework captured best-case, intermediate, and worst-case trajectories, ensuring transparent and reproducible assessment of invasive species spread in Uganda. Finally, using ArcGIS version 10.8 software [39], the climate scenario data were spatially downscaled and retrieved to the extent of this study area.

The MaxEnt Algorithm

The Maximum Entropy (MaxEnt) model is a machine learning algorithm and one of the SDM tools. It’s mostly used for modeling and predicting species distributions or the suitability of habitat using occurrence data of species and associated environmental variables [37, 40, 41]. MaxEnt offers numerous advantages compare to other modeling techniques. These include its ability to handle big and small sample sizes, incorporating both categorical and continuous environmental variables, and producing interpretable ecological output data [42].

MaxEnt is also computationally efficient and provides valuable ecological insights through variable importance analysis and response curves [43]. MaxEnt is normally used to predict the probability distribution of habitat suitable for particular species based on the principle of maximum entropy, which is common in biodiversity studies [39, 44].

The study used MaxEnt version 3.4.4 [29, 41], and *L. camara* occurrence records were divided into two (25% for model validation and 75% for model training), which is a widely accepted ratio in SDM [45–47]. We enabled linear, quadratic, and product features to ensure that the model capture the relationships between environmental predictors and species presence. This is align with best practices for modeling invasive species, where nonlinear responses are common issue [48].

The number of background points was set to 10,000, a widely recommended default that balances adequate representation of environment variables with computational efficiency [29, 42, 47]. To minimize overfitting and maintain the model's ability to generalize while retaining significant ecological information, a regularization multiplier was set to 3 [39, 49].

To improve the model robustness and account for variability, we ran 10 replicates, which provides averaged performance metrics and reduces bias from single random partitions [41, 50]. To guarantee model convergence even under complex feature combinations, the maximum iterations were set at 5,000 [29, 41]. Finally, we adopted the 10-percentile training presence threshold for binary conversion. This is because it’s a conservative approach that excludes the lowest suitability records and has been widely used in invasive species distribution modeling to minimize commission errors [45].

The Area Under Curve (AUC) of the Receiver Operating Characteristic Curve (ROC) was used to analyze the performance of the model [29, 41]. The AUC values range between 0–1, where values were interpreted as follows: no better than random (AUC ≤ 0.5), poor to fair low performance (0.5 ≤ AUC ≤ 0.7), good to very good (0.7 AUC ≤ 0.9), and excellent (AUC > 0.9) [21, 36]. Finally, we used Jackknife tests for the examination of each environmental variable's contributions to the model [29, 40, 47]. The conceptual workflow of this study is illustrated below (Fig. 2).

The Model Statistical and Spatial Analysis

In order to estimate the likely suitable area, we used ArcGIS 10.8, and we did a reclassification of habitat suitability projected in future years. The logistic probability of presence thresholds generated by the model was used for the classification of different habitat suitability levels for the *L. camara* [22]. The map generated by the model was reclassified into four clusters of suitability according to [51] as: (0-0.25), not suitable, (0.25–0.50), least suitable, (0.50–0.75), moderately suitable, and (0.75-1.0), highly suitable [41].

The distribution area changes of *L. camara* were calculated, using ArcGIS, and we obtained the future area suitability for the period 2050s (2041–2060) and 2070s (2061–2080) under three Shared Socio-economic Pathways (SSPs): SSP1-2.6, SSP2-4.5, and SSP5-8.5. The year range 2041–2060 is averaged to get values for 2050s and 2061–2080 for 2070s. This time span is chosen for comprehending of mid-term and long-term effects of the species. Thus, offering near future early detection and long-term crucial planning, decision -making framework informed by future *L. camara* distribution pattern.

Area Change Analysis

To evaluate the change in suitable habitat for the species, we primarily identified areas, where habitat non-suitability and suitability status changes as projected in to the 2050s and 2070s. According to the methodology of [52], The indicators used to evaluate the climate change impacts on *L. camara* habitat distribution were: (1) Suitable habitat percentage gain the proportion of new habitats predicted to become more suitable for the distribution of *L. camara* by the 2050s and 2070s, (2) Loss percentage of suitable habitat- the proportion of currently suitable habitats Predicted to become unsuitable for the distribution *of L. camara* under future climate scenarios, and (3) Net change in suitable habitat (AC) the overall balance between habitat gained and lost, expressed as a percentage of the suitable habitat by 2050s and 2070s (AC).

Computation was done as:

$$AC = \frac{Af - Ac}{Ac} \times 100\% \qquad (1)$$

Where *AC* is the loss or gain by 2050s and 2070s, *Ac* is the projected non-suitable area under the current scenario, and *Af* is the projected suitability area for *L. camara* in the future.

Results

Performance of the Model

The Maximum Entropy (MaxEnt) model used for this study had a strong discriminatory power between unsuitable and suitable habitats, as seen by their mean and test AUC of 0.79 (Fig. 3). A satisfactory model fit was indicated by the training AUC of 0.84. Therefore predicting that the locations where *L. camara* is most likely to be found in the areas having conditions of favorable environmental and climatic factors needed for the growth and spread of *L. camara* [9, 15].

Additionally, the strong level of consistency between the test and training data suggests that the MaxEnt model effectively predicted suitable regions for *L. camara* in Uganda. Land use is the primary determinant of *L. camara* habitat followed by diurnal range, and elevation (Fig. 4).

The omission and predicted area curves provided insight into the reliability of the species distribution model for *L. camara* in Uganda. The close alignment between the predicted omission (black line) and the mean omission on test data (blue line) indicates that the model generalizes well which supports confidence in the spatial habitat predictions of the model. The relatively narrow confidence intervals around both the mean predicted area (red line) and omission rates suggest stable performance of the model across thresholds.

Relative Importance of Environmental Variables

The Jackknife test indicated that when used in isolation, land-use was the most importance predictor of *L. camara* distribution in Uganda, with the highest AUC (AUC ≈ 0.71). This was followed by soil pH (AUC ≈ 0.69), then followed by elevation and mean diurnal temperature range (BIO2) with AUC ≈ 0.65, and temperature seasonality (BIO4; AUC ≈ 0.64) (Fig. 4).

The result also showed that variables related to vegetation condition yielded lower predictive power in isolation, with minimum NDVI producing AUC ≈ 0.60 and maximum NDVI producing the lowest AUC of about 0.57. There was also relatively lower contribution (AUC ≈ 0.62) of soil texture to the model prediction of *L. camara's* habitat range shift, while precipitation of the coldest quarter (BIO19) was the least contributor (AUC ≈ 0.56) among the all environmental variable used (Fig. 4). Overall, the results of the study indicated that land-use, soil pH, elevation, and temperature variability plays key roles in influencing spatial range shift of *L. camara's* habitat in Uganda. On the contrary, vegetation indices (minNDVI and maxNDVI) and precipitation variables contributed comparatively less to the model prediction, according to our jackknife (Fig. 4).

The Current and future Lantana camara Habitat Suitability range in Uganda

The model revealed that only 6.8% (16,423 km^2) of Uganda is showing high habitat suitability for *L. camara* in the current climate scenario; meanwhile, 47.2% (113,992 km^2) under the same conditions is unsuitable. We found that, under the current climatic conditions, an additional 27.8% (67,139 km^2) and 18.2% (43,954 km^2) of Uganda's land constitute the least and moderately suitable habitat for *L. camara*, respectively (Table 2).

In comparison to the current suitability status, by 2050s, the total highly suitable habitats under all the three Shared Socio-economic Pathways; SSPs1-2.6, SSPs2-4.5 and SSPs5-5.8 will gradually increase up to 8.7% (21,011 km^2), 10.3% (24,875 km^2), and 14.0% (33,745 km^2) respectively. Unsuitable habitats under SSPs1-2.6, SSPs2-4.5 and SSPs5-5.8, will consistently decline by 22.9% (26,083 km^2), 16.3% (18,596 km^2), and 33.0% (37,596 km^2) respectively by 2050s (Table 2; Table 3).

Under the mid future scenario (2050s), SSPs1-2.6, SSPs2-4.5, and SSPs5-5.8, moderately suitable habitats are projected to increase by 73.6% (32,363 km^2), 57.7% (25,359 km^2), and 85.9% (37.758 km^2), respectively (Table 3). In comparison, by the late future (2070s), under SSPs1-2.6, SSPs2-4.5, and SSPs5-5.8 climatic conditions, unsuitable habitat is predicted to decrease to 35.3% (85,267 km^2), 31.8% (76,813 km^2), and 32.8% (79,228 km^2), respectively (Table 2). In the same period (2070s), under SSPs1-2.6, SSPs2-4.5, and SSPs5-5.8, highly suitable areas projected to increase by 22.1% (3,626 km^2), 172.1% (28,264 km^2), and 225.0% (36,960 km^2), respectively (Table 3).

Overall, by the 2070s under SSPs1-2.6, SSPs2-4.5, and SSPs5-5.8 scenarios, the least suitable habitats in Uganda will experience a decrease to 27.0% (65,219 km^2), 19.8% (47,827 km^2), and 17.8% (42,996 km^2), respectively (Table 2). However, in that same period under SSPs1-2.6, SSPs2-4.5, and SSPs5-5.8 scenarios show that the moderately suitable habitats for *L. camara* will increase to 29.4% (71,016 km^2), 29.9% (72,223 km^2), and 27.3% (65,943 km^2) respectively (Table 2). Under the current conditions (Fig. 6), moderately and highly suitable habitats for *L. camara* are projected to expand mostly to the eastern, central, and southwestern parts of Uganda. The northern part of Uganda was projected to be less affected, with most of the part having least to no suitability areas for the invasion of *L. camara* (Fig. 6; Fig. 7; Fig. 8).

Table 2
Area suitability for *L. camara* in Uganda under current and future climate scenarios (2050s' and 2070s').

Period	Scenario	Area Suitability Range in Km^2 (%)			
		Not suitable ($0 \le r \le 0.25$)	Least suitable ($0.25 \le r \le 0.5$)	Moderately ($0.5 \le r \le 0.75$)	Highly suitable ($0.75 \le r \le 1$)
Current	-	113992 (47.2)	67139 (27.8)	43954 (18.2)	16423 (6.8)
2041–2060	SSPs1-2.6	87909 (36.4)	56271 (23.3)	76317 (31.6)	21011 (8.7)
	SSPs2-4.5	95396 (39.5)	51924 (21.5)	69313 (28.7)	24875 (10.3)
	SSPs5-8.5	76409 (31.7)	49172 (20.4)	81712 (33.9)	33745 (14.0)
2061–2080	SSPs1-2.6	85267 (35.3)	65219 (27.0)	71016 (29.4)	20049 (8.3)
	SSPs2-4.5	76813 (31.8)	47827 (19.8)	72223 (29.9)	44687(18.5)
	SSPs5-8.5	79228 (32.8)	42996 (17.8)	65943 (27.3)	53383 (22.1)

Projected Habitat Suitability Change: Gain and Loss

Projected changes in habitat suitability reveal significant increases in moderately and highly suitable areas across all scenarios. By 2041–2060 under SSPs1-2.6, SSPs2-4.5, and SSPs5-8.5 climate scenarios, highly suitable habitat increases by 27.9% (4,588 km^2), 51.5% (8,452 km^2), and 105.5% (17,322 km^2), respectively. These increases were even greater by 2061–2080, with gains of 22.1% (3,626 km^2), 172.1% (28,264 km^2), and 225.0% (36,960 km^2) for the same scenarios (Table 3).

The most substantial expansion occurs under the SSPs5-8.5 (high carbon emissions scenario) for both decades, 2050s and 2070s (Fig. 7; Fig. 8). Thus, indicating a strong positive correlation between climate warming and habitat favorability for *L. camara*. Conversely, not suitable and least suitable habitats were predicted to decline. Substantial decrease by 30.5% (34,764 km^2) for not suitable habitat and by 36.0% (24,143 km^2) for least suitable habitat is predicted by 2061–2080 under SSPs5-8.5 (Table 3). These reductions reflect a likely range shift and expansion into areas previously considered marginal or not suitable for the distribution of *L. camara*.

The predicted habitat suitability for *L. camara* under SSPs1-2.6, SSPs2-4.5, and SSPs5-5.8 scenario will extend in most parts of Uganda by 2050s (Table 2; Fig. 7) and further expansion will be anticipated by the 2070s (Table 2; Fig. 8). In most part of Uganda, the moderately suitable and highly suitable habitats for *L. camara* distributions were predicted to increase (gained) under SSPs1-2.6, SSPs2-4.5, and SSPs5-5.8 climate scenarios, respectively, during the periods 2050s and 2070s (Table 2; Table 3; Fig. 7; Fig. 8).

The overall results indicated a consistent pattern of habitat range expansion for *L. camara* distribution in Uganda under future climate scenarios. While currently suitable habitats are more limited to small area of the country, the study projection result show a remarkable increase in moderate to high suitability zones especially under SSPs5-8.5 scenario. This result of the study highlights the potential of *L. camara* invasion with the increasing climate change. This calls for the need for early detection and strategic control mechanisms, more especially in a more vulnerable ecosystems and protected areas.

Table 3
Projected habitat gains/loss of *L. camara* in Uganda under climate scenarios (2050s' and 2070s').

Period	Scenario	Habitat Gain/Loss (Km² and % Change)			
		Not suitable (0 ≤ r ≤ 0.25)	Least suitable (0.25 ≤ r ≤ 0.5)	Moderately (0.5 ≤ r ≤ 0.75)	Highly suitable (r = 0.75 ≤ r ≤ 1)
Current	-				
2041–2060	SSPs1-2.6	-26083(-22.9%)	-10868(-16.2%)	+ 32363(+ 73.6%)	+ 4588(+ 27.9%)
	SSPs2-4.5	-18596(-16.3%)	-15215(-22.7%)	+ 25359(+ 57.7%)	+ 8452(+ 51.5%)
	SSPs5-8.5	-37596(-33.0%)	-17967(-26.7%)	+ 37758(+ 85.9%)	+ 17322(+ 105.5%)
2061–2080	SSPs1-2.6	-28725(-25.2%)	-1920(-2.9%)	+ 27062(+ 61.6%)	+ 3626(+ 22.1%)
	SSPs2-4.5	-37179(-32.6%)	-19312(-28.8%)	+ 28269(+ 64.3%)	+ 28264(+ 172.1%)
	SSPs5-8.5	-34764(-30.5%)	-24143(-36.0%)	+ 21989(+ 50.0%)	+ 36960(+ 225.0%)

(+) for area suitability gain, (-) for area suitability loss in projected decades of 2050 and 2070.

Discussion

Performance of the model in predicting suitable habitats

The models used for this study have shown a very high mean test and training AUC value, which indicates very strong predictive accuracy. A test AUC value (0.79) attained by this model, showing its strong predictive power and reflecting the effectiveness of the model in categorizing *L. camara* habitat suitability distribution. It indicates that the MaxEnt model approach, together with the selected variables, accurately categorized the *L. camara* habitat distribution in Uganda.

The areas with high potential threats to invasion remarkably gained valuable insights from the ability of the model by accurately capturing the species' habitats. This is shown by a high AUC value close to 1, which implies perfect discrimination power of the model used [53, 54]. Furthermore, with a 0.84 training

AUC value, indicating that the model and variables selected perfectly captured and predicted *L. camara* suitable habitats.

Our MaxEnt model made an accurate prediction of areas where the *L. camara* species is likely to be absent (true negative) and where they are present (true positive), as stated by [55, 56]. This indicates the MaxEnt model's effectiveness, with a high-test AUC (0.79) showing the strength in differentiating suitable habitats from unsuitable habitats. This is indicated by a high training AUC confirming its strength in projecting the habitat suitability range of *L. camara*. The finding from the study provides insight scientific baseline for further understanding of the potential shift of *L. camara* habitat in Uganda. Thus, offers a valuable clue for early detection and intervention in order to minimize their spread in the future.

Key environmental variables for L. camara distribution

Lantana camara is recognized among the worst plant invaders in East Africa, and it imposes a serious threat on ecosystems and people's livelihoods globally [57]. It has the potential to invade a wide area owing to remarkable, unique traits that help it to survive in harsh conditions where other plant species cannot. Their invasion are normally highly favored in an open land with optimum exposure to sunlight, but face difficulty under a thick canopy because of its high demand for sunlight [58]. The invasion risk of *Lantana camara* as one of the invasive alien plant species (IAPS) tend to be severe in disturbed or stressed environment due to climate change[59].

Our results revealed land use, soil pH, and elevation to be the most significant variables affecting *L. camara* distribution in Uganda. Furthermore, temperature and rainfall related variables such as diurnal range temperature (Bio2) and temperature seasonality (Bio4), also made a remarkable contribution in determining *L. camara* distribution in Uganda. This is consistent with recent similar studies, which also indicated that precipitation, temperature, elevation, and land use are the most important variables in determining invasive species distributions [30, 60].

According to [61], a slight temperature increase can impact the physiological and allelopathic/chemical reaction of *L. camara*, which in turn can trigger an increase in their growth rate. Our findings further complement the [30] predictive hypothesis that invasion by plant species such as *L. camara* to a new area with a warmer climate can be amplified by climate change.

Furthermore, the invasion by IAPS such as *L. camara* is predicted to accelerate due to climate-induced temperature and precipitation patterns change, which cause further displacement of native plant species [11]. Based on those findings, it’s safe to draw conclusion that *L. camara* is most likely to find new climatic niches within Uganda. This is due to the erratic rainfall patterns and temperature rise of 1.5 to 2.5°C by 2050s, especially in higher elevations which are currently unsuitable for *L. camara* invasion [62].

Habitats shift prediction under three SSPs climate scenarios.

Invasive alien plant species (IAPS) have numerous ways they respond to environmental change. For example, “niche conservatism, and niche expansion along multiple or very specific climatic or other environmental variables, or by shifting into a new niche” [63, 64]. Invasive alien plant species range shift and expansion, which are induced by climate change, are one of the top threats to ecosystems [65, 66]. This study shows that *L. camara* has the potential to greatly increase its geographic distribution in Uganda in the future. Thus, complements [7] finding that *L. camara* species adaptation to do so well in a warmer tropical area of East Africa.

Our study’s, prediction of habitat shift and further distribution of *L. camara* in Uganda in the future, also complements findings by [67], which found that most central and eastern parts of Africa are predicted to be suitable for *L. camara* invasion. Moreover, our results further predicted expansion of *L. camara* to a wetter region of Uganda around Lake Victoria and nearby districts (Busia, Masaka, Rakai, and Mukono districts). Further expansion is also expected in the south south-eastern region of a cooler area (Tororo and Bukedea districts), and also the western region (Mbarara, Rukungiri, Ibanda, and Kanungu districts).

In comparison, the drier semi-arid districts (Kotido, Moroto, Kitgum, Lamwo, Karenga, Kabong, and Moyo districts) remained not /or least invaded compared to any other regions in Uganda. This is because these districts often receive erratic rainfall, and experience hot temperatures, especially

the semi-arid regions of Karamoja rangeland. This is in line with other findings by [68, 69], that *L. camara* can thrive best in areas with sufficient rainfall, and cool temperatures distributed throughout the year to support its survival. This clearly reflects why the regions that receive higher rainfall and experience cool temperatures throughout the year, like around Lake Victoria, will be highly invaded (Fig. 7; Fig. 8) in both years of the 2050s and 2070s.

According to the current situation, over 25% (18.2% moderate + 6.8% highly suitable) (Table 2) of Uganda is already moderate to highly suitable for *L. camara* invasion. This also complements earlier findings by [10] showing that *L. camara* has a great capacity to invade and establish itself in tropical settings with open canopies and disturbed habitats. Up to 225.0% (36,960 km^2) increase in highly suitable habitats are predicted by the high-emissions scenario by the 2070s. Thus, indicating that *L. camara* may exert more invasion pressure on Uganda's ecological zones, especially in the central, eastern, and southwestern parts. This study further predicts that suitable habitat increases with increasing elevation. This is in agreement with [70] 's finding that elevation highly determines *L. camara* invasion of South African savannah.

Furthermore, our findings have shown a gradual shrinkage of unsuitable habitats for *L. camara*, suggesting a future shift of habitat suitability to semi-arid and highland regions of Uganda. Thus, endangering biodiversity hotspots in the country like the Albertine Rift and mountain forest ecosystems [18]. This is evidenced by the unsuitable habitats' shrinkage of 14.4% (from 47.2% to 32.8%) by the 2070s (Table 2) in the high carbon emissions SSPs5-5.8 climate scenario. This shift comes with risks not only to the native plant species but also to the ecosystem services [71]. Needless to mention, further loss and gain of suitable habitats can be triggered by human-induced climate change [54, 72].

Although climate change undoubtedly increases the likelihood of plant species invasion, human activities like road construction, agricultural expansion, and changes in land use may favor further invasion by *L. camara* [73]. Therefore, our study findings also complement [74]'s finding that the potential invasion of *L. camara* will be favored by the future climatic scenarios. The finding from this study highlights the necessity of proactive national approaches to track and control the invasion of *L. camara*, particularly in situations of climate uncertainty. Furthermore, policy frameworks that incorporate the management of invasive species into climate adaptation measures and ecological restoration in degraded areas will be crucial [75].

Conclusion

Based on this study, habitat suitability for *Lantana camara* is projected to extend across most areas of Uganda. This is evidenced with highly suitable habitats increasing more than 225.0% by the 2070s, thereby posing an increasing ecological threat to biodiversity and ecosystems. This expansion has the potential to severely impact native biodiversity, deteriorate ecosystem services, and endanger livelihoods dependents on ecosystem if not properly monitored and managed, particularly in Uganda's most vulnerable ecological hotspots such as the Albertine rift.

A collaborative invasive plant species management strategy is key, and predictive modeling must be implemented to address this escalating problem. It is vital to integrate management strategies for *L. camara* into national biodiversity strategy and action plan (NBSAP) frameworks, with early detection and control serving an important measure. Furthermore, regional cooperation among the neighboring countries to monitor its entry into the country due to transportation is very crucial in the control and management of the introduction and spread of *L. camara* from other neighboring countries.

Abbreviations

ACCESS-CM2: Australian Community Climate and Earth System Simulator – Climate Model version 2

AUC: The **Area Under Curve**

CMIP6: Coupled Model Intercomparison Project Phase 6

GBIF: Global Biodiversity Information Facility database

GCMs: Global Climate Models

IAPS: Invasive Alien Plant Species

IPCC: Intergovernmental Panel on Climate Change

IUCN: International Union for Conservation of Nature

MaxEnt: Maximum Entropy modeling

MIROC6: Model for Interdisciplinary Research on Climate, version 6

MPI-ESMI-2-HR: Max Planck Institute Earth System Model, Version 1.2 – High Resolution

NBSAP: National Biodiversity Strategy and Action Plan

NEMA: National Environment Management Authority

ROC: Receiver Operating Characteristic Curve

SDMs: Species Distribution Models

SSPs: Shared Socio-economic Pathways

UBOS: Uganda Bureau of Statistics

WCRP: World Climate Research Program

Declarations

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Author contributions

Otim Lawrence performed the data extraction, cleaning, analysis, and wrote the draft manuscript. Elie Kany Luganda also helped in data cleaning and analysis. Nega Tassie Abate, and Anteneh Belayneh Desta**,** reviewed and approved the final version of the manuscript.

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Data availability

Datasets shall be available from the corresponding author on request.

Ethics approval and consent to participate

This study did not require any ethical approval.

Consent for publication

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Competing interests

The authors declare no competing interests.

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Figures

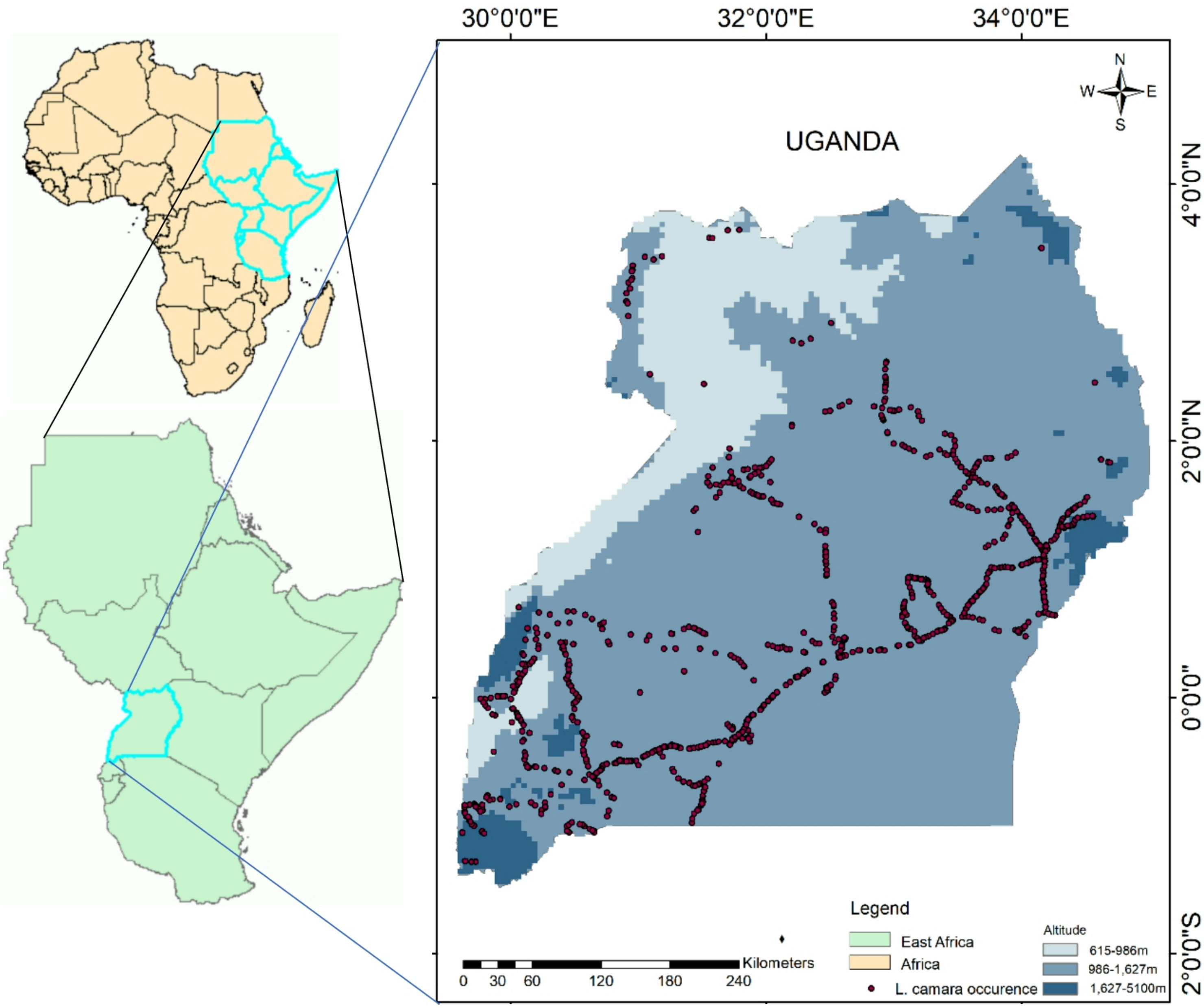

Figure 1

Map of Uganda illustrating elevation and L. camara occurrence point (red dots).

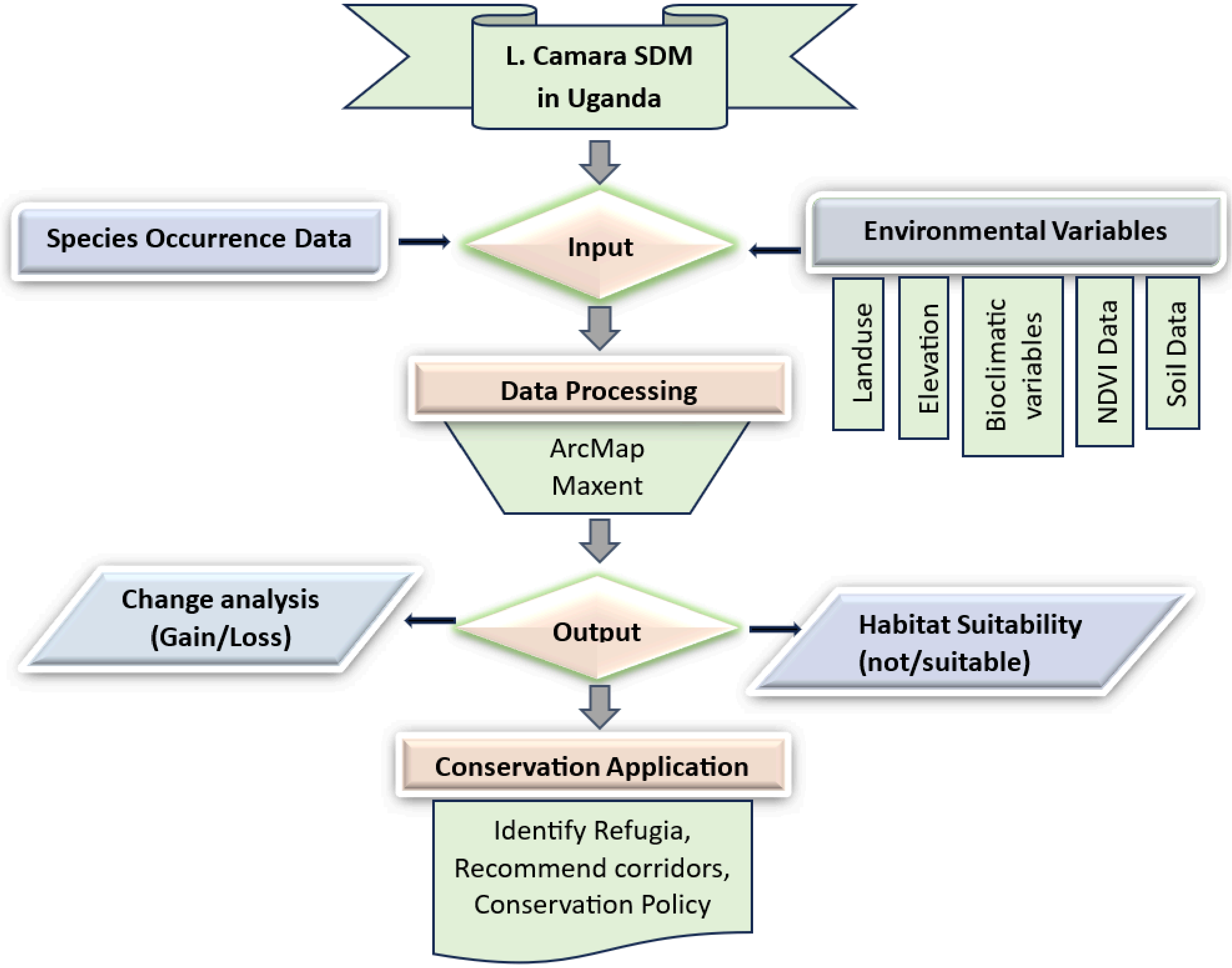

Figure 2

Conceptualized framework in modeling L. camara distribution in Uganda.

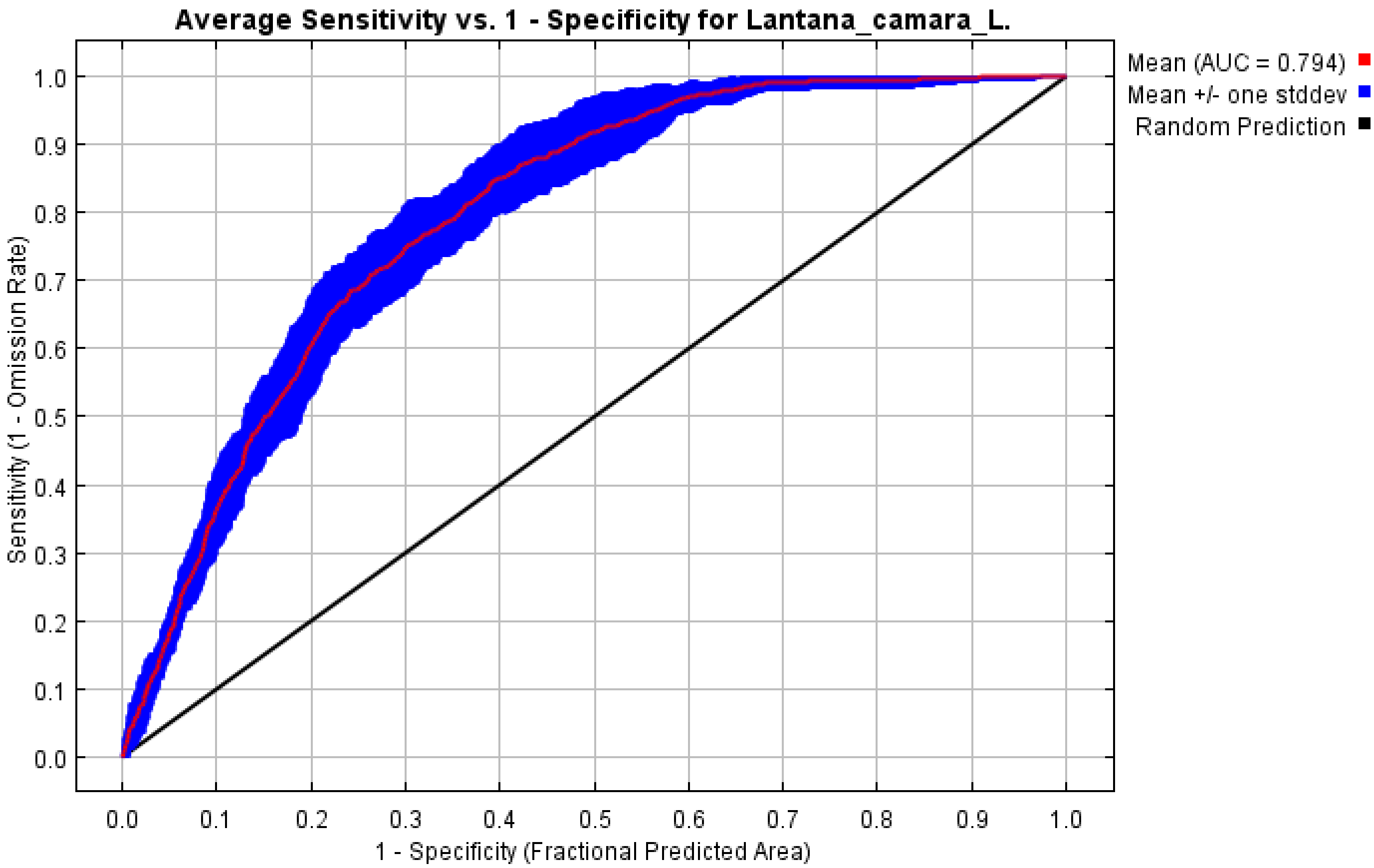

Figure 3

Model performance for L. camara habitat suitability predictions in Uganda.

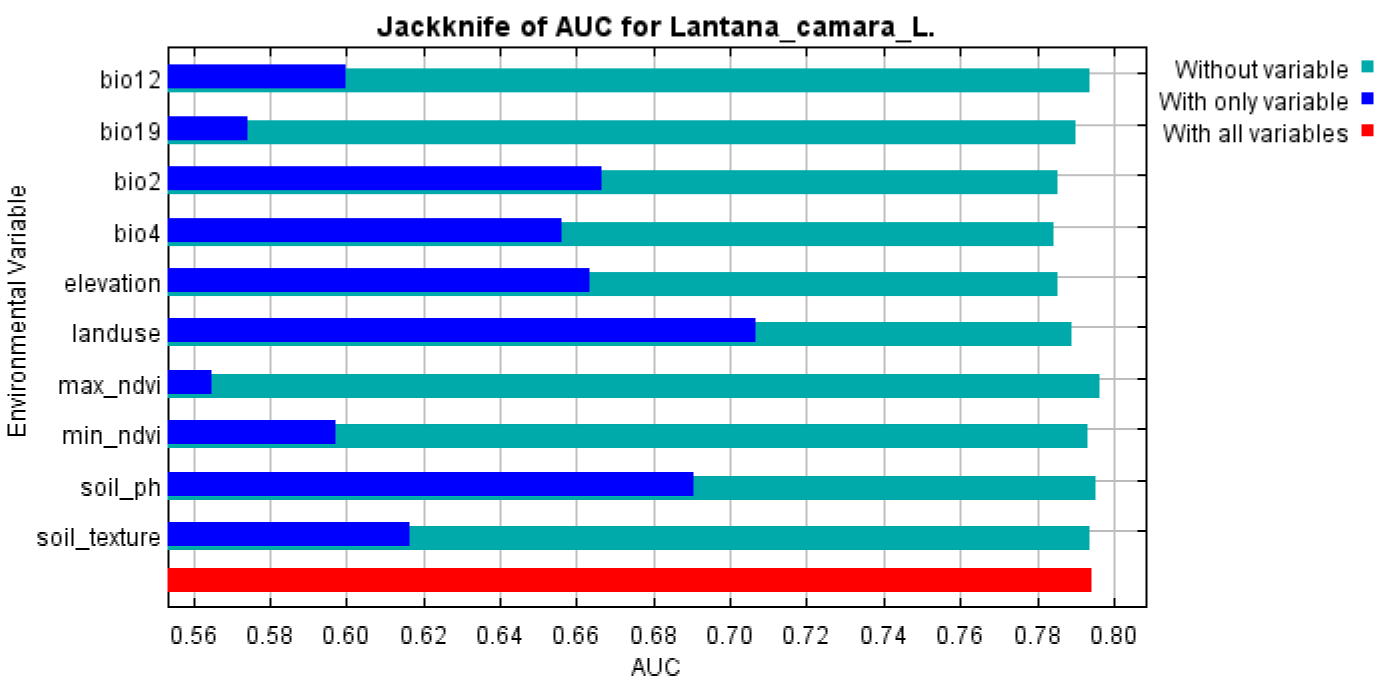

Figure 4

Jackknife test result showing the contribution of variables.

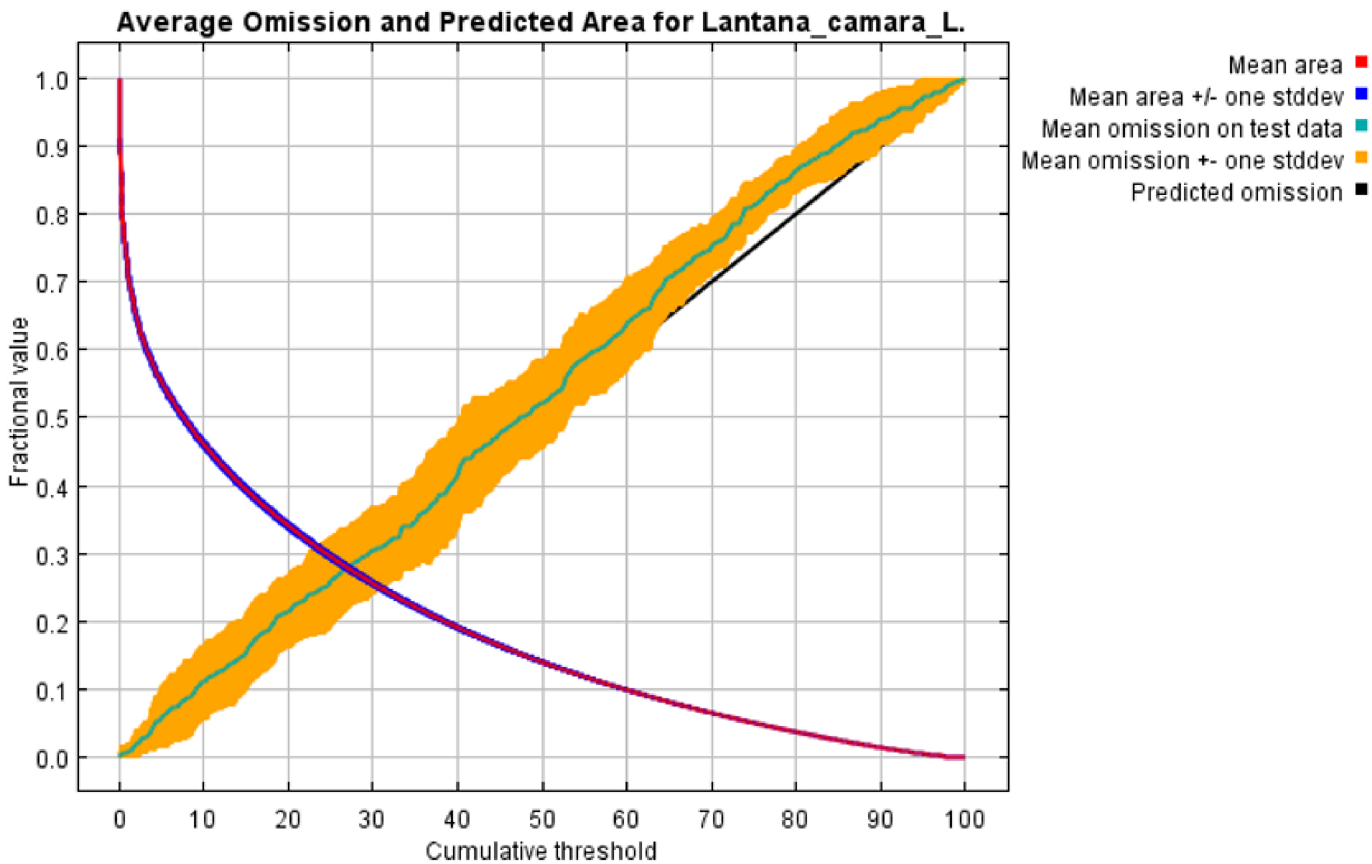

Figure 5

Average omission and predicted area for distribution of L. camara in Uganda.

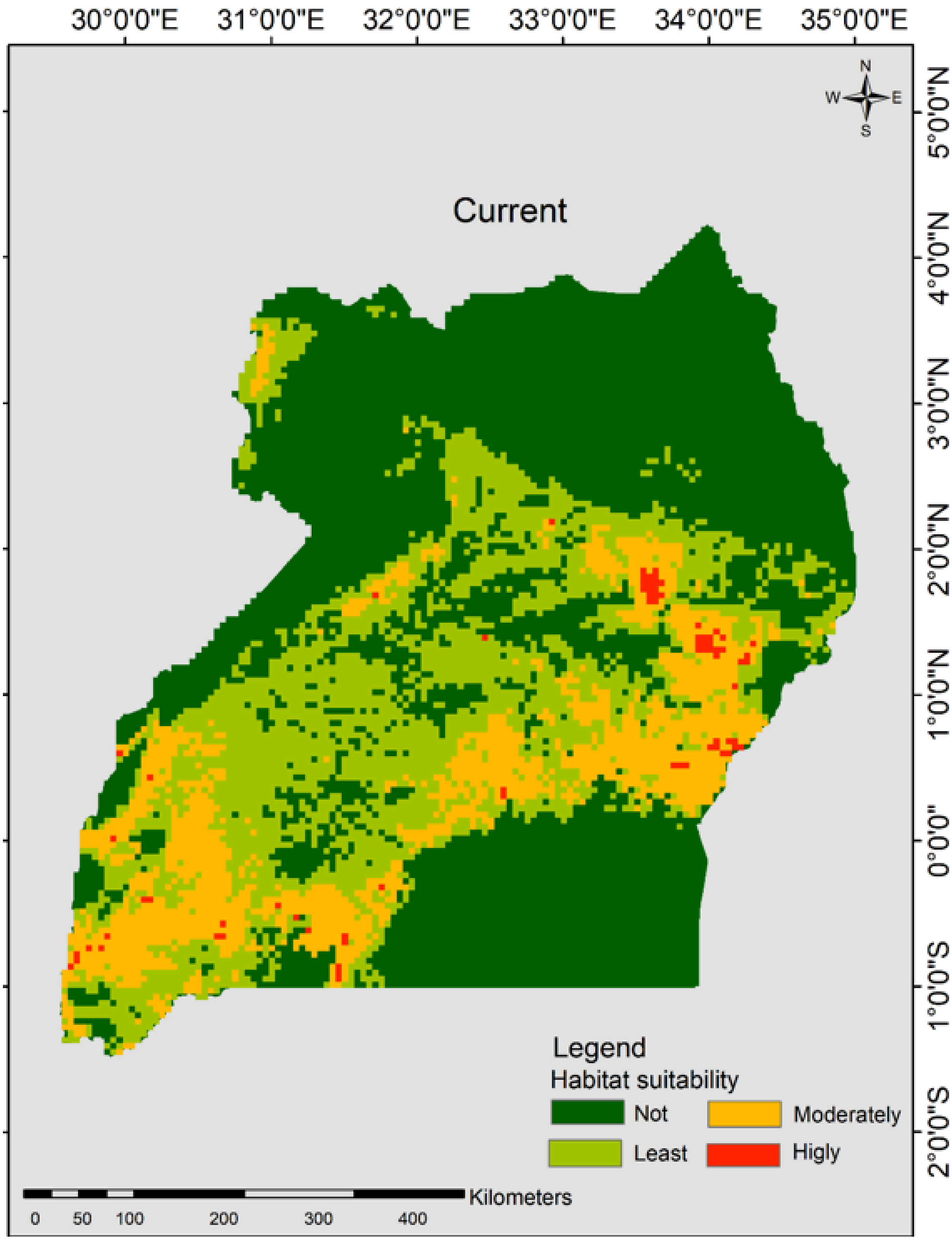

Figure 6

Map illustrating predicted current habitat suitability for L. camara in Uganda.

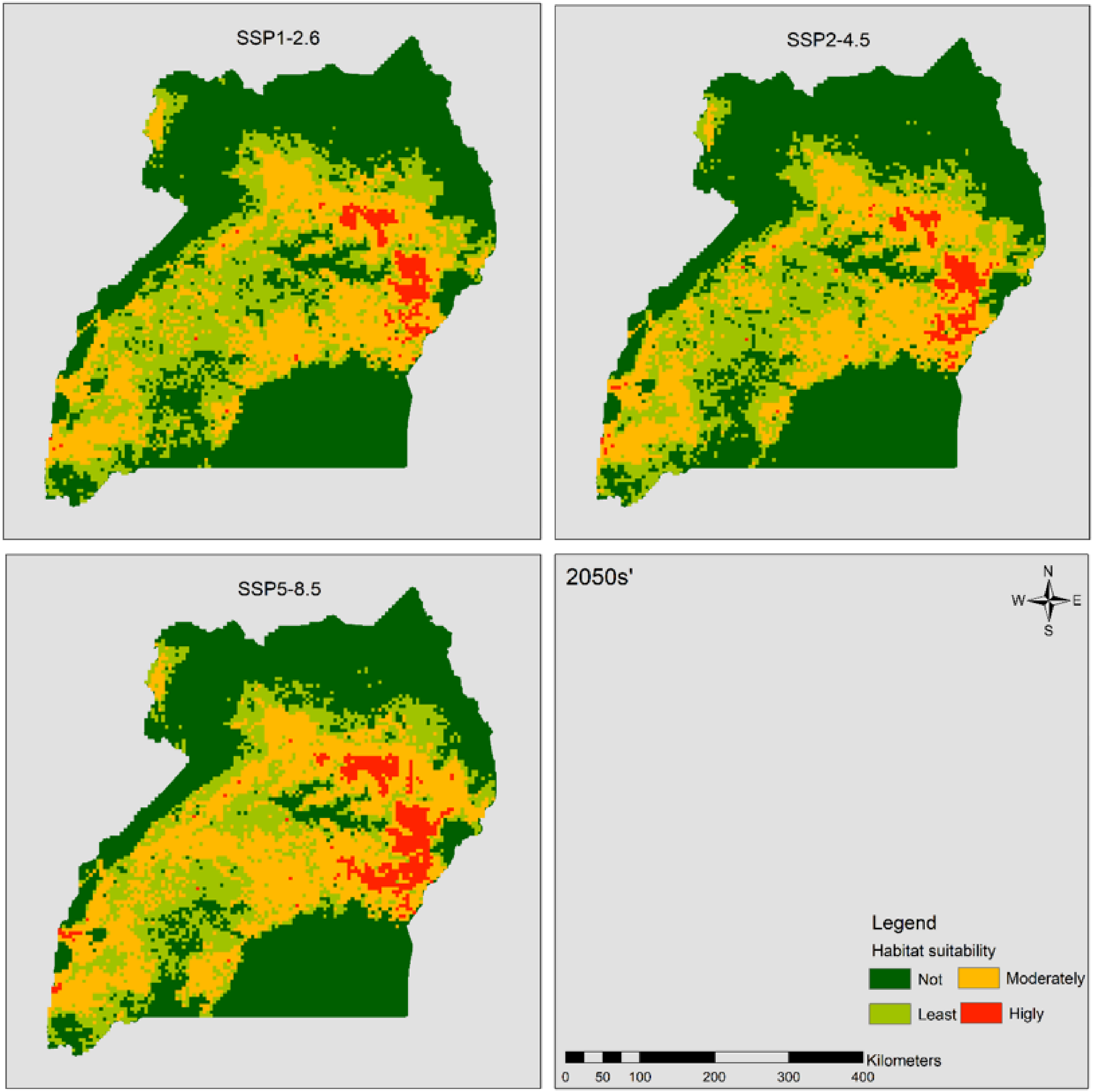

Figure 7

Prospective habitat suitability range for L. camara under difference climate scenarios in Uganda by 2050s'.

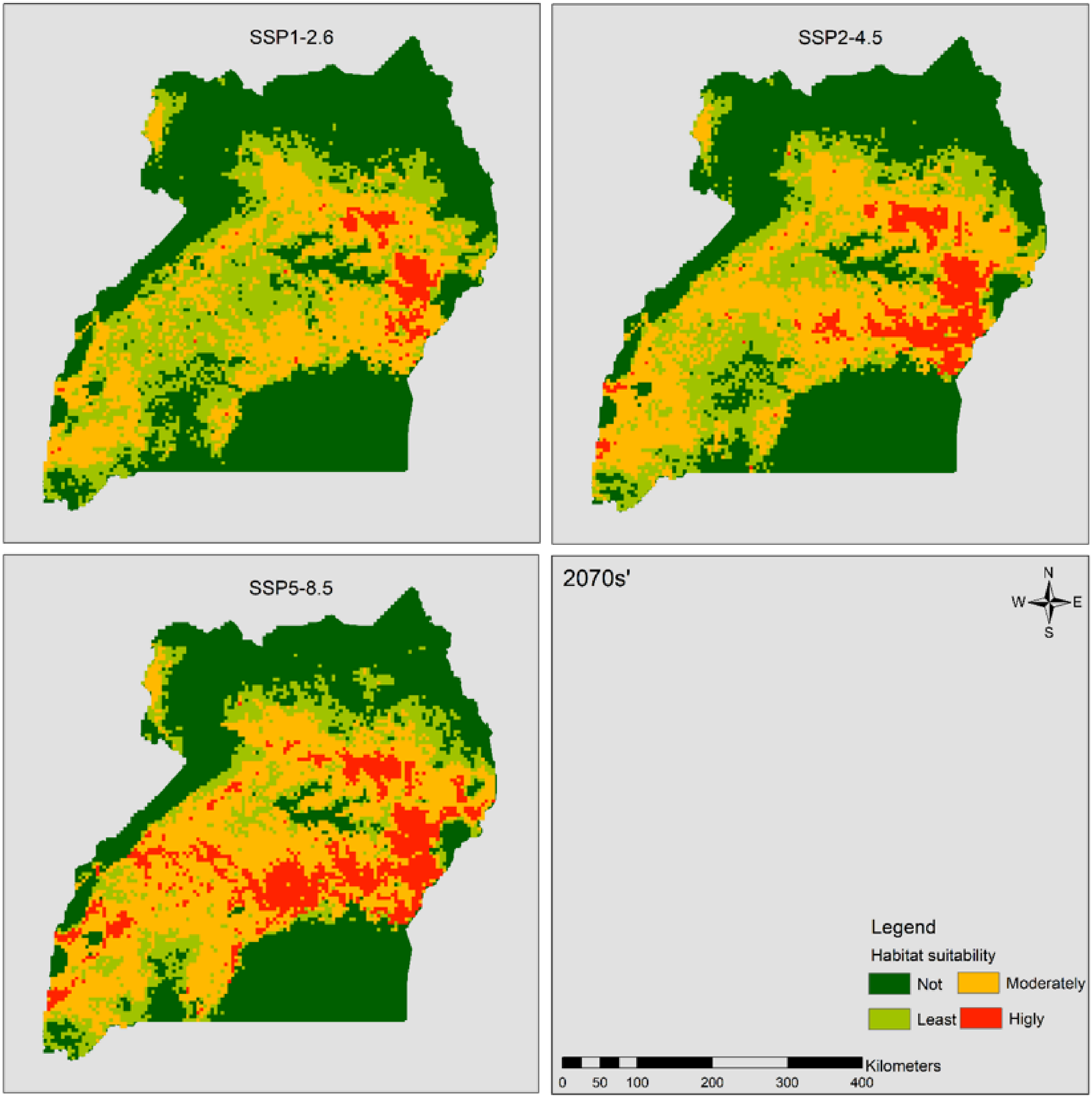

Figure 8

Prospective habitat suitability range for L. camara under difference climate scenario in Uganda by 2070s’.