Modelling habitat suitability of the invasive tick *Rhipicephalus microplus* in West Africa

Short running title: Modelling *R. microplus* suitability in West Africa

Olivier M. Zannou[1,2], Daniele Da Re[3], Achille S. Ouedraogo[2,4], Abel S. Biguezoton[2], Emmanuel Abatih[5], Kouassi Patrick Yao[6], Souaïbou Farougou[7], Laetitia Lempereur[4], Sophie O. Vanwambeke[3] and Claude Saegerman[1]

[1] Research Unit in Epidemiology and Risk Analysis applied to veterinary sciences (UREAR-ULiège), Fundamental and Applied Research for Animal and Health (FARAH) Center, Department of Infectious and Parasitic Diseases, Faculty of Veterinary Medicine, University of Liège, Liege, Belgium

[2] Vector-borne Diseases and Biodiversity Unit (UMaVeB), International Research and Development Center on Livestock in Sub-humid Areas (CIRDES), Bobo Dioulasso, Burkina Faso

[3] Georges Lemaître Center for Earth and Climate Research, Earth and Life Institute, UCLouvain, Louvain-la-Neuve, Belgium

[4] Laboratory of Parasitology and Parasitic Diseases, Fundamental and Applied Research for Animal and Health (FARAH) Center, Faculty of Veterinary Medicine, University of Liège, Liège, Belgium

[5] Department of Applied Mathematics, Computer Sciences and Statistics, Ghent University, Gent, Belgium

[6] UFR Biosciences, Université Félix Houphouët-Boigny, Abidjan, Côte d'Ivoire

[7] Communicable Diseases Research Unit (URMaT), Polytechnic School of Abomey-Calavi, University of Abomey-Calavi, Republic of Benin

Corresponding author: claude.saegerman@uliege.be

This article has been accepted for publication and undergone full peer review but has not been through the copyediting, typesetting, pagination and proofreading process, which may lead to differences between this version and the Version of Record. Please cite this article as doi: 10.1111/tbed.14449.

BSTRACT

Background: Ticks have medical and economic importance due to their ability to transmit pathogens to humans and animals. In tropical and sub-tropical countries, tick-borne diseases (TBD) are among the most important diseases affecting livestock and humans. The fast spread of ticks and TBD requires a quick development and application of efficient prevention and/or control programs. Therefore, prior investigations on TBD and related vectors epidemiology, for instance through accurate epidemiological models are mandatory. This study aims to develop models to forecast suitable habitat for *Rhipicephalus microplus* distribution in West Africa. **Methods and principal findings:** Tick occurrences were assembled from ten different studies carried out in six West African countries in the past decade. Six statistical models (Maximum Entropy in a single model and Generalized Linear Model, Generalized Additive Model, Random forest, Boosted Regression Tree and Support Vector Machine model in an ensemble model) were applied and compared to predict the habitat suitability of *R. microplus* distribution in West Africa. Each model was evaluated with the area under the receiver operating characteristic curve (AUC), the true skill statistic (TSS) and the Boyce index (BI). The selected models had good performance according to their AUC (above 0.8), TSS (above 0.7) and BI (above 0.8). Temperature played a key role in MaxEnt, while normalized difference vegetation index (NDVI) was the most important variable in the ensemble model. The model predictions showed coastal countries of West Africa as more suitable for *R. microplus*. However, some Sahelian areas seems also favourable. **Conclusions and significance:** We stress the importance of vector surveillance and control in countries that have not yet detected *R. microplus* but are in the areas predicted to host suitable habitat. Indeed, awareness-raising and training of different stakeholders must be reinforced for better prevention and control of this tick in these different countries according to their status.

Keywords: *Rhipicephalus microplus*; West Africa; Maximum Entropy; Random forest; Generalized Linear Model; Generalized Additive Model; Boosted Regression Tree; Support Vector Machine; Ensemble modelling.

INTRODUCTION

Livestock plays a key role in the macroeconomy of West Africa and provides livelihoods for millions of people. The main cattle rearing strategy in West Africa is pastoralism, including transhumance: i.e. a seasonal migration of cattle with their herders. This adaptive strategy aims to optimize livestock access to water and pastures. However, it can favour pathogens and vectors transboundary spread.

Ticks are an important threat to livestock and human health worldwide. These vectors are of medical and economic importance due to their ability to transmit various pathogens to animals and humans (Jongejan and Uilenberg, 2005; Duvallet et al., 2017). Tick-borne diseases (TBD) including protozoan diseases (e.g. theileriosis and babesiosis), rickettsial diseases (e.g. anaplasmosis and heartwater), viral disease (e.g. Tick-Borne Encephalitis, Crimean Congo Haemorrhagic Fever and Lumpy Skin Disease) and bacterial diseases (e.g. dermatophilosis and Q fever) represent major health and management problems of livestock in many developing countries. In Tanzania, Kivaria, (2006) reported economic losses from tick-borne diseases in livestock of US$ 364 million. These losses included the deaths of 1.3 million cattle representing 7.34% of the country's livestock population (Kivaria, 2006).

The most important *Ixodidae* ticks species hampering livestock improvement in West Africa belong to the genera *Hyalomma*, *Rhipicephalus* and *Amblyomma* (Frans, 2000). Among these species, the invasive tick, *Rhipicephalus microplus* was the most studied during the last two decades since its introduction in West Africa in 2002-2004 (Maxime Madder et al., 2007 and 2012). *Rhipicephalus microplus,* the cattle tick originating from Asia is distributed in the tropical and subtropical regions of the world and has commercial importance (Frisch, 1999; Labruna et al., 2009). Initially in Africa, this tick has been established in southern and eastern countries such as South Africa, Mozambique, Zimbabwe, Malawi, Zambia, Tanzania, and Kenya (Walker et al., 2003). Its first occurrence in West Africa was reported in Ivory Coast (Maxime Madder et al., 2007) and Benin (de Clercq et al., 2012; Maxime Madder et al., 2012). After its introduction in this part of Africa, it has spread to several other countries such as Burkina Faso, Togo, Mali (Adakal et al., 2013), Nigeria (Opara and Ezeh, 2011; Musa et al., 2014; Adedayo and Olukunle, 2018), and Cameroon (Silatsa et al., 2019).

The complex epidemiology of TBD includes relationships with environmental factors (e.g. temperature, humidity, and vegetation) that influence vector abundance, host availability, and pathogen transmission (Robinson et al., 2015). The rapid spread of ticks and TBD suggests the need for implementing rapid and efficient prevention and/or control programs. Developing relevant control programs for ticks spread and the various TBD requires a deep understanding of the biology of these ticks and related TBD and the use of accurate epidemiological models.

Modelling is a powerful tool for informing policies development for the prevention and control of animal diseases. It has become a widely used tool to support the evaluation of various disease management activities (Eisen and Eisen, 2011). For animal health domain, models may be useful in various ways like retrospective analysis, contingency planning, resource planning, training, surveillance targeting, and real-time decision support (Taylor, 2003).

Ticks are not host-permanent parasites. They alternate between non-parasitic and parasitic phases. Therefore, their survival and development are strongly related to the characteristics of the biotic (e.g. host) and abiotic (e.g. host habitat, temperature, and humidity) environment (Duvallet et al., 2017). To study the distribution of ticks, it is important to use models that are best suited to their biology, such as species distribution models (SDM). These later, also known as climate envelop models, habitat suitability models and ecological niche models, use the environmental records for sites of occurrence (presence) of a species to forecast a response variable. This may be, for instance, suitability for a site where the environmental conditions are appropriate for the survival of that species and therefore where it can be reasonably expected to be found. SDM compare the locations where a species has been observed to other location where i) it has not been observed (true absence), ii) it is not believed to be observable (pseudo-absences), iii) the background environment (background points) (Guisan et al., 2017).

One of the main applications of this method is to predict the ranges of vector species with climatic data as predictors. Modelling the habitat of a vector species requires prior knowledge of its biology and ecology. In the lifetime of ticks, they alternate between non-parasitic life phases, during which metamorphosis, egg-laying and incubation take place, and parasitic phases, during which they feed on the blood of their vertebrate host (Duvallet et al., 2017). During their non-parasitic life, they need climatic and environmental conditions (e.g. temperature, humidity, vegetation) adapted to each species to fulfil the different off-host phases of their biological cycle. The availability of suitable and specific hosts is also crucial for their survival in a given environment, as these ectoparasites are exclusively haematophagous. These conditions are therefore very important for the installation and expansion of a tick species in an environment (Sonenshine and Roe, 2013). A risk assessment of the introduction and spread of a tick species must address these different biological parameters.

Rhipicephalus microplus is widely distributed in tropical and subtropical areas of the world where it is responsible for a major problem for livestock owners as it causes important economic losses to animal production. It is present in Africa, Southeast Asia, South and Central America, including Argentina, Brazil, Cambodia, Malaysia, Mozambique, Panama, Philippines, Taiwan and Texas, South China, Bangladesh, India, Myanmar, Nepal, and Pakistan (Labruna et al., 2009; Agustín Estrada-Peña et al., 2012; Burger et al., 2014; Low et al., 2015; Roy et al., 2018). It is a species native to South East Asia which spread elsewhere through the cattle trade (Walker et al., 2003). To improve the African cattle breed productivity, dairy cattle from Brazil were introduced in West Africa in the 2000s. Unfortunately, the invasive tick species has been also introduced through Côte d'Ivoire (Maxime Madder et al., 2007) and Benin (Maxime Madder et al., 2012). Since its introduction in the West African sub-region in the 2000s, *R. microplus* has not stopped spreading. New locations for its establishment have been reported over the last ten years (Boka et al., 2017; Kamani et al., 2017). Then, thanks to transhumance, *R. microplus* distribution area increased.

The objective of this study was to highlight the current extent of the spread of *R. microplus* in West Africa and to show the suitability of the parts of West African environment for the habitat of *R. microplus* using species distribution models. These models were used individually or gathered (ensemble modelling) according to analyses.

MATERIALS AND METHODS

Study area

The study area included the West African countries located between 18°E - 15°W and 4°N - 16°N (**Fig. 1**). West Africa has three major climatic zones: the Guinean zone which extends approximately between 6°- 8°N, the Sudanian zone approximately between 8°- 12°N and the Sahelian zone between 12°- 16°N (Kouassi et al., 2010).

One of the main assumptions of correlative species distribution modelling applied to invasive species is the niche conservatism of the native environmental niche into the invaded area (Pearman et al., 2008). While usually tested using ordination techniques, here, due to lack of a sufficient number of occurrences in the native area with temporal consistency with the occurrences in West Africa, we proposed a qualitative analysis based on the similarity of the

Koppen-Geiger climatic classification for the native (South East Asia, **Appendix S1)** and the invaded areas (South America and sub-Saharan Africa) to test this assumption (Romero et al., 2021).

Data

Tick occurrence data

A collection of the sampling locations was built and used here as occurrence (i.e. presence) and non-occurrence (i.e. absence) data (**Fig 1**). These different surveys, conducted between 2008 and 2017, revealed the presence of *R. microplus* in 316 locations (**Table 1**).

Table 1. Rhipicephalus microplus distribution studies in West Africa since its introduction

Place of ticks collection	Period of ticks collection	Number of occurrences	References
Côte d'Ivoire	2008	21	Madder et al., 2011
Benin	2008	33	Madder et al., 2012
Benin	2011	52	de Clercq et al., 2012
Burkina Faso; Mali and Togo	2011	12	Adakal et al., 2013
Ivory Coast	2011 to 2012	25	Toure et al., 2014
Burkina Faso	2013	23	Unpublished
Benin and Burkina Faso	2012 to 2013	8	Biguezoton et al., 2016
Ivory Coast	2015	99	O. Boka et al., 2017
Nigeria	2014 to 2015	4	Kamani et al., 2017
Benin and Burkina Faso	2017	39	Ouedraogo et al., 2021

Predictors

A set of 13 relevant variables (**Table 2**) related to the environment of the tick and its host were selected. The biotic predictor selected was cattle density, as *R. microplus* was described as a specific and the most significant parasite for cattle (Bellgard et al., 2012). The abiotic predictors selected were temperature, rainfall, vegetation index and land cover. Vegetation (pasture for herds) were considered as dependent on climatic factors (rainfall and temperature). It plays a key role in the life of the tick host (cattle). The availability of pasture and water are determinants for the presence of cattle in an area.

Abiotic factors (temperature, humidity, vegetation index and land cover) are crucial for the survival of the tick during its off-host stages (Apanaskevich and Oliver, 2014).

The rainfall and the temperature data used in this study were climate data set for the earth land surface areas at a spatial resolution of 1 km. The rainfall data and the temperature data were annual mean patterns for the period of 1979-2013; http://chelsa-climate.org/bioclim/ (**Table 2**).

The cattle density dataset contains the global distribution of cattle in 2010 expressed in the total number of cattle per pixel (5 min of arc) according to the Gridded Livestock of the World database (GLW 3) (**Table 2**).

The Normalized difference vegetation index (NDVI) data used here is the calculation of the mean of the NDVI raster of the twelve months of 2015 downloaded from the MODIS NDVI; https://lpdaac.usgs.gov/products/mod13a3v006/ with a resolution of 1 km (**Table 2**).

The annual (2015) land cover variables (Cropland, Mosaic tree and shrub, Mosaic herbaceous cover, Shrubland, Grassland, Sparse vegetation, Urban areas, Bares areas and Water bodies) were downloaded from https://www.esa-landcover-cci.org, with a resolution of 1 km (**Table 2**).

Variable pre-processing

A collinearity test on the predictors was used to check for linear associations between two or more explanatory (predictors) variables. Two variables are perfectly collinear if there is an exact linear relationship between them. For the diagnosis of collinearity, we used the Variance Inflation Factor (VIF) method to see which variables are really necessary for the computation of the different models (Akinwande et al., 2015). A VIF in the range of 5 to 10 shows a high correlation which can be problematic. If the VIF rises above 10, it can be argued that the regression coefficients are misestimated because of multi-collinearity, which must be treated appropriately (Akinwande et al., 2015). Variables with VIF greater than five will not be used further. The correlation of the predictors with the presence of the tick was highlighted by the multivariate regression preceding the VIF analysis and included in the collinearity analysis. This helped in the selection of relevant predictors for the modelling (**Table 2**). Variables with many missing values were removed from the list of predictors. The number of presence and absence data was balanced accordingly. In our data, the number of absence points was higher than the number of presence points, so we randomly sampled 316 points (total number of presence points) from all absence points. In addition, all predictors' rasters resolutions were harmonized at the spatial resolution of 10 km.

Table 2. Rhipicephalus microplus potential predictors and associated variables, sources, and their variance inflation factors

Predictors	Description	VIF	Type	Period	Sources
Rainfall	Annual rainfall [mm/year]	2.17	Climatic	1979-2013	http://chelsa-climate.org/bioclim/
Temperature	Annual Mean Temperature [°C*10]	2.15	Climatic	1979-2013	http://chelsa-climate.org/bioclim/
Cattle	Cattle density (Head/Km^2)	1.32	Host	2010	https://dataverse.harvard.edu/dataset.xhtml?persistentId=doi:10.7910/DVN/GIVQ75; (Nicolas et al., 2016; Gilbert et al., 2018)
NDVI	Normalized difference vegetation index	2.23	Environmental	2015	https://lpdaac.usgs.gov /products/mod13a3v006/
Crop (code: 10)	Cropland	2.29	Environmental (Land cover)	2015	https://www.esa-landcover-cci.org
Mosaic TSHC (code: 100)	Mosaic tree and shrub (>50%) / herbaceous cover (<50%)	1.03	Environmental (Land cover)	2015	https://www.esa-landcover-cci.org
Mosaic	Mosaic herbaceous cover	1.01	Environmental	2015	https://www.esa-landcover-

Predictors	Description	VIF	Type	Period	Sources
HCTS (code: 101)	(>50%) / tree and shrub (<50%)		(Land cover)		cci.org
Shrub (code: 120)	Shrubland	1.47	Environmental (Land cover)	2015	https://www.esa-landcover-cci.org
Grass (code: 130)	Grassland	1.31	Environmental (Land cover)	2015	https://www.esa-landcover-cci.org
Vegetation (code: 150)	Sparse vegetation (tree, shrub, herbaceous cover) (<15%)	0.00	Environmental (Land cover)	2015	https://www.esa-landcover-cci.org
Urban (code: 190)	Urban areas	56.54	Environmental (Land cover)	2015	https://www.esa-landcover-cci.org
Bare (code: 200)	Bare areas	0.00	Environmental (Land cover)	2015	https://www.esa-landcover-cci.org
Water (code: 210)	Water bodies	0.00	Environmental (Land cover)	2015	https://www.esa-landcover-cci.org

Legend: VIF, Variance inflation factors; NDVI, Normalized difference vegetation index; HCTS, Mosaic herbaceous Cover Tree and Shrub.

Modelling

Six models were used in this study. The Maximum Entropy Model (MaxEnt) was used alone with only *R. microplus* presence data, while five other models, i.e. Generalized Linear Model (GLM), Generalized additive model (GAM), Random Forest (RF) model, Boosted regression tree (BRT) and Support vector machine model (SVM), were used to produce an ensemble model using *R. microplus* presence and absence data via the R package "sdm" (Naimi and Araújo, 2016).

In addition, a sensitivity analysis was carried out to assess the contribution of each predictor used in models through the variables importance analysis in each modelling technique. The variable importance was addressed in the Maximum Entropy (MaxEnt) model by the permutation importance values.

Maximum Entropy (MaxEnt)

MaxEnt is a machine learning technique using a set of environmental grids and georeferenced locations of occurrence to model niches and species distributions (Phillips et al., 2006; Jane Elith et al., 2011; Zeng et al., 2016; Phillips et al., 2017). Our MaxEnt model was trained and tuned using the ENMeval package (Muscarella et al., 2014). We used the function ENMevaluate with nine arguments: "occ", env, "bg.coords", "method", "algorithm", "kfold", "RMvalues", "fc" and "parallel". The "occ" argument here was *R. microplus* occurrences data. The predictor layers were stacked in the argument "env" and we sampled 10000 background coordinates for the argument "bg.coords". We chose the "block" method for data partitioning, the algorithm of "maxent.jar" and the number of bins used in the k-fold cross-validation was k=10. The features combination used in the argument "fc" were: L, LQ, LQP and LQPH (L=linear, Q=quadratic, P=product and H=hinge). The selected model was the one with the lowest Akaike information criterion (AIC) (Warren et al., 2010). The MaxEnt model's running and prediction were made with the following arguments: "replicates=10", "replicatetype=crossvalidate", "doclamp=FALSE", "extrapolate=TRUE", "maximumiterations=5000", "betamultiplier=1.5", "randomseed", "removeduplicates", "writeplotdata", and "pictures".

Ensemble modelling

Various methods exist for ensemble modelling and can be defined in the method specification. In this study, the R package "sdm" was used for the ensemble modelling (Naimi and Araújo, 2016). First, we created a data object "d" with the function "sdmData" including the argument "species" and "predictors". The arguments of "species" summarize the presence and absence points of *R. microplus* and "predictors" the seven selected explanatory variables. We used the "weighted average" method and the evaluation statistic was the TSS. The selected models are Generalized linear model (GLM), Generalized additive model (GAM), Random Forest, Boosted regression tree (BRT) and Support vector machine model (SVM). The validation methods used were cross-validation with (cv.folds=5) and bootstrapping (n=10).

Generalized linear model (GLM)

Generalised Linear Models (GLM) highlight the relationship between the response variable and a set of predictor variables by searching for the most suitable and parsimonious model (Thuiller et al., 2003).

Generalized additive model (GAM)

GAMs are useful when the relationship between variables is expected to be of a more complex form, not easily fitted with standard parametric functions of the predictors (e.g. GLM with a linear or quadratic response), or where there is no priori reason for using a particular shape (Hastie and Tibshirani, 1990; Guisan et al., 2017). A GAM can be used in addition to a GLM, to explore the general shape of the response function and to implement it in the best possible way in a GLM (Guisan et al., 2002).

Random Forest (RF)

Random forest (RF) is a supervised learning algorithm. The "forest" that it builds is a set of decision trees, usually trained by the "bagging" method (Peters et al., 2011).

Boosted regression tree (BRT)

The BRT is a technique that aims to improve the performance of a single model by fitting many models and combining them for prediction. This technique uses two algorithms: the classification and regression tree (decision tree) group of models, and boosting builds and combines a collection of models (Elith et al., 2008).

Support vector machine model (SVM)

The SVM model is able to strike the most rational balance between species adaptability and complexity in order to achieve the most likely distribution given the constrained information in the data sample (Drake et al., 2006).

Cross-validation and bootstrapping

Cross-validation is a resampling procedure used to evaluate machine learning models on a limited data sample. The procedure has a single parameter called k that refers to the number of groups that a given data sample is to be split into. The model will train k models, each with k-1 folds, and the k^{th} (last fold) will be used to test it (Hijmans, 2012). Overall accuracy is calculated by the average of the accuracy from all k models.

Bootstrapping replicates a sampling method with replacement, each time a sample of equal size to the original data is drawn and used as training data. Observations that are not selected are used for evaluation in each round (Naimi and Araújo, 2016).

To evaluate the performance of the models three parameters were considered: the Area Under the receiver operating Curve (AUC), the True Skill Statistics (TSS) and the Boyce Index. We use AUC, TSS and Boyce index for the MaxEnt model and AUC and TSS for the ensemble modelling.

A model with no predictive power would have an AUC of 0.5 (e.g. a diagonal line), while a perfect model would correspond to an AUC of 1 (Boyce et al., 2002; Allouche et al., 2006).

A TSS value of +1 indicates perfect agreement and values of zero or less indicate performance no better than random (Allouche et al., 2006).

Boyce's index is an evaluation tool adapted for models predicting species distribution based on presence-only data (Di Cola et al., 2017). The Boyce index is ranged from -1 to +1 and positive values indicate consistent predictions of species presences. Values close to zero mean that the pattern is no different from a random pattern and negative values indicate counter-predictions, i.e. prediction of areas of presence more frequent as it is highly relevant to the species (Boyce et al., 2002; Hirzel et al., 2006).

Softwares

Analyses were carried out with R software version 4.0.5 (R Core Team 2021). The following R packages were used: dismo, ENMeval, and sdm (Hijmans and Elith, 2013). The MaxEnt m odel was implemented using R packages rJava and dismo. The ensemble modelling with the f ive models (GLM, GAM, RF, BRT and SVM) was implemented using the R package “sdm” (Naimi and Araújo, 2016).

The cartographic outputs were computed using the software QGIS version 3.18.1 (Quantum GIS Development Team, 2021).

RESULTS

Variables and models selected

The collinearity analysis revealed that only one variable (urban area) had a variance inflation factor above 10 (i.e. 56.54). This variable that was showing a high multi-collinearity furthermore did not significantly correlate with the presence of *R. microplus*.

Seven out of the 13 predictors were significantly (*p*-value < 0.05) correlated with the presence of *R. microplus* through multivariate analysis preceding the VIF. These predictors are Rainfall, Temperature, NDVI, Cattle density, Cropland, Grassland and Shrubland.

Characteristics of the predictors according to presence or absence of *R. microplus* in the study area

The investigation to check if there was difference between the various predictors according to areas where the tick was found or not revealed that the rainfall was significantly ($p<0.001$) higher in areas where *R. microplus* was present (annual rainfall average: 1202.23 +/-252.24 mm) than areas where it was absent (annual rainfall average: 881.62+/- 231.71 mm). The tick was found in areas with higher rainfall than where it was absent (**Appendix S2**). Temperature was significantly ($p<0.001$) higher in areas where *R. microplus* was absent (annual temperature average: 27.99+/-0.99°C) than areas where it was present (annual temperature average: 26.44+-/0.77°C). Areas where the tick was found, are cooler than places where it was absent (**Appendix S2**). On the other hand, cattle density was significantly ($p<0.001$) higher in areas where *R. microplus* was absent (average head/Km^2: 229.32+/-196.48) than in area where it was present (average head/Km^2: 99.76 +/-118.02). The hosts were more concentrated in areas where the tick was absent (**Appendix S2**). The NDVI was significantly ($p<0.001$) higher in areas where *R. microplus* is present (monthly NDVI average: $5681.17*10^{-4}$+/-$1024.29*10^{-4}$) than in area where it is absent (monthly NDVI average: $3837.59*10^{-4}$). The NDVI was better in places the tick was found than where it was absent (**Appendix S2**). The cropland was significantly ($p<0.001$) more important in areas where *R. microplus* was absent (annual cropland classes unit average: 0.73 +/- 0.35) than in area where it was present (annual cropland classes unit average: 0.52 +/- 0.41). The tick was found more frequently on cattle living in uncropped areas than cropped ones. The proportion of grassland was significantly higher ($p<0.001$) in areas where *R. microplus* was absent (annual grassland classes unit average: 0.05 +/- 0.18) than in area where it was present (annual grassland classes unit average: 0.00 +/-0.01). The tick was found more frequently on cattle living in an environment where there was less grassland (**Appendix S2**).

And lastly, shrublands were found more ($p<0.001$) in areas where *R. microplus* is present (annual shrubland classes unit average: 0.09 +/- 0.18) than areas where it was absent (annual shrubland classes unit average: 0.06 +/-0.01). The tick was found more frequently on cattle living in an environment where there is shrubland (**Appendix S2**).

Variable importance

The analysis of the contribution of the different predictors to the MaxEnt model highlighted that temperature and rainfall were the main variables. Temperature contributed to more than 39% and rainfall contributed more than 19% of the model accuracy. Shrubland (1.8%) and grassland (1.8%) contributed less to the model predictions (**Appendix S3A**). The relative variable importance based on the Pearson correlation metric in the ensemble model revealed that NDVI played an important role in the model. This variable was the most important in the five models that make up our ensemble model set. NDVI was the most important predictor in the ensemble model and the cropland and shrubland were the less important ones (**Appendix S3B**). In the GLM model, NDVI (88%) was the most important predictor while cattle density contributed the least to the model with 0.1% (**Appendix S3C**). In the GAM model, it was the rainfall that contributed the most with 39.3% and the cropland contribute the least with 2.4% (**Appendix S3D**). In the RF model, NDVI was the most important contributor among the predictors (20.3%) and grassland has the lowest contribution (0.4%) (**Appendix S3E**). The NDVI also was the largest contributor to the BRT model (62.6%) and grassland did not contributed (0%) to the model (**Appendix S3F**). In the fifth model (SVM), the most important predictor was NDVI (18.5%) and the least important was Grassland (1.9%) (**Appendix S3G**).

Habitat suitability for *Rhipicephalus microplus* in West Africa

The maps revealed high suitability of the coastal areas of West Africa. On the other hand, the tick *R. microplus* seems very poorly adapted to the environment of the Sahelian region, a desert area (**Fig. 2**). However, the southern regions of some Sahelian countries, contiguous to the coastal areas, are also suitable for *R. microplus*. Some differences can be noted in these outputs according to the type of model implemented. The MaxEnt model predicts differently the presence of the tick in the Sahelian region where it is not expected at all or the probability is very low to find it (**Fig. 2A**). On the opposite side, the other five models grouped in the ensemble model predict a significant presence of the tick in the Sahelian region (**Fig. 2B**). Furthermore, the suitability level of the coastal areas predicted by the MaxEnt model is lower than the four other models grouped in the ensemble model.

Model evaluation

The Random forest model and the BRT model had the highest AUC (0.95) and the GLM had the lowest AUC (0.93) (**Table 3**). The GAM and the SVM models had the same AUC (0.94). The Random forest model had the highest TSS (0.80) and other models had the same TSS (0.79) (**Table 3**).

The boxplot graphics in **Appendix S4A** highlighted the variability in the AUC among the bootstrap and cross-validation runs for each model. This figure revealed that the RF and BRT models AUC medians were above the other models ones for both bootstrap and cross-validation runs.

The boxplot graphics in Appendix S4B highlighted the variability in the TSS among the bootstrap and cross-validation runs for each model. Appendix S4B revealed that for the RF and GLM models, TSS medians were above the other models ones respectively for bootstrap and cross-validation runs.

Table 3: Evaluation parameters of the various models

Models	Average AUC	Average TSS	Average Boyce index
GLM	0.93	0.79	NA
GAM	0.94	0.79	NA
RF	0.95	0.80	NA
BRT	0.95	0.79	NA
SVM	0.94	0.79	NA
MaxEnt	0.87	NA	0.87

Legend: NA: Not available; AUC: Area Under the Curve; TSS: True skill statistic.

DISCUSSION

This study aimed to characterise the habitat suitability of the invasive tick *R. microplus* in West Africa. Results of the habitat suitability modelling exercise showed that the coastal areas host more suitable areas for the tick than the Sahelian zone located in the north. The coastal zone, which receives more rainfall and is cooler than the Sahel has also a higher vegetation index. Moreover, the host (cattle) density is higher in the Sahel than in the coastal zone.

Model evaluation

According to the classification of Swets (1988), the MaxEnt model is "Useful" and all the ensemble models are "Highly accurate".

For the ensemble models, TSS values indicate that the selected models were accurate.

The MaxEnt model was built with presence data only. These two accuracy parameters (AUC and TSS) are known to use sensitivity and specificity in their computation (Shabani et al., 2018).

The MaxEnt model has a lower AUC value than other models built with presence and absence data, so it was less accurate than these models according to this parameter. However, on the other hand, the MaxEnt model had a high Boyce index that is an adapted parameter for presence-only models evaluation. The Boyce index is used to measure how well a model can predict the presence of species. The MaxEnt model was confirmed by its Boyce index value to be a model that does not require absence data to model species distribution.

The RF was the most accurate model among the ensemble models regarding its AUC and TSS means level and variance between both cross-validation and bootstrap runs. Cross-validation tends to be less biased but has a relatively large variance. On the other side, bootstrapping tends to reduce the variance considerably but gives more biased results. Combining the two methods, as is the case here in a model set, could lead to fairly accurate prediction results without too much bias and very little variance.

Characterization of predictors and their importance in the models

The process of selecting variables for the construction of the models allowed the selection of seven variables including the annual average rainfall, the annual average temperature, the annual average vegetation index and the density of the host (cattle) and three land cover variables (cropland, grassland and shrubland).

Ticks are found in areas with significantly higher rainfall and moderate temperature. Water and temperature are important factors in tick biology, especially in one-host ticks since the non-parasitic (and therefore environment-dependent) stage is the egg and larva stage. Ticks are very sensitive to desiccation while searching for a host, as they constantly lose water through the integument of their body surface in dry conditions through transpiration. They also lose water through their spiracles in connection with respiration during locomotor activity (Randolph and Storey, 1999; Herrmann and Gern, 2015). The development and mortality of ticks are strongly influenced by these two factors (Estrada-Peña et al., 2015). Our models show quite clearly that areas that are wetter and cooler are more suitable for *R. microplus*. Previous studies have shown in Benin and Eastern Burkina Faso that the *R. microplus* tick prefers areas of moderate temperature and high rainfall (De Clercq et al., 2015; Zannou et al., 2021). The results seem to show that high temperatures are a limiting factor for the presence of the tick in an environment of West Africa. However, it is important to note that other factors such as humidity (represented here by rainfall and the vegetation index) also contribute to the presence of the tick. So in an environment with good rainfall and adequate vegetation, the temperature could not be the only limiting parameter. It is not uncommon to find in areas where the tick is present temperatures exceeding 28°C at certain times of the year. But generally, in West Africa the regions that often experience high temperatures are the countries of the Sahel which are generally very dry (low rainfall) and therefore unsuitable for the tick.

The NDVI of areas where the tick was found was higher than where it was not. The vegetation index, itself dependent on temperature and humidity (F. Hao et al., 2012), is an important variable in that it provides information on the presence, vitality and photosynthesis activity of vegetation. Engorged *R. microplus* female after dropping off the host need shelter under vegetation with convenient temperature and humidity to lay eggs (Latif and Walker, 2004). Eggs are sensitive to heat and risk desiccation when exposed to high temperatures and dry areas. Incubation and hatching of eggs are only possible under some particular climatic conditions (Pfäffle et al., 2013). Our results indicate that this variable is positively correlated with the presence of the tick and the models developed show that it took a large part in predicting the presence of the tick. De Clercq et al., (2015) in Benin and Zannou et al., (2020) in Benin and Burkina Faso have also evidenced the importance of the NDVI on a smaller scale.

Host (cattle) density was higher in areas where the tick is absent than in areas where it was present. In West Africa, the cattle population is more concentrated in the Sahelian countries, which are less watered and warmer. As the tick is more inclined to areas with more water and less heat, a negative correlation between these two variables appears. Nevertheless, the frequent and periodic movements of herds between these two ecosystems enabled by transhumance should be considered. Indeed, in dry season herds in search of pasture and water are forced to reach areas that are still wet at that time and therefore heavily infested by ticks (Zannou et al., 2021). These regular movements and stays expose the animals to *R. microplus* and the main pathogen it transmits: i.e *Babesia bovis* and *Babesia bigemina*. These pathogens are responsible of extensive production losses (Waldron and Jorgensen, 1999; Jonsson, 2006).

Croplands were significantly higher in areas where *R. microplus* was absent than in areas it was present. Cropland is known to be the site of much human activity. Before the crops are planted, the land is well ploughed to help destroy ticks nests. During the vegetative cycle of the different crops, farmers carry out several weeding operations or use herbicides. Pesticides are also regularly used to protect these plants and guarantee a good harvest at the end of the season. All these anthropic actions do not allow the establishment of the non-host phase of the ticks in such environments. It must also be said that *R. microplus* is a specific tick and should be found in the areas most frequented by its bovine host. Cattle are kept away from the farmlands to avoid the destruction of crops by them. They are only tolerated in cropping areas in the dry season to take advantage of crop residues and fertilise the fields.

Rainfall was by far the most important predictor in the MaxEnt model followed respectively by NDVI, cropland, temperature, cattle density and shrub. The grassland did not play a role in the MaxEnt model prediction. The ensemble model revealed that NDVI was by far the most important predictor followed respectively by rainfall, temperature, cattle density, cropland, shrubland and grassland.

While most existing studies (De Clercq et al., 2015; Sungirai et al., 2018) on the projection of the tick distribution only take into account climatic variables, our results showed the importance of other predictors such as cropland, host density in the modelling. The type of vegetation does not seem to be very important in predicting the presence of *R. microplus*. However, it should be noted that shrub vegetation seems to have a better predictive value than grassland. Shrubland provides a better canopy for the ticks and protects them from desiccation during the off-host phase. Grass is only really useful during the quest phase of the host. However, it is important to put the importance of these two variables into perspective because the collections were made on the animals and not on the ground by flagging. Similar results on vegetation preference were observed in the study of Omodior et al., (2021) in the United States of America.

Habitat suitability for *R. microplus* in West Africa

This work qualitatively provides a broader view compared to the previous study by De Clercq et al (2015) and according to the model outputs the coastal areas seem globally more adapted to the tick. This previous *R. microplus* distribution modelling used occurrences data from 2011. Recent work (Ouedraogo et al., 2021) had revealed the presence of the tick in areas where it was previously absent (2015). Therefore, the present work has taken into account presence data from several countries, compared to the work from De Clercq et al., (2015), which only sampled and modelled data from Benin. When looking at habitat suitability maps generated in the current study in Benin in comparison to the study of De Clercq et al., (2015), it can be noticed that our models predicted suitable habitats for the species also in the northern part of Benin, while De Clercq et al., (2015) predictions emphasise mostly the southern one. This may be due to the larger dataset of observations used, as well as different predictors and the tuning of the MaxEnt model. The MaxEnt model as well as the ensemble model predicts a higher risk of tick presence in northern Benin than De Clercq et al., (2015) study. This work provides a larger view of the situation of *R. microplus* in West Africa. It also uses different methods, the ensemble models which are based on the consensus of several models to predict the habitat suitability for *R. microplus*. The interest of the ensemble modelling is that it relies on the principle of the "wisdom of the crowd" to make a better prediction than those models used individually (T. Hao et al., 2019).

The ensemble model seems to predict a stronger fit of the Sahelian zone to the tick than the MaxEnt model. When we consider the contribution of the variables to the prediction of the models we notice that the pattern is not the same. For the MaxEnt model it is the temperature variable that holds the greatest importance while for the ensemble model it is the NDVI. This may have contributed to this difference in prediction, since the Sahel countries are significantly warmer than the coastal countries, but there is still vegetation in some parts of the Sahel around the oases. It should also be underlined that the ensemble model is a consensus model among several models, so its predictions must be given special attention. Precautions must be taken in some Sahelian countries that are at risk due to the extensive livestock farming methods used. These farming methods could favour the importation of the tick, which could adapt and continue its invasion.

According to the updated Koppen-Geiger climatic map provided by Beck et al. (2018), the coastal areas of West Africa show climatic similarities with southern Asia and South America respectively native area and previously invaded area of the tick *R. microplus*. These climatic similarities could be part of the factors that enabled the rapid adaptation and spread of the tick in the environment of some West African countries.

All six models clearly show that countries in the southern part of West Africa (coastal countries) are more suitable for *R. microplus* than those in the Sahel. As expected, temperature, humidity and vegetation influenced most the biology of the tick. Indeed the Sahelian countries are drier and hotter than the coastal countries. Moreover, the vegetation is less developed there. In spite of the higher density of cattle in the Sahel, the off-host life will be difficult for *R. microplus* larvae because of the unfavourable climatic conditions. However, as the habitat suitability maps show, the risk of having the tick in some parts of the Sahel is not null. In some Sahelian countries there are areas such as permanent water points that could provide conditions for the tick to establish itself, especially when the species is known to be highly invasive and adaptive. Recent unpublished work has revealed its establishment in the central plateau of Burkina Faso, a fairly hot area compared to the usual places where it is found (Abel Biguezoton, personal communication). In recent years, Burkina Faso has developed water reservoirs, which have the dual function of being used for the cultivation of vegetables and for watering cattle herds. These environments can present risks of the introduction and dissemination of ticks from herds returning from transhumance in coastal countries. The valleys of perennial rivers also represent biotopes that can favour the establishment of the invasive tick as they are very frequented during the dry season by herds in search of water and pasture.

Although native to Asia, *R. microplus* has invaded Sub-Saharan Africa and is probably replacing progressively the indigenous *R. decoloratus and R. annulatus* (M. Madder et al., 2011; Adakal et al., 2013; Gomes and Neves, 2018). This rapid expansion was also favoured by the extensive livestock farming practised by more than 70% of cattle farmers in sub-Saharan Africa (Boka et al., 2017).

Management options faced to *R. microplus* in West Africa

This study provides a broader view of habitat suitability for *R. microplus*. It allows decision-makers in West African countries to have a better idea of the level of suitability of their area for the invasive tick. It is therefore a tool to identify areas where the emphasis should be placed on raising awareness among livestock stakeholders.

In areas favourable to the tick and not yet infested, measures must be taken to prevent or detect quickly its introduction. For instance, management options should be awareness campaign, avoiding the purchase of cattle originating from infested areas, avoiding herd movement to already infested areas, and capacity building for detection of *R. microplus*. This capacity building should concern farmers, para-veterinarians, private veterinarians and veterinary officers. Other actions could consist to strengthen surveillance of the veterinary acaricides drug market.

Furthermore, in areas where the tick is already established, it will be necessary to raise awareness of the measures to be implemented to limit its spread and, ultimately, its control (e.g. campaign of information, adequate protocol of acaricide treatment, follow up of acaricide resistance, training veterinary agents in tick identification, strengthen the surveillance of the veterinary drug market).

In areas identified here as not favourable to the tick, veterinary services should put in place measures to avoid the introduction and the establishment of the invasive tick (e.g. avoid the introduction of animals from infested areas without appropriate measures, control the movement of animals from infested areas and strengthen the capacity of veterinary services agents in tick detection).

This study is a tool to help in the development of sub-regional and local control plans for *R. microplus* tick and consequently the pathogens it transmits. The direct consequence is the improvement of cattle production and productivity and in turn food security. Good knowledge of the risk for ticks with veterinary and/or medical importance establishment in an area allows for careful management of financial resources dedicated to their control.

CONCLUSION

All the coastal countries of West Africa are suitable areas for *R. microplus*. The southern region of some Sahelian countries (Mali and Burkina Faso) also seems favourable but to a lesser extent. This new study revealed that the risk of *R. microplus* establishment is higher in some areas than previously predicted (case of Benin). It also gave a broader view of the risk over the whole West African sub-region compared to previous studies. It would be advisable for the veterinary authorities of countries that have not yet detected the tick but are in the risk area to take mitigation measures to prevent its introduction. Surveys should be carried out in all countries at risk to determine their status with respect to the tick in order to take appropriate measures. Countries where the tick is already present should raise awareness of the responsible use of acaricides because of the resistant nature of this tick. Countries not yet infested with *R. microplus* should strengthen measures to protect their livestock. This will require better control of animal movements in an extensive livestock context. The modelling the distribution of the invasive tick with several methods (single models and ensemble models) also allowed us to assess their behaviour and performance with the available data.

ACKNOWLEDGEMENTS

This study was funded by the Academy of Research and Higher Education (ARES) through the Research for Development Project (PRD) entitled “Support to the epidemiological surveillance network of animal diseases and related sociological aspects in West Africa (Acronym: TransTicks)”, which involve Burkina Faso and Benin. Olivier Mahuton Zannou is currently doing a PhD at the University of Liège. His research focuses on epidemiological aspects of ticks and tick-borne diseases on transhumant cattle between Burkina Faso and Benin. Daniele Da Re is supported by F.R.S – F.N.R.S.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

ETHICS STATEMENT

The activities of the research project "Support to epidemio-surveillance networks for animal diseases and associated sociological aspects in West Africa (Acronym: TransTicks)" was approved by the Ethics Committee of the International Centre for Research and Development on Livestock in Sub-humid Zones (CIRDES) (Ref. 001-02/2017/CE-CIRDES) under the strict respect of the protocol submitted to the members of the Committee and their unannounced control.

AUTHOR CONTRIBUTIONS

Conceptualization, O.M.Z., A.S.B., K.P.Y., L.L. and C.S.; methodology, O.M.Z., D.D.R., S.O.V. and C.S.; software, O.M.Z., D.D.R., S.O.V. and C.S.; validation, O.M.Z., D.D.R., S.O.V. and C.S; formal analysis, O.M.Z.; investigation, O.M.Z., A.S.O.; resources, A.S.B. and C.S.; data curation, O.M.Z., D.D.R. and C.S.; writing—original draft preparation, O.M.Z.; writing—review and editing, all; visualization, O.M.Z., D.D.R. S.O.V. and C.S.; supervision, A.S.B., S.F., D.D.R., S.O.V. and C.S.; project administration, C.S. All authors have read and agreed to the published version of the manuscript.

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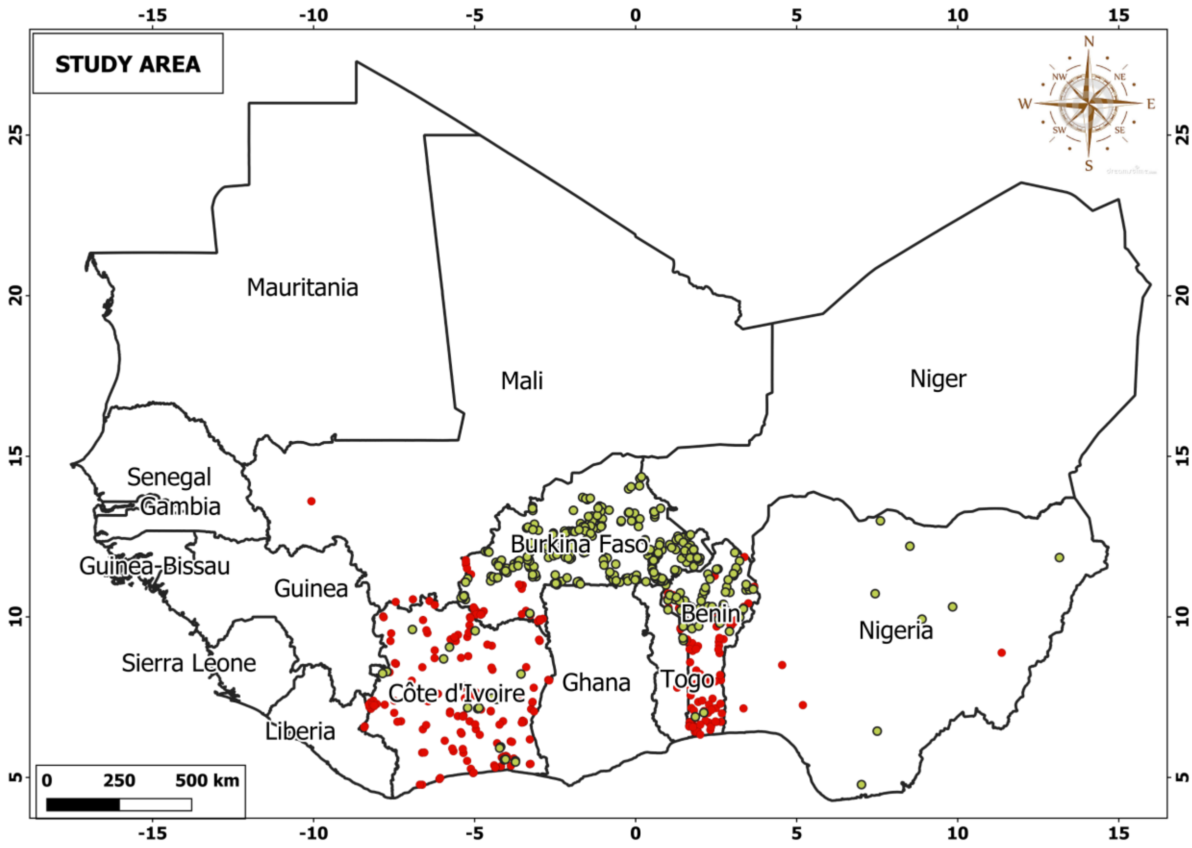
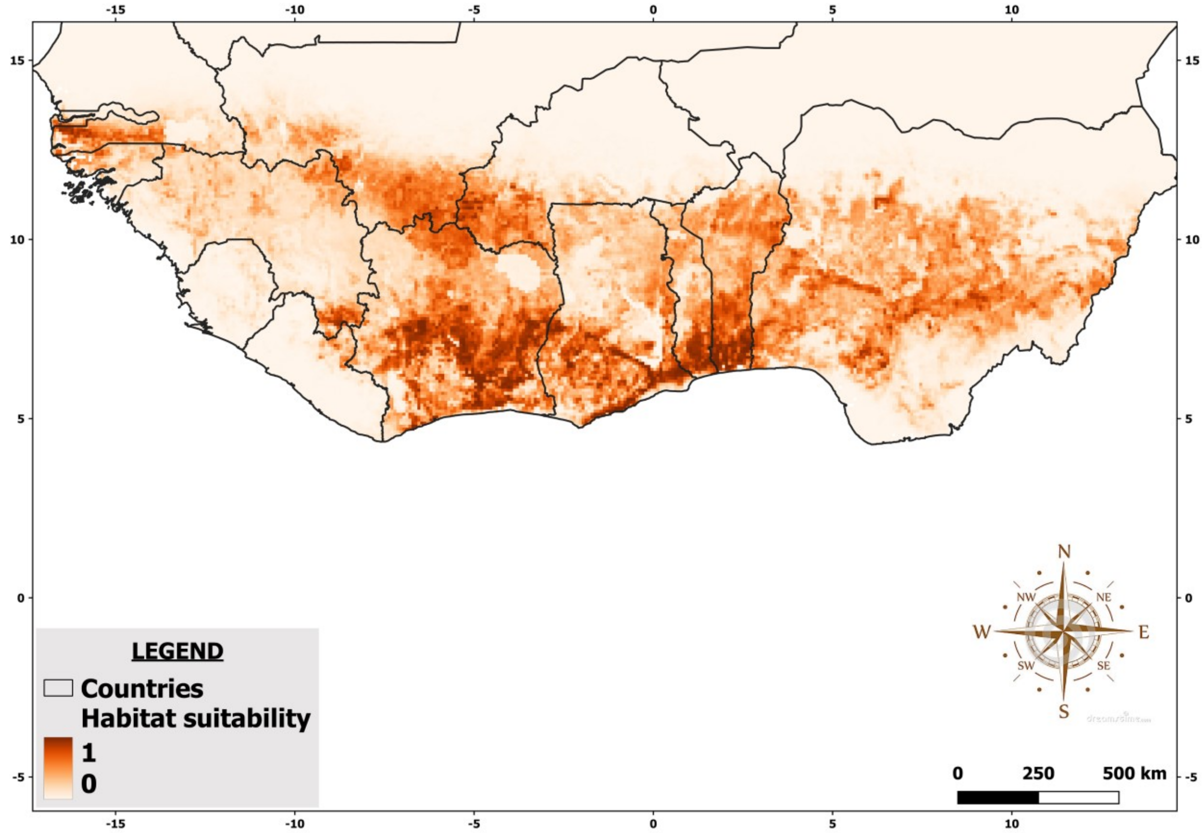


Fig. 1: Study area with different occurrences of R. microplus

Legend: Red dot, presence of *R. microplus*; Green dot, absence of *R. microplus*.


LEGEND
Countries
Habitat suitability
1
0
N
NW
NE
W
E
SW
SE
S
0
250
500 km
-15
-10
-5
0
5
10
15

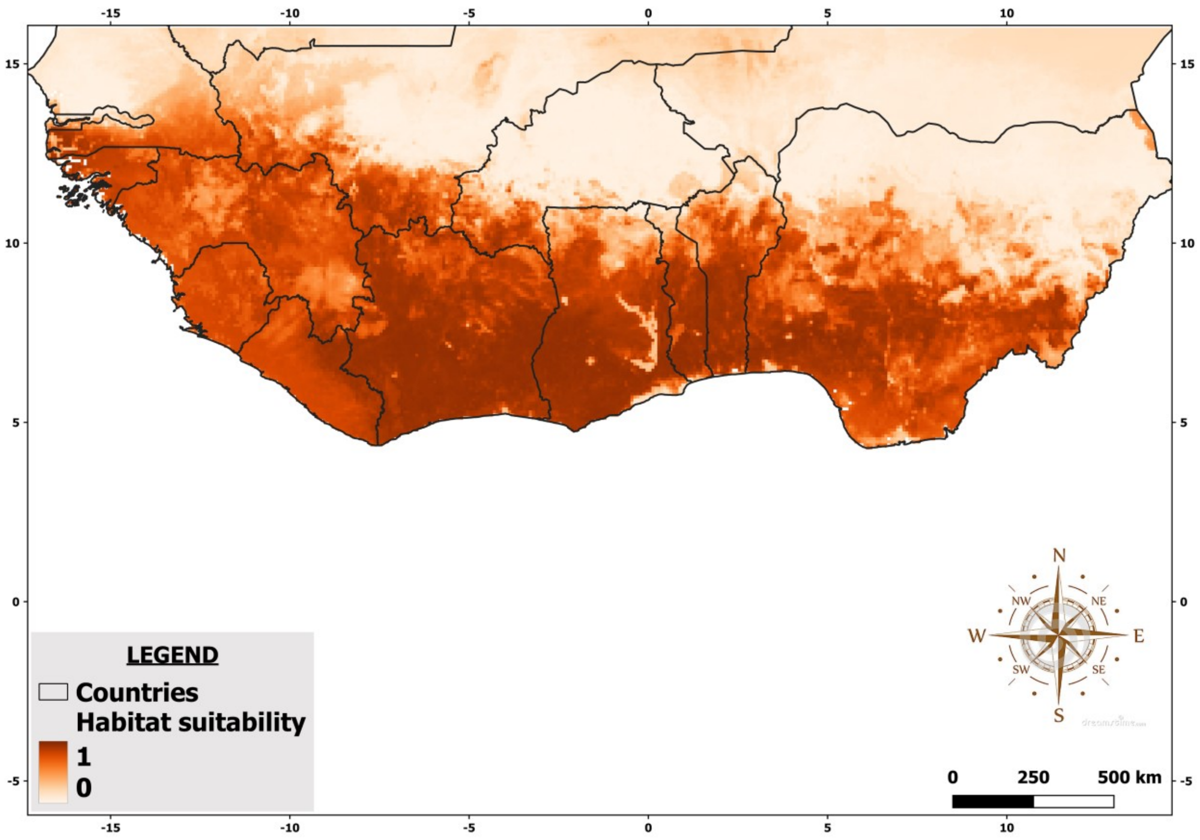


Fig. 2. Habitat suitability maps of R. microplus in West Africa with seven predictors (rainfall, temperature, cattle density, normalized difference vegetation index, cropland, grassland and shrubland). [A] MaxEnt model with only presence data; [B] Ensemble modelling suitability map with presence and absence data