Veterinary Parasitology 338 (2025) 110528

Contents lists available at ScienceDirect

Veterinary Parasitology

journal homepage: www.elsevier.com/locate/vetpar

Predicting tick distributions in a changing climate: An ensemble approach for South Africa

R.F. Motloung [a,1], M.E. Chaisi [a,b,2], M.S. Sibiya [a,3], N. Nyangiwe [c,*,4], T.C. Shivambu [d,5]

[a] Foundational Biodiversity Science, South African National Biodiversity Institute, Private Bag x101, Pretoria, South Africa
[b] Department of Veterinary Tropical Diseases, University of Pretoria, P/Bag X04, Onderstepoort, Pretoria 0110, South Africa
[c] College of Agriculture and Environmental Sciences, Department of Agriculture and Animal Health, Florida Science Campus, University of South Africa, Johannesburg 1710, South Africa
[d] College of Agriculture and Environmental Sciences, Department of Environmental Sciences, Florida Science Campus, University of South Africa, Johannesburg 1710, South Africa

ARTICLE INFO

Keywords:
CMIP6
Ecological niche shift
Public health
Species distribution models
Vector distribution
Tick management

ABSTRACT

Predicting the potential distribution of disease vectors is crucial for vector management and disease transmission surveillance. This study aims to assess changes in the geographic projection of the ecological niche of ticks of veterinary, public health, and economic importance in South Africa, and to predict areas suitable for their establishment under current and future climate scenarios. We used a suite of six algorithms within the ensemble modelling framework of the biomod2 package in R version 4.4.2 to produce species distribution models for current (2021–2040) and future (2041–2060) climate scenarios. Six bioclimatic variables, representing a range of biophysical and anthropogenic factors, were used in combination with tick presence-only occurrence data submitted to SANBI's Integrated Publishing Toolkit by tick species experts. The model outputs indicate that all 10 tick species will likely experience range shifts over time (2021–2060). All species are projected to gain significant portions of suitable ranges in the future. Notably, *Rhipicephalus microplus* is predicted to gain the most, with a 14 % increase in its suitable range in South Africa. This predicted range expansion could potentially disrupt ecological balances in the ecosystems it is likely to occupy. Native species such as *Amblyomma hebraeum* and *Hyalomma rufipes* are predicted to expand their ranges by 10 and 9 %, respectively, while others may gain less than 6 % of their potential ranges The overall predicted range expansion could also introduce new disease dynamics, potentially leading to increased pathogen transmission, host switching and higher incidences of diseases in humans and animals in currently unaffected areas. The study provides baseline information to support ongoing monitoring and adaptive management strategies to mitigate the negative impacts associated with ticks on ecosystems, public health, and agriculture. The results will help inform tick control programs in South Africa and other similar environments. South Africa must adopt a comprehensive One Health approach to tick management to address the challenges posed by invasive species like *R. microplus*, which threaten livestock health and have significant veterinary and economic impacts.

1. Introduction

Ticks are blood-feeding acarine species that play significant roles in both ecology and public health (Nejash, 2016; Obaid et al. 2022). They perform unique ecosystem services and functions like regulating populations of some animals (e.g. deer and rodents) through disease transmission (Hurtado and Giraldo-Ríos, 2018; Burtis et al. 2019). Animals like birds, reptiles, amphibians and other arthropods use ticks as

* Corresponding author.
E-mail addresses: r.motloung@sanbi.org.za (R.F. Motloung), M.Chaisi@sanbi.org.za (M.E. Chaisi), M.Sibiya@sanbi.org.za (M.S. Sibiya), nyangn@unisa.ac.za (N. Nyangiwe), shivatc@unisa.ac.za (T.C. Shivambu).
[1] https://orcid.org/0000–0002-2173–7701
[2] https://orcid.org/ 0000–0002-2365–1039
[3] https://orcid.org/0000–0002-1263–8277
[4] https://orcid.org/0000–0002-2685–1896
[5] https://orcid.org/0000–0002-9336–9813

https://doi.org/10.1016/j.vetpar.2025.110528
Received 24 November 2024; Received in revised form 6 June 2025; Accepted 6 June 2025
Available online 28 June 2025

their food source (Samish and Rehacek, 1999; Anderson and Magnarelli, 2008). There are about 900 tick species known to science currently, comprising approximately 191 species of soft ticks in the family Argasidae, 701 species of hard ticks in the family Ixodidae, and one species of Nuttallidae (Pfäffle et al. 2013). However, ticks are the second most notorious vector of human and animal diseases, following mosquitoes (de la Fuente et al., 2008). They are obligate blood-feeders of terrestrial vertebrates (Brites-Neto et al. 2015). Ticks transmit a variety of pathogens such as viruses (Flavivirus and Nairovirus), bacteria (*Anaplasma* and *Rickettsia*), protozoa (*Babesia* and *Theileria*) and helminths (Ledger et al. 2021). Ticks of different genera, such as *Amblyomma*, *Haemaphysalis*, *Ixodes*, *Rhipicephalus,* and *Hyalomma* transmit these pathogens during their blood meal. With each blood meal, ticks can acquire or spread tick-borne diseases (hereafter, TBDs) either horizontally (stage-to-stage), vertically (female-to-egg) or by co-feeding (Hrnková et al. 2021).

Ticks and the associated TBDs pose a significant global threat to animal and human health (Zannou et al. 2021; de la Fuente et al., 2023). Theileriosis, babesiosis, rickettsiosis, Crimean–Congo hemorrhagic fever, tick-borne relapsing fever, and ehrlichiosis are the most economically important TBDs in southern Africa (Chitanga et al. 2014). These diseases increase public health burdens associated with diagnosis, treatment, and prevention (Rochlin and Toledo, 2020). They lead to production losses in livestock farming, reducing incomes, raising customer costs, and threatening global trade markets (Hurtado and Giraldo-Ríos, 2018; Ali et al. 2020; Johnston et al. 2024).

Given that ticks transmit diseases to humans, livestock, and wildlife, it is especially important to understand tick distribution for several reasons. Firstly, changes in tick distributions could lead to the emergence of TBDs in new regions where they were previously uncommon or absent, posing new animal or public health risks (Githaka et al. 2021; Ogden et al. 2021). Secondly, climate change and other anthropogenic factors may cause shifts in species ranges as new suitable ranges are formed, enabling ticks to establish propagule pressure in new ecosystems (Zannou et al. 2021). In the process, they harm native wildlife populations that are not adapted to tick infestations, potentially leading to biodiversity declines (Janzén et al. 2024). This can disrupt ecosystems and food webs in regions where wildlife plays a critical role in ecological balance (Léger et al. 2013). Climate change may also alter tick life cycle and behaviour by extending the active periods and promoting faster development rates (Estrada-Peña, De La Fuente, 2014; Nuttall, 2022). For example, warmer temperatures may prolong the duration of tick activity throughout the year, while mild winters could favour tick survival even in seasons when they would typically die off, leading to greater tick abundance and a higher likelihood of disease transmission (Dennis and Fisher, 2018; Wright et al. 2021). Temperature increase in South Africa may accelerate the developmental stages of ticks and potentially lead to more generations produced per year, increasing tick population size and disease transmission (von Maltitz et al., 2024). Understanding how these dynamics unfold is vital for anticipating disease outbreaks and implementing effective public health interventions.

Despite increased efforts to study TBDs in South Africa, there is a lack of studies prioritizing ticks and the associated disease risk based on the species' ecological niche breadth. Additionally, there is a lack of studies that have investigated the impact of climate change on the distribution of ticks in the whole country (Makwarela et al. 2024). Previous studies have shown that factors like transhumance, wide ecological adaptability, and specialized phenotypes play a role in the displacement of certain species in regions where they are not typically found (Nyangiwe et al. 2017; Nyangiwe et al. 2018). However, no study has listed ticks based on their ecological niche breadth and their implications on animal and human health in South Africa. This study addresses this gap by selecting 10 tick species of medical and veterinary importance in South Africa to determine current and future habitat suitability using species distribution models.

Predicting the current and future distribution of the ticks is essential to support vector management programmes and to identify disease risk zones (Pillay et al. 2022; Tawana et al. 2022). The availability of species occurrence records, advanced species distribution modelling (SDMs) techniques, Global Circulation Models (GCMs), and climate data allows researchers to test various hypotheses. This includes modelling the potential impacts of climate change on tick distributions and the diseases they transmit (Rousseau et al. 2017; Ncube et al. 2020). Although "single" SDMs (i.e., models based on one algorithm) come with errors and uncertainties, these techniques still hold significant value (Guisan and Thuiller, 2005; Johnson et al. 2016; Naimi and Araújo, 2016). However, to deal with the errors and uncertainty related to single models, researchers use ensemble models (eSDMs) because such modelling increases accuracy by applying different algorithms simultaneously within a consensus framework (Thuiller et al. 2009; Hao et al. 2019). Ensemble models were indicated to have a high predicting power compared to individual models (Hao et al. 2019).

This study aimed to assess the impact of climate change on the distribution of veterinary and economic importance ticks in South Africa and predict areas which may be suitable for establishment under current and future climate scenarios. This study combined ensemble models using six algorithms—random forest (RF), generalized boosted forest (GBM), generalized linear models (GLM), classification tree analysis (CTA), artificial neural networks (ANN), and multiple adaptive regression splines (MARS)—along with two climatic models based on a single Representative Concentration Pathway to predict the potential effects of climate change on tick distribution. This study will inform targeted tick control and management strategies, helping to mitigate the risks posed by shifting tick distributions under changing climate conditions.

2. Materials and methods

2.1. Study Area

South Africa is the southernmost country in Africa, covering a land area of 1220,000 km^2 and is located between 22 and 35°S and 16–33°E (Roffe et al. 2021) (Fig. 1). The country shares its borders with the following neighbouring countries: Namibia on the northwestern side, Botswana and Zimbabwe on the northern side, and Mozambique on the eastern side, with Lesotho and Eswatini landlocked within the country (Fig. 1). According to the South African National census conducted in 2023 by Statistics South Africa, the country's population is estimated at 61.5 million (Statista, 2023). Agriculture (livestock farming) contributes significantly to the country's economy, especially in rural areas. Some country inhabitants depend on crops and livestock for their livelihoods (Johnston et al. 2024). However, cattle, sheep, and goat farming experience significant economic losses due to tick-borne diseases, which are particularly common among African resource-poor farmers (Mapholi et al. 2022; Makwarela et al. 2023).

The variable climatic conditions of South Africa support high tick diversity and prevalence by providing suitable habitats and microclimates. The Indian Ocean surrounds the country on the east and the Atlantic on the west, resulting in subtropical climates with mild temperatures in the east, which experience rainfall throughout the year. On the western side, the climate is more of a Mediterranean type characterized by heavy winter rainfall and warm, dry summers. The northwestern side of the country experiences desert and semi-desert climatic conditions with low rainfall in summer and variation of temperatures between hot days and cold nights. Finally, the savannah climate forms part of the northeastern side of the country characterized by the distinct wet and hot seasons in summer and dry season in winter. The region's topography comprises the coastal plains, mountains, and a central plateau. The Drakensberg Mountain range runs along the eastern border, with mountain peaks reaching over 3400 m above sea level and providing a range of suitable habitats for different species (Finch and Meadows, 2019).

South Africa's diverse climatic conditions have led to the

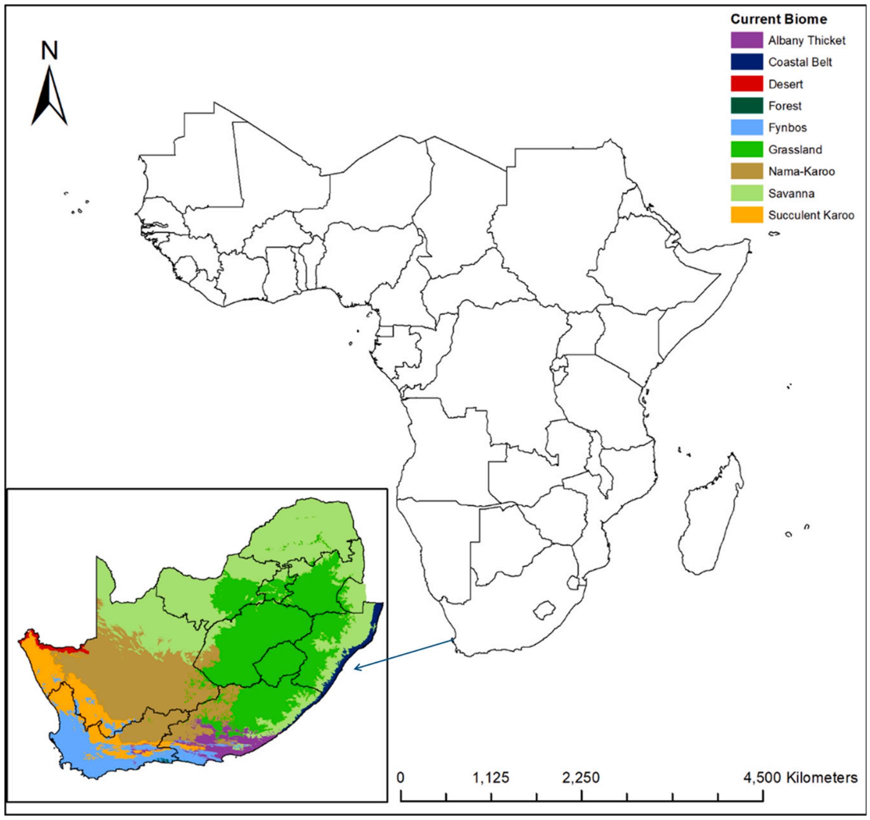

Fig. 1. The map of Africa south of 18° N latitude with an inset zoom of South Africa showing the current biomes of South Africa, highlighting various ecological zones. The biomes are colour-coded as indicated in the legend.

development of various biomes and bioregions (Fig. 1). A biome is a large area with similar vegetation shaped by shared micro-climates and factors like competition, disturbances, and time. The Succulent Karoo is arid with winter rainfall, low annual rainfall, and extreme temperature variations, and it supports diverse succulent plants. The Savanna is the largest biome, with summer rainfall and warm temperatures, featuring a mix of grasses and trees. The Grassland is found in the cooler, elevated interior of the country, with summer rainfall and moderate temperatures, supporting various grasses and herbivores. The Indian Ocean Coastal Belt (IOCB) lies along the eastern coast. It is warm and humid with high year-round rainfall, supporting tropical and subtropical forests. The Desert is in the northwest, with very low rainfall and extreme temperatures, with some areas receiving winter or summer rainfall. The Albany Thicket, in the Eastern Cape, has an intermediate climate between Savanna, Nama-Karoo, and Subtropical Forest, experiences moderate rainfall and temperatures. Nama-Karoo: Mainly has summer rainfall, arid conditions, low species richness, and low to moderate rainfall. Afrotemperate Forest: In the southern part of the country, is cooler and moist with high rainfall, supporting a rich diversity of plants and animals.

2.2. *Tick species selection criteria*

For this study, we selected ten tick species based on the following criteria: 1) their significance to veterinary and public health; 2) the majority of these species (70 %) are generalists, meaning they infest a wide range of hosts (Horak et al. 2018); 3) they are widespread in their geographic distribution (e.g. *Amblyomma hebraeum*) which is important for understanding the regional disease dynamics and TBDs emergence. Lastly, some of the selected ticks have unique biological traits, such as differing host preferences or resistance to acaricides (e.g. *Rhipicephalus decoloratus* and *R. microplus* (Rodriguez-Vivas et al., 2018; Juache-Villagrana et al., 2023), selected to provide insights into their ecology and potential control measures (Dalen and Jansen 2023). As per the criteria used, the findings of this study will inform the use of resources while addressing key public health and veterinary challenges in the country. Of the selected tick species, only *R. microplus* is alien to South Africa.

2.3. *Modelling framework*

We employed an ensemble species distribution modelling (SDM) approach within the Biomod2 package in R version 4.4.2 (R Core Team, 2025) to predict the current and future distribution of ticks of veterinary and economic importance in South Africa, integrating multiple machine-learning algorithms to improve predictive accuracy and reliability. The analysis followed several key steps: data preparation, model calibration, projection, and evaluation.

2.4. *Data preparation*

2.4.1. *Presence and absence*

Presence-only occurrence records for ten tick species were obtained from publicly available databases, including the SANBI Integrated Publishing Toolkit (SANBI IPT) available at https://ipt.sanbi.org.za/resource?r=ticks (Robertson et al. 2014; Horak, 2016). Additionally, we manually searched and retrieved species occurrence data from the Global Biodiversity Information Facility (GBIF; Table 1). For two species (*Amblyomma hebraeum* amd *A. marmoreum*), the GBIF downloaded DOIs were saved at the time of data acquisition in August 2024. To ensure complete and properly referenced datasets, occurrence records for the remaining eight species were re-downloaded from GBIF in May 2025, and the corresponding DOIs have been included. GBIF provides a comprehensive occurrence dataset sourced from accredited

Table 1
Species names, their corresponding GBIF accession numbers, and the dates on which the data were accessed from the online database.

Species	Accession number	Date accessed
Amblyomma hebraeum	https://doi.org/10.15468/dl.zv5cns	6 August 2024
Amblyomma marmoreum	https://doi.org/10.15468/dl.hg6buk	6 August 2024
Haemaphysalis elliptica	No records	
Hyalomma rufipes	https://doi.org/10.15468/dl.s2v6c4	16 May 2025
Rhipicephalus appendiculatus	https://doi.org/10.15468/dl.cca7rd	16 May 2025
Rhipicephalus decoloratus	https://doi.org/10.15468/dl.mk9um4	16 May 2025
Rhipicephalus evertsi evertsi	https://doi.org/10.15468/dl.2yw38m	16 May 2025
Rhipicephalus microplus	No records	16 May 2025
Rhipicephalus simus	https://doi.org/10.15468/dl.948szv	16 May 2025
Rhipicephalus zambeziensis	No records	

institutions, international museums, and peer-reviewed literature (Petrosyan et al. 2023).

The compiled occurrence records were cleaned by removing duplicates, overlapping occurrences, and records with missing latitude or longitude coordinates using the R packages *Biogeo* (Robertson et al., 2016) and *CoordinateCleaner* (Maldonado et al. 2015) as well as ArcGIS (ESRI, 2020). Records falling outside the study area were also excluded. After data cleaning, 975 occurrence records remained and are provided in Supplementary Material: Appendix S1 to enhance transparency and facilitate future research. All South African records of *Haemaphysalis leachi* were renamed to *Ha. elliptica* (Apanaskevich et al. 2007). Since the data were collected opportunistically, they exhibit inherent spatial biases, particularly toward more accessible locations (Koldasbayeva et al. 2023; Baker et al. 2024; Xu et al. 2024). Uncorrected spatial bias can lead to inaccurate model predictions and erroneous ecological interpretations (Ranc et al. 2017; Baker et al. 2024). To address this issue, we applied a sampling bias correction approach using Kernel Density Estimation (KDE) from the *sm* package (Worton, 1989; Bowman and Azzalini, 2021). This approach generates a bias surface reflecting the sampling effort, allowing for improved pseudo-absence selection. We generated a set of pseudo-absences for each species, with the number of pseudo-absence points to five times the number of presence records. These points were randomly selected based on the KDE-derived bias surface within South Africa (Phillips et al. 2009).

2.4.2. Climate data

Although factors such as host availability, transhumance, and vegetation cover are important for predicting tick range shifts, they were not included in this study. Instead, we focused on assessing the impact of climate change on tick distributions using exclusively climate-related variables (Nyangiwe et al. 2018; Sungirai et al. 2018; Sili et al. 2021) (Table 2). To achieve this goal, we incorporated a global circulation model (GCM) from the Coupled Model Intercomparison Project 6 (phase 6) from a single climate change scenario called Shared Socioeconomic Pathways 1–2.6 (SSP 1–2.6). The SSP1–2.6 represents a low-carbon emission, sustainability-focused pathway where the global temperature rise is limited to approximately 1.5 ℃ to 2 ℃ above the pre-industrial levels by the end of the 21st century (IPCC 2021). This scenario was selected as it aligns with the goals of the Paris Agreement and is used to explore how mitigated future climate might affect tick distribution and habitat suitability. Specifically, we selected the ACCESS-CM2 general circulation model (GCM) as it has global and regional climate simulation capabilities, high-resolution projections, and a proven track record in studying vector-borne diseases and biodiversity under climate change (Ogden et al. 2014). Additionally, it has compatibility with species distribution modelling methods, as it can capture the complexities of climate in regions like South Africa, and its capacity to simulate diverse climate scenarios makes it an ideal tool for predicting future habitat suitability for tick species(Song et al. 2024; Pham et al. 2025).

Table 2
A set of non-collinear environmental variables used as predictor variables for modelling the current and future climatic conditions of tick species found in South Africa.

Variable code	Description	Units	VIF value (2020 s)	VIF value (2050 s)
BIO2	Mean diurnal range (Mean of monthly (max temp—min temp))	°C	4.93	5.20
BIO3	Isothermality (BIO2/BIO7) (×100)	%	2.45	2.23
BIO13	Precipitation of the wettest month	mm	4.42	6.27
BIO14	Precipitation of the driest month	mm	6.89	8.77
BIO15	Precipitation seasonality	mm	5.14	7.60
BIO19	Precipitation of the coldest quarter	mm	8.58	7.50

We obtained nineteen bioclimatic variables from WorldClim version 2 for both the baseline (2021–2040) and future (2041–2060) climate scenarios at a 10-arc minute resolution in GeoTIFF format (Booth et al. 2014; Fick and Hijmans, 2017). Correlations amongst the 19 bioclimatic variables for current and future climate scenarios were tested using the Variable Inflation Factor function in R using the uSDM package VIF (Marquaridt, 1970) and Pearson (r) correlation coefficients to identify multicollinearity. This is because multicollinearity impacts model performance and prediction, as well as effects on the SDM, such as model uncertainty and overfitting (Dormann et al. 2013; De Marco and Nóbrega, 2018). We applied a threshold of $|\rho| < 0.7$ to exclude highly correlated variable pairs and used a VIF threshold of less than 10 to remove variables showing high multicollinearity in the multivariate context (Dormann et al. 2013). Following these criteria, six non-collinear bioclimatic variables were selected for each species (Table 2).

2.5. Model calibration, fitting and evaluation

To select algorithms that exhibit similar responses to the same optimization method for pseudo-absence selection (Barbet-Massin et al. 2012) we initially employed eight non-linear and non-parametric machine learning techniques. These included Classification Tree Analysis (CTA), Generalized Boosting Model (GBM), Random Forest (RF), Artificial Neural Networks (ANN), Generalized Linear Models (GLM),

Table 3
A set of eight algorithms employed as a statistical method for modelling ten selected tick species in South Africa.

Algorithm	code	Dependent packages	References
Generalized Linear Models	GLM	*stats*	
Classification Tree Analysis	CTA	*rpart*	(Breiman et al., 1984)
Artificial Neural Networks	ANN	*nnet*	
Generalized Boosted Models	GBM		
Multiple Adaptive Regression splines	MARS	*mda*	
Randon Forest	RF	*randomForest*	
Surface Range Envelope	SRE	*biomod2*	(Thuiller et al., 2009)
Flexible Discriminant Analysis	FDA	*mda*	(Hastie, Tibshirani and Buja, 1994)

Multiple Adaptive Regression Splines (MARS), Surface Range Envelope (SRE), and Flexible Discriminant Analysis (FDA) (Table 3).

To ensure high model performance, only models meeting the thresholds of TSS > 0.6 and AUC > 0.8 were retained for ensemble predictions (Table 2). Consequently, SRE and FDA models were excluded from further analysis. The remaining six models (GLM, CTA, ANN, GBM, MARS, RF) were used to construct ensemble models via the BIOMOD_projection function (Komac et al. 2016).

For the species R. zambeziensis, due to the limited number of occurrence records (n = 33), we selected fewer complex models (GLM, CTA, MARS) to avoid overfitting and improve model generalizability. These models are known to perform well with small datasets, as they are less likely to overfit compared to more complex algorithms. The used models can capture key ecological relationships while minimizing the risk of overfitting, which is particularly important when the number of available occurrence records is constrained (Wisz et al. 2008; Gomez et al. 2015; Breiner et al. 2018).

Model performance was evaluated through fivefold cross-validation, where the dataset was split into 80 % training and 20 % testing subsets. The ensemble model for each species was computed using a weighted mean approach, averaging the predictions of the six retained algorithms (Hao et al. 2019; Hao et al. 2020). The maximum specificity plus sensitivity threshold was used to determine presence-absence cutoffs, ensuring models with TSS ≥ 0.6 were retained (Petrosyan et al. 2023). The resulting binary habitat suitability maps were created in ArcMap 10.8.1.

To account for errors and uncertainties in our models, we employed the *BIOMOD_EnsembleModeling* function, with parameters that compute the coefficient of variation (EMcv) for ensemble predictions. This approach allows us to quantify the variability in model outputs and assess the robustness of our predictions. Models were selected based on performance metrics, retaining only those with TSS > 0.6 and AUC > 0.8. The coefficient of variation values was used to represent uncertainty in predicted range sizes for each species. To enhance the visibility of variability in our graphical representations, coefficients of variation (CVs) were scaled by a factor of 100 or 10,000 to improve clarity in the display of error bars. This adjustment was applied solely for visualisation purposes and does not affect the interpretation of the model outputs. The resulting uncertainty estimates are presented in supplementary material Fig. A1.

Model performance was assessed using the partial receiving operating characteristic (partial ROC) utilizing the true skill statistic (TSS) and the area under the curve (AUC) (Allouche et al. 2006; Hardlife et al. 2020; Tagwireyi et al. 2022). The AUC values were interpreted as follows: < 0.7: Poor model performance, 0.7–0.9: Good performance, and > 0.9: Excellent performance (Mohammadi et al. 2019)). TSS values ranged from −1–1, with values > 0.6 considered excellent (Araújo et al. 2019). Instead of the jackknife procedure, which can overestimate predictive power, we evaluated cut-off thresholds, sensitivity, and specificity to ensure model accuracy.

2.6. Model prediction

The outputs of the ensemble model were utilized to generate spatially continuous suitability maps for current conditions, indicating areas with varying probabilities of occurrence (0 = unsuitable, 1 = highly suitable). Variable importance was assessed using 999 permutations within biomod2, and model evaluation metrics were produced to assess performance. In addition to these maps, we adopted the *Biomod_RangeSize* function to quantify and measure predicted species distribution changes induced by future predictions under a given management regime. These changes were computed to identify using the number of pixels: a) climatically suitable or unsuitable areas for each tick species under current and future climate scenarios, b) the loss or gain of climatically suitable habitats, c) habitats predicted as climatically suitable and the species is observed to occur (stable 1), (sable 1), and d) habitats predicted as climatically unsuitable and where the species is unobserved (stable 0). The function also calculates overall species range change, percentages of gain and loss per species, and the current range size. Lastly, the function measures species' potential distribution change under full and no dispersal scenarios.

2.7. Statistical analysis

Potential range size changes were calculated using binary maps using the raster zonal geometry calculation function in desktop ArcGIS version 10.8.1 for present and future predictions (blue and black pixels in 2041–2060. To determine whether there is a significant association between current and future habitat suitability, a Pearson's Chi-squared test (χ^2) was performed using R statistical software version 4.4.2 (Tagwireyi et al. 2022).

3. Results

3.1. Model fitting and evaluation

Individual model performances showed high intra- and inter-model variability using the evaluation metrics (ROC and TSS). The weighted mean ROC values varied across algorithms, ranging from 0.76 for MARS to 1 for RF (excluding *R. zambeziensis*). According to TSS, the lowest weighted mean was 0.78 for MARS and 1 for RF. Our results indicate that RF models were better calibrated than other algorithms, based on the evaluation metrics (Appendix S2).

By selecting the best individual models (TSS > 0.6 and AUC > 0.8) and excluding poorly calibrated and validated models, based on the cross-validation procedure, good ensemble models were achieved. The ensemble models were satisfactory and showed low variability, with evaluation metrics ranging from 0.74 to 1 for TSS (± 0.09 SD) and 0.87–1 for AUC (± 0.04 SD).

3.2. Model predictions

3.2.1. Variable importance

The ensemble model used in this study to predict the current and future distribution of selected ticks incorporated an average of six bioclimatic variables for each of the two Global Circulation Models (Table 2). The most important variables across both climate scenarios were BIO13 (precipitation of the wettest month), BIO19 (precipitation of the coldest quarter), and BIO14 (precipitation of the coldest month). Conversely, BIO3 (isothermality) contributed the least to the model for all species except *R. decoloratus* and *R. simus*. Precipitation during the wettest quarter (BIO13) was the most significant variable for modelling species distributions across all tick species except for *R. zambeziensis*. For this species, precipitation seasonality (BIO15 was the most relevant variable (Table 4).

3.2.2. Model evaluation metrics

The ensemble models successfully predicted the current habitat suitability of the ten tick species in South Africa with an AUC value of 0.87 and a mean TSS value of 0.74 (Table 5). Of the ten tick species, the ensemble models for threshold-independent scores (AUC) performed well for all ticks with scores above 0.8. The threshold-dependent scores (TSS) models performed well for all species and only *A. hebrauem* (TSS = 0.74), *Hy. rufipes* (TSS = 0.74) and *R. decoloratus* (TSS = 075) have scores lower than 0.8. Overall, in terms of the evaluation metrics used, the six algorithms performed well for the ten tick species selected. The assessment of model performance indicates satisfactory levels of accuracy, reliability, and performance, as reflected in the measures like sensitivity and specificity values for each species (Table 5, Fig. 4, Appendix A2).

Table 4
Top three variables important in predicting tick species distribution under current and future climate scenarios.

Species	Variables of importance
Amblyomma hebraeum	Precipitation of the wettest month (Bio13), precipitation seasonality (Bio15), mean diurnal temperature (Bio2)
Amblyomma marmoreum	Precipitation of the coldest quarter (Bio19), Precipitation of the wettest month (Bio13), Precipitation of the driest month (Bio14)
Haemaphysalis elliptica	Precipitation of the wettest month (Bio13), precipitation of the coldest quarter (Bio19), precipitation seasonality (Bio15)
Hyalomma. rufipes	Precipitation of the wettest month (Bio13), Precipitation of the driest month (bio14), precipitation of the coldest quarter (Bio19)
Rhipicephalus appendiculatus	Precipitation of the wettest month (Bio13), precipitation of the coldest quarter (Bio19), and mean diurnal range (Bio2),
Rhipicephalus decoloratus	Precipitation of the wettest month (bio13), Isothermality (Bio3), precipitation of the driest month (Bio14)
Rhipicephalus evertsi evertsi	Precipitation of the wettest quarte (Bio13), mean diurnal range (bio2), precipitation seasonality (Bio15)
Rhipicephalus microplus	Precipitation of the wettest month (Bio13), precipitation of the coldest quarter (bio19), Precipitation of the driest month (Bio14)
Rhipicephalus simus	Precipitation of the wettest month (Bio13), Isothermality (Bio3), mean diurnal range (Bio2),
Rhipicephalus zambeziensis	Precipitation seasonality (Bio15), precipitation of the coldest quarter (Bio19), precipitation of the driest month (Bio14)

3.2.3. Potential range size changes

The predicted changes in habitat suitability for the ten modelled tick species indicate significant changes under both the current and future climate scenarios (χ^2 = 569.66, df = 9, p-value < 2.2e-16). The ensemble model predictions under the two climate scenarios have indicated an overall increase in the potential distributions of all ticks, thereby affecting their range sizes in South Africa (Fig. 2). Interestingly, most of the tick species studied are predicted to retain their current ranges in the future, maintaining stable occupancy (stable1) in areas they currently inhabit. Additionally, they are predicted to remain absent (stable 0) in most regions where they are not presently found (Fig. 3).

While all the studied tick species are predicted to expand their potential ranges, the extent of potential habitat gain varies for each species in response to climate change. Interestingly, the models predicted that the alien species, *Rhipicephalus microplus*, is the most likely to gain potential range (14 %) more than the native species. Secondly, *A. hebraeum* is predicted to likely increase its potential range by 10 %, while *Hy. rufipes* is predicted to expand by 9 % (see Figs. 2 and 4). The species predicted to have the smallest increase in potential range, at 3 %, is *R. e. evertsi*. All species' potential ranges are more likely to expand towards the interior regions of the country, except *R. zambeziensis* which is more likely to expand the range to the coastal regions (Fig. 4). For instance, *R. microplus* range is likely to expand into the interior parts of the Northern Cape, Free State, Eastern Cape and up into the Limpopo Province. The models also predicted that this species is likely to expand its potential range to the Coastal parts of KwaZulu-Natal (Fig. 4). In contrast, *R. decoloratus* is predicted to potentially increase its range towards the eastern side of the North West province, but not much into the Northern Cape (Fig. 4).

Conversely, the studied tick species exhibit varying levels of potential habitat loss in response to climate change, with values ranging from 0.2 % to 6 %. While some species are predicted to face significant reductions in suitable areas, others are less affected. For example, R. microplus and A. hebraeum are projected to lose 6 % and 5 % of their current suitable habitat under future climate scenarios, respectively. In contrast, all other species are predicted to likely lose less than 2 % of their habitat, with R. appendiculatus expected to lose only 0.2 % (see Fig. 3). These differences highlight the diverse sensitivities of species to climate change, shaped by their unique ecological requirements and environmental tolerances.

3.3. Ecosystems at risk of tick infestations

Based on ensemble species distribution models, the predicted habitat suitability for current and future conditions varies but follows a consistent pattern. Predicted suitable areas are primarily located in the eastern half of South Africa, encompassing the Savanna biome, Indian Ocean Coastal Belt, Grassland and Albany thicket biomes (Fig. 4). *Amblyomma* species exhibit distinct potential distribution patterns under current and future climates, with *A. marmoreum* likely to occupy parts of all eastern provinces (Limpopo, Gauteng, KwaZulu-Natal, half of the North West and Free state provinces. Interestingly, the predicted future distribution of *A. hebraeum* indicates that the species is likely to spread further down into the central North West.

Under future climatic conditions, the country's eastern half is predicted to be suitable for *Hy. rufipes* and the species is more likely to spread into other parts of KwaZulu-Natal, the east side of Mpumalanga, Free State, Limpopo and North West provinces in the future. The potential distribution of *Ha. elliptica* in the future indicates key areas for range expansion as a belt around the western parts of the North West, the Free State, down into the Eastern Cape.

The *Rhipicephalus* species exhibit intriguing, predicted distribution patterns. Notably, *R. decoloratus* and *R. microplus* are both predicted to likelyspread westward into the North West, with *R. microplus* also likely to extend into the Northern Cape province. Additionally, *R. microplus* is predicted to spread into the western side of the Eastern Cape and the north-eastern KwaZulu-Natal. *Rhipicephalus appendiculatus, R. simus* and *R. e. evertsi* are also predicted to spread into the eastern side of the Northern Cape, the Western Free State (*R. e. evertsi*), and the Eastern Cape. *Rhipicephalus zambeziensis* is a fascinating tick species, recorded in Limpopo and parts of Mpumalanga, with a few records in the Free State, Eastern Cape, and Western Cape. However, the predicted distribution suggests it will likely occupy a much larger range, covering almost the

Table 5
Model evaluation metrics for various tick species with current climate (2020–2040). The table provides the number of occurrence records, sensitivity, specificity, True Skill Statistic (TSS), and Area Under the Curve (AUC) for each species.

Species	Presence	Absence	Sensitivity (ROC)	Specificity (ROC)	AUC	Sensitivity (TSS)	Specificity (TSS)	TSS	Model SD	Model mean
A. hebraeum	169	845	0.87	0.88	0.87	0.87	0.87	0.74	0.528	−0.264
A. marmoreum	99	495	0.94	0.91	0.92	0.94	0.91	0.85	0.524	−0.349
Ha. elliptica	71	355	0.94	0.95	0.95	0.96	0.95	0.91	0.546	−0.438
Hy. rufipes	78	390	0.92	0.83	0.87	0.92	0.82	0.74	0.520	−0.283
R. appendiculatus	130	650	0.98	0.95	0.97	0.98	0.95	0.93	0.539	−0.476
R. decoloratus	122	610	0.88	0.87	0.88	0.90	0.85	0.75	0.540	−0.394
R. evertsi	162	810	0.95	0.93	0.94	0.95	0.93	0.88	0.544	−0.537
R. microplus	55	275	0.89	0.93	0.91	0.89	0.92	0.81	0.529	−0.230
R. simus	86	430	0.97	0.80	0.89	0.97	0.80	0.87	0.564	−0.468
R. zambeziensis	33	165	1.00	1.00	1.00	1.00	1.00	1.00	0.556	−0.586
Total / Average	**975**	**5535**	**0.92**	**0.90**	**0.91**	**0.92**	**0.90**	**0.84**	0.528	−0.264

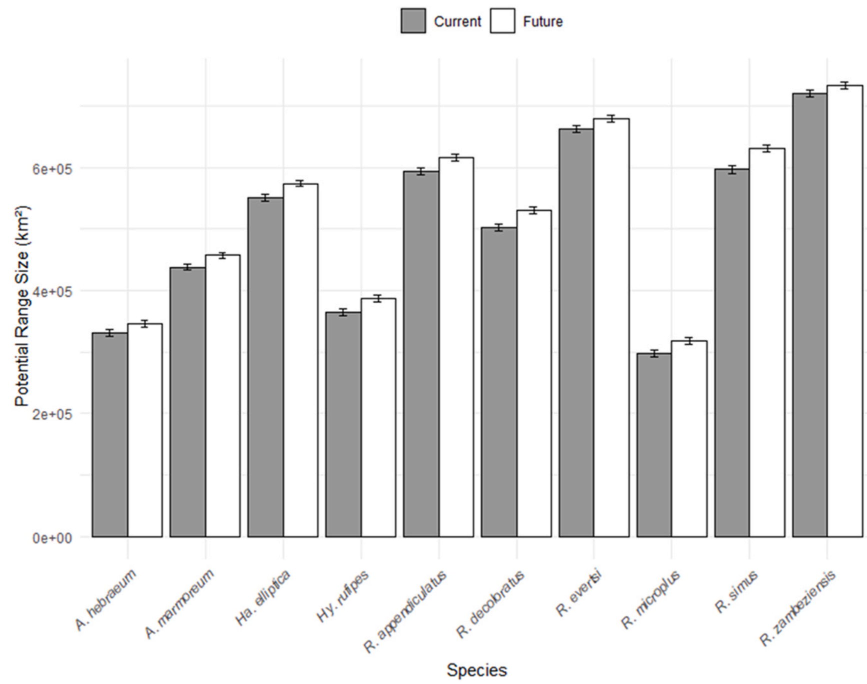

Fig. 2. Comparative analysis of the changes in the predicted current and projected future range sizes (in square kilometres) for various tick species in South Africa. Notably, some species are predicted to undergo significant expansions in their habitats.

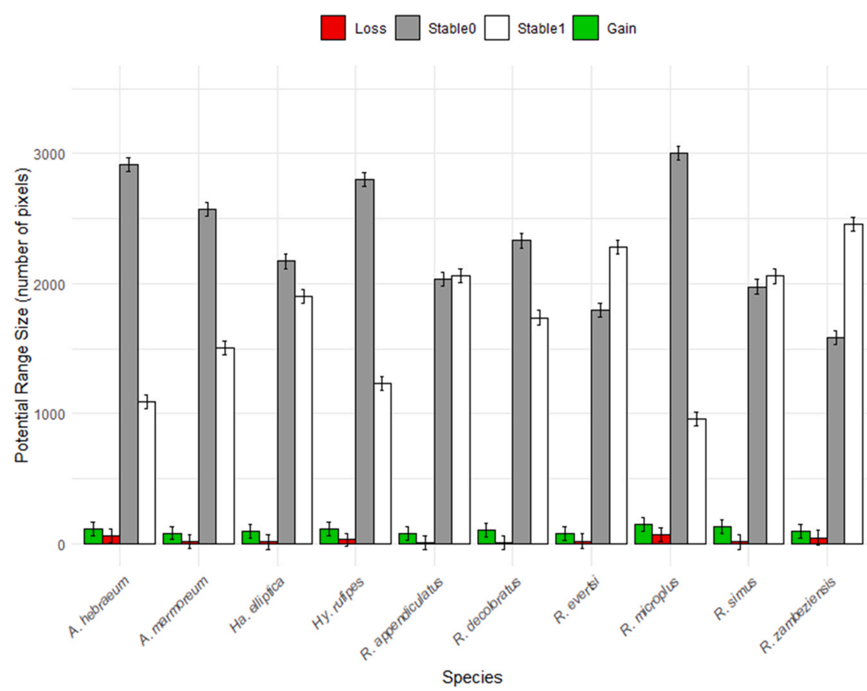

Fig. 3. Potential range size changes for different tick species based on future climate scenarios. The bar plot shows the count for each species categorized into four variables: habitat loss (red), stable unsuitable areas (grey), stable suitable areas (white), and habitat gain (green).

entire country. Only parts of the Western Cape and Eastern Cape are predicted to be less likely suitable. The predicted probability of occurrence for this species is high in all seven provinces of South Africa.

4. Discussion

The main objective of this study was to investigate the potential effects of climate change on the spatial distribution of the ten tick species of veterinary, public health, and economic importance. The outputs from the ensemble SDMs were validated using current known tick distributions, and current and future projections were compared across time periods to assess potential range shifts, expansions, and contractions in tick habitat suitability. Our results indicated that significant changes in tick distributions may occur even under the relatively mild and optimistic SSP 1–2.6 climate scenario.

The two covariates, i.e., rainfall and temperature, are essential in explaining the predicted spatial distribution of ticks under both the current and future climate scenarios. These covariates directly affect the

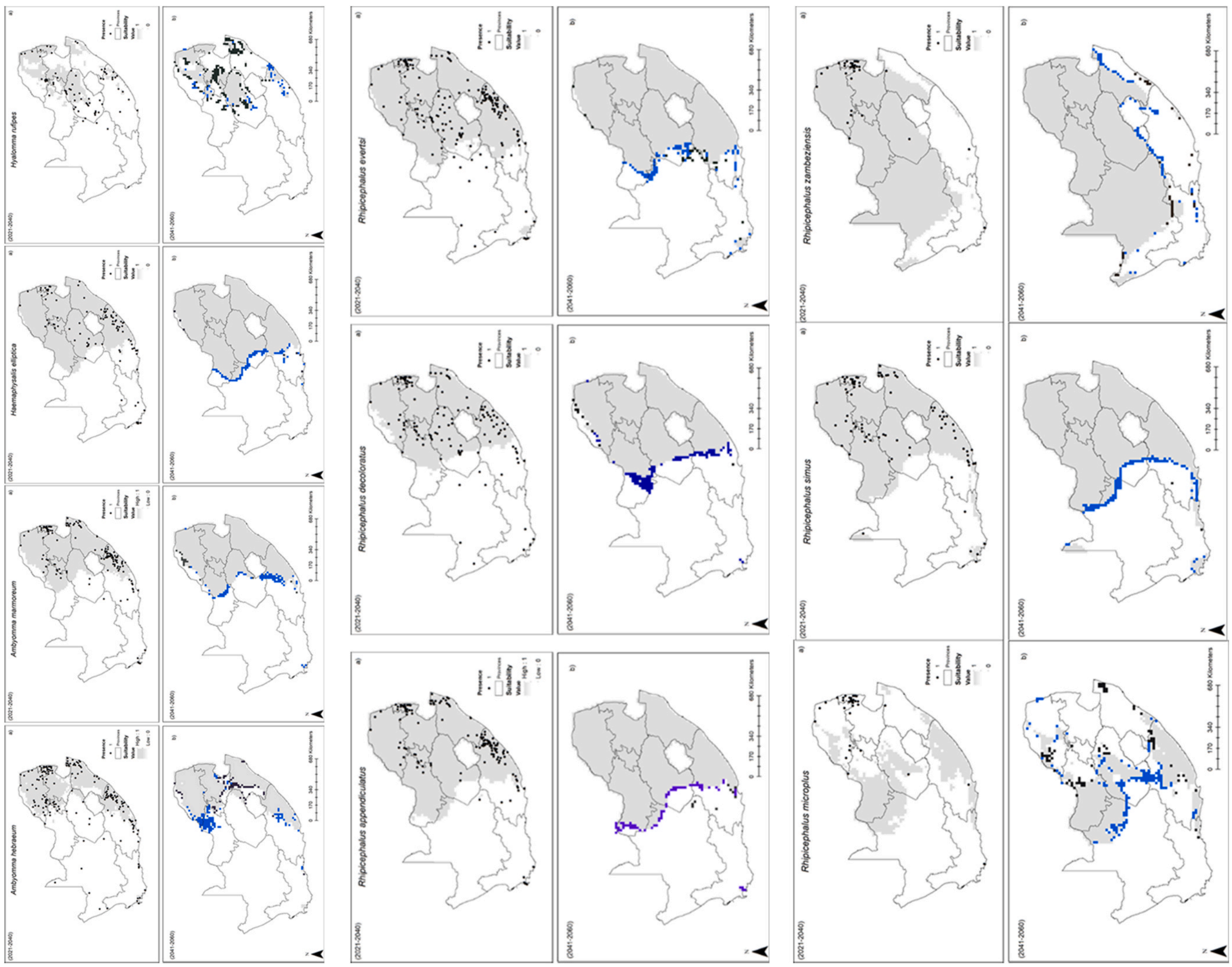

Fig. 4. Habitat suitability maps for different tick species in South Africa under current (a) (2021–2040) and future (b) (2041–2060) climatic conditions. Suitability values are shown on a gradient from 0 (unsuitable, no fill) to 1 (highly suitable, grey). In panel (a), black pixels indicate species occurrence locations based on presence records. In panel (b), blue pixels represent areas of predicted suitable range gain, while black pixels indicate areas of predicted suitable range loss under future climate scenarios.

ticks and their host's living conditions in several ways (Ndaimani et al. 2016). Studies have shown that ticks thrive best in areas of moderate to high rainfall and temperatures (Sungirai et al. 2018). In South Africa, moderate to high rainfall and temperature appear to favour all species, with peaks observed at temperatures from 16 to > 26 °C and rainfall from 400 mm to > 1200 mm. Rainfall below 400 mm appears unfavourable for all species, while an increase in temperatures inland appears to give species like *R. zambeziensis* an advantage in the future.

An important result of this study is that bio13, bio14 and bio19 have the highest prediction power when compared with other bioclimatic variables. This correlates in part with the two studies carried out in Zimbabwe by Sungirai et al. (2018) and Tagwireyi et al. (2022), which show that *R. decoloratus* and *R. microplus* prefer areas of moderate temperatures (between 18 and 20ºC) and rainfall (between 500 and 750 mm). In the study by Tagwiyeri et al. (2022), *A. hebraeum* was shown to thrive in areas with moderate temperatures (between 26 and 29ºC) and its range restricted by an increase in temperature (bio5). However, in South Africa, *A. hebraeum* range size is likely restricted by the precipitation of the wettest (bio13), precipitation seasonality (bio15) and mean diurnal temperature (bio2). If the precipitation seasonality becomes less pronounced, with longer wet periods and shorter dry seasons, the species' habitat may become more suitable, leading to range expansion. This is because variations in rainfall and temperature can favour the ticks' life cycle and increase the availability of microhabitats.

The projected changes in the range sizes of various tick species, as illustrated in Fig. 4, highlight these species' complex and varied responses to climate change. The significant range size expansion for species like *Rhipicephalus microplus*, *A. hebraeum*, and *Hy. rufipes* under current and future climatic conditions suggests that changing climatic conditions will favour them. Although the distribution of *R. microplus* has not yet fully reached equilibrium, the predicted distribution indicates that this species is more likely to spread than *R. decoloratus*, which is predicted to increase its potential range by 6 % compared to 14 %. *Rhipicephalus microplus* will likely displace *R. decoloratus* in other parts of the country, like the North West and Free State, due to its predicted range expansion and adaptability to changing climatic conditions (Tønnesen et al. 2004; Nyangiwe et al. 2013).

The model output indicates that the potential habitat suitable for *R. microplus* in South Africa continues to expand, showing a patchy yet continuous distribution in the central parts of the country, including the Eastern Cape, Free State, Northern Cape, and Limpopo. While *R. decoloratus* still has a wider distribution across the country, there are areas where both species coexist, with the potential for *R. decoloratus* to be displaced in regions highly suitable for *R. microplus*. These results suggest that *R. microplus* is predicted as more likely to establish in most parts of the country, especially if it spreads into new areas, such as through cattle movement. These results indicate a strong association between climate change, tick phenology and the role of life history traits of the invasive vs. native species. While both ticks are one-host species, *R. microplus* has a high reproductive ability, i.e. lays more eggs than *R. decoloratus*, is more adaptable to a broader range of environments and has shown increased resistance to acaricides (Cruz et al. 2020; Léger et al. 2013).

Conversely, the model outputs indicate that all species are likely to lose smaller parts of their predicted suitable ranges compared to the gained range in the future (Fig. 4). In general, all species are likely to benefit from the changing climate, possibly due to their broader ecological niches or greater adaptability. It also indicates that the future climate in such areas will likely be more semi-arid to arid. This is particularly true because these ticks prefer hotter regions and are well-adapted to survive in areas with moderate to high temperatures. The warm climates of high temperatures and moderate to lower rainfall support the tick's activity and development (Mtambo et al. 2007). As such, these ticks require more humid environments and are more likely found in the eastern provinces like KwaZulu-Natal, Eastern Cape, Free State, Gauteng, Limpopo and North West (Fig. 4).

The primary limitation of our study lies in the reliance on publicly available occurrence records, such as those from the Global Biodiversity Information Facility, and data provided by a single subject-matter expert. This approach inadvertently excludes data from literature sources and other inaccessible records maintained by additional experts in the field. The accuracy of species distribution models for ticks, such as *R. microplus* and *R. zambeziensis*, is significantly affected by small sample sizes. Additionally, *Hy. rufipes* is much more widely distributed in South Africa than the model predicts (Norval and Horak, 2004; Spickett et al. 2011; Horak et al. 2018). Limited data can lead to biased predictions and increased variability, as the models may not capture the full range of environmental conditions where the species is likely to occur (Ribeiro et al. 2019; Sillero et al. 2021; Soley-Guardia et al. 2024). This can result in underestimating or overestimating the tick's potential distribution, highlighting the need for more comprehensive sampling to improve model reliability (Elith et al. 2006; Wisz et al. 2008; Ribeiro et al. 2019).

Future research could improve the modelling process by using more comprehensive occurrence records by searching the literature and exploring the use of species distribution models with more ticks. Although land use, host availability and vegetation contribute strongly to tick distribution, they cannot be used in climate change scenarios or combined with bioclimatic variables at different spatial and temporal resolutions (Aguilar-Domínguez et al. 2021; Polo et al. 2024). However, the findings of this study are useful because of the three major strengths of our approach. The first is using authenticated bioclimatic variables with global spatial coverage. As such, the variables and occurrence data are available for other researchers to validate our findings. Secondly, ensemble models with the six best algorithms maintain high validity and reliability of the model (Eisen et al. 2016; Tagwireyi et al. 2022). Lastly, they also highlight the critical role of dispersal ability in shaping future range dynamics and the necessity for comprehensive models that incorporate both climatic and ecological factors to accurately predict the impacts of climate change on tick distributions. This information is vital for developing effective control measures and mitigating economic and public health impacts of tick-borne diseases.

5. Conclusion

The results of this study indicate that climate change, even under a more optimistic scenario (SSP 1–2.6), will significantly impact the distribution of tick species in South Africa. According to our study, all modelled tick species are likely to expand their ranges into the country's interior regions. None of the species will experience a reduction in suitable habitat to the extent of the observed range expansion, particularly along the eastern coastal and inland areas. These findings are consistent with global trends that link climate change to shifts in species distributions. However, the unique climatic and ecological conditions of South Africa contribute to regional variability in species responses. Overall, the range size changes highlight the need for ongoing monitoring and adaptive management strategies to mitigate the negative impacts of ticks on ecosystems, public health, and agriculture. The study provides baseline data for ongoing monitoring and adaptive management strategies to mitigate the negative impacts associated with ticks on ecosystems, public health, and agriculture in South Africa and similar environments. South Africa must implement a comprehensive approach to tick management due to the significant challenges posed by invasive species like *Rhipicephalus microplus*. This tick species and others pose a serious threat to livestock health, leading to substantial veterinary and economic impacts.

A One Health approach may be a solution with its interdisciplinary approach, which integrates the health of humans, animals, and the environment, is crucial in addressing these challenges. By adopting this approach, South Africa can effectively manage tick populations, reduce the spread of tick-borne diseases, and mitigate the economic losses associated with tick infestations. This holistic strategy will ensure the well-being of livestock, safeguard public health, and protect the country's agricultural economy.

Declaration of Generative AI and AI-assisted technologies in the writing process

While preparing this work, the author(s), R. Motloung, used artificial language editing software such as Grammarly to edit and improve the manuscript's readability. After using this tool/service, the authors ensured that the manuscript's context remained unchanged and took full responsibility for its final version.

Declaration of Competing Interest

The authors declare that they have no financial or personal relationships that may have inappropriately influenced them in writing this article.

Acknowledgements

We extend our gratitude to Dr. Tagwiyeri (University of Zimbabwe) for generously sharing the R code from their study and to Dr K. Faulkner (SANBI) for her invaluable assistance and expertise in Species Distribution Modelling. This article would not have been possible without the occurrence records made available through SANBI's Integrated Publishing Toolkit, which greatly contributed to the success of this research.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.vetpar.2025.110528.

References

Aguilar-Domínguez, M., Moo-Llanes, D.A., Sánchez-Montes, S., Becker, I., Feria-Arroyo, T.P., de León, A.P., Romero-Salas, D., 2021. Potential distribution of *Amblyomma mixtum* (Koch, 1844) in climate change scenarios in the Americas. Ticks Tick. borne Dis. 12 (6), 1–9. https://doi.org/10.1016/j.ttbdis.2021.101812.

Ali, A., Mulenga, A., Vaz Jr, I.S., 2020. Tick and tick-borne pathogens: molecular and immune targets for control strategies. Front. Physiol. 11, 1–4. https://doi.org/10.3389/fphys.2020.00744.

Allouche, O., Tsoar, A., Kadmon, R., 2006. Assessing the accuracy of species distribution models: Prevalence, kappa and the true skill statistic (TSS). J. Appl. Ecol. 43 (6), 1223–1232. https://doi.org/10.1111/j.1365-2664.2006.01214.x.

Anderson, J.F., Magnarelli, L.A., 2008. Biology of Ticks, 22, 195–215. https://doi.org/10.1016/j.idc.2007.12.006.

Apanaskevich, D.A., Horak, I.G., Camicas, J.L., 2007. Redescription of *Haemaphysalis (Rhipistoma) elliptica* (Koch, 1844), an old taxon of the Haemaphysalis [*Rhipistoma leachi* group from East and southern Africa, and of *Haemaphysalis (Rhipistoma) leachi* (Audouin, 1826) (Ixodida, Ixodidae). Onderstepoort J. Vet. Res. 74 (3), 181–208. https://doi.org/10.4102/ojvr.v74i3.122.

Araújo, M.B., Anderson, R.P., Barbosa, A.M., Beale, C.M., 2019. Standards for distribution models in biodiversity assessments. Sci. Adv. 5 (1), 1–10. https://doi.org/10.1126/sciadv.aat4858.

Baker, D.J., Maclean, I.M.D., Gaston, K.J., 2024. Effective strategies for correcting spatial sampling bias in species distribution models without independent test data. Divers. Distrib. 30 (3), 1–13. https://doi.org/10.1111/ddi.13802.

Barbet-Massin, M., Jiguet, F., Albert, C.H., Thuiller, W., 2012. Selecting pseudo-absences for species distribution models: How, where and how many? Methods Ecol. Evol. 3 (2), 327–338. https://doi.org/10.1111/j.2041-210X.2011.00172.x.

Booth, T.H., Nix, H.A., Busby, J.R., Hutchinson, M.F., 2014. BIOCLIM: the first species distribution modelling package, its early applications and relevance to most current MAXENT studies. Divers. Distrib. 20 (1), 1–9.

Bowman, A.W. and Azzalini, A. 2021. Package "sm" Title Smoothing Methods for Nonparametric Regression and Density Estimation.

Breiner, F.T., Nobis, M.P., Bergamini, A., Guisan, A., 2018. Optimizing ensembles of small models for predicting the distribution of species with few occurrences. Methods Ecol. Evol. 9 (4), 802–808. https://doi.org/10.1111/2041-210X.12957.

Brites-Neto, J., Duarte, K.M.R., Martins, T.F., 2015. Tick-borne infections in human and animal population worldwide. Vet. World 8 (3), 301–315. https://doi.org/10.14202/vetworld.2015.301-315.

Burtis, J.C., Yavitt, J.B., Fahey, T.J., Ostfeld, R.S., 2019. Ticks as Soil-Dwelling Arthropods: An Intersection between Disease and Soil Ecology. J. Med. Entomol. 56 (6), 1555–1564. https://doi.org/10.1093/jme/tjz116.

Chitanga, S., Gaff, H., Mukaratirwa, S., 2014. Tick-borne pathogens of potential zoonotic importance in the southern African region. J. South Afr. Vet. Assoc. 85 (1), 1–3. https://doi.org/10.4102/jsava.v85i1.1084.

Cruz, B.C., de Lima Mendes, A.F., Maciel, W.G., Dos Santos, I.B., Gomes, L.V.C., Felippelli, G., Teixeira, W.F.P., Ferreira, L.L., Soares, V.E., Lopes, W.D.Z., da Costa, A.J., 2020. Biological parameters for *Rhipicephalus microplus* in the field and laboratory and estimation of its annual number of generations in a tropical region. Parasitol. Res. 119 (8), 2421–2430. https://doi.org/10.1007/s00436-020-06758-5.

de la Fuente, J., Estrada-Pena, A., Venzal, J.M., Kocan, K.M., Sonenshine, D.E., 2008. Overview: Ticks as vectors of pathogens that cause disease in humans and animals. Front Biosci. 13, 6938. https://doi.org/10.2741/3200. PMID: 18508706.

de la Fuente, J., Estrada-Peña, A., Rafael, M., Almazán, C., Bermúdez, S., Abdelbaset, A. E., Kasaija, P.D., Kabi, F., Akande, F.A., Ajagbe, D.O., Bamgbose, T., 2023. Perception of ticks and tick-borne diseases worldwide. Pathogens 12 (10), 1258.

De Marco, P., Nóbrega, C.C., 2018. Evaluating collinearity effects on species distribution models: An approach based on virtual species simulation. PLoS ONE 13 (9), 1–25. https://doi.org/10.1371/journal.pone.0202403.

Dennis, S., Fisher, D., 2018. Climate Change and Infectious Diseases: The Next 50 Years. Ann. Acad. Med. Singap. 47 (10), 401–404. https://doi.org/10.47102/annals-acadmedsg.v47n10p401.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36 (1), 27–46. https://doi.org/10.1111/j.1600-0587.2012.07348.x.

Eisen, R.J., Eisen, L., Beard, C.B., 2016. County-Scale Distribution of *Ixodes scapularis* and *Ixodes pacificus* (Acari: Ixodidae) in the Continental United States. J. Med. Entomol. https://doi.org/10.1093/JME/TJV237.

Elith, J., H. Graham, C., P. Anderson, R., Dudík, M., Ferrier, S., Guisan, A., J. Hijmans, R., Huettmann, F., R. Leathwick, J., Lehmann, A., Li, J., 2006. Novel methods improve prediction of species' distributions from occurrence data. Ecography 29 (2), 129–151. https://doi.org/10.1111/j.2006.0906-7590.04596.x.

ESRI, 2020. ArcGIS Desktop: Release 10.8.1. Environmental Systems Research Institute: Redlands, CA, USA.

Estrada-Peña, A., De La Fuente, J., 2014. The ecology of ticks and epidemiology of tick-borne viral diseases. Antivir. Res. 108 (1), 104–128. https://doi.org/10.1016/j.antiviral.2014.05.016.

Fick, S.E., Hijmans, R.J., 2017. WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. Int. J. Climatol. 37 (12), 4302–4315. https://doi.org/10.1002/joc.5086.

Finch, J.M. and Meadows, M.E. 2019. South African biomes and their changes over time. The geography of South Africa: Contemporary changes and new directions, pp. 57–69.

Githaka, N., Kanduma, E., Bishop, R., 2021. Role of Climate and Other Factors in Determining the Dynamics of Tick and Tick-Transmitted Pathogen Populations and Distribution in Western, Central and Eastern Africa. Clim. Ticks Dis. (Dec.) 486–491. https://doi.org/10.1079/9781789249637.0070.

Gomez, C., Williams, A.J., Nicol, S.J., Mellin, C., Loeun, K.L., Bradshaw, C.J.A., 2015. Species distribution models of tropical deep-sea snappers. PLoS ONE 10 (6), 1–17. https://doi.org/10.1371/journal.pone.0127395.

Guisan, A., Thuiller, W., 2005. Predicting species distribution: offering more than simple habitat models. Ecol. Lett. 8 (9), 993–1009.

Hao, T., Elith, J., Guillera-Arroita, G., Lahoz-Monfort, J.J., 2019. A review of evidence about use and performance of species distribution modelling ensembles like BIOMOD. Divers. Distrib. 25 (5), 839–852. https://doi.org/10.1111/ddi.12892.

Hao, T., Elith, J., Lahoz-Monfort, J.J., Guillera-Arroita, G., 2020. Testing whether ensemble modelling is advantageous for maximising predictive performance of species distribution models. Ecography 43 (4), 549–558. https://doi.org/10.1111/ecog.04890.

Hardlife, M., Henry, N., Paradzayi, T., Mpakairi, K.S., Eliah, G., 2020. Predicting the invasion of a southern African savannah by the black wattle (*Acacia mearnsii*). J. For. Res. 31, 1995–2003. https://doi.org/10.1007/s11676-019-00975-0.

Horak P.I. 2016. University of Pretoria: South African Ticks (Acari: Ixodidae). v1.2. South African National Biodiversity Institute. Dataset/Occurrence. ⟨https://ipt.sanbi.org.za/resource?r=ticks⟩, accessed in August 2024.

Horak, I.G., Heyne, H., Williams, R., Gallivan, G.J., Spickett, A.M., Bezuidenhout, J.D., Estrada-Peña, A., 2018. The ixodid ticks (Acari: Ixodidae) of southern Africa. Springer.

Hrnková, J., Schneiderová, I., Golovchenko, M., Grubhoffer, L., Rudenko, N., Černý, J., 2021. Role of zoo-housed animals in the ecology of ticks and tick-borne pathogens—a review. Pathogens 10 (2), 1–26. ⟨https://doi.org/10.3390/pathogens10020210⟩.

Hurtado, O.J.B., Giraldo-Ríos, C., 2018. Economic and health impact of the ticks in production animals. Ticks Tick. borne Pathog. 1–19.

Janzén, T., Choudhury, F., Hammer, M., Petersson, M., Dinnétz, P., 2024. Ticks - public health risks in urban green spaces. BMC Public Health 24 (1), 1–17. https://doi.org/10.1186/s12889-024-18540-8.

Johnson, T.L., Bjork, J.K.H., Neitzel, D.F., Dorr, F.M., Schiffman, E.K., Eisen, R.J., 2016. Habitat suitability model for the distribution of *Ixodes scapularis* (acari: Ixodidae) in Minnesota. J. Med. Entomol. 53 (3), 598–606. https://doi.org/10.1093/jme/tjw008.

Johnston, P., Egbebiyi, T.S., Zvobgo, L., Omar, S.A., Cartwright, A. and Hewitson, B. 2024. Climate change impacts in South Africa.

Juache-Villagrana, A.E., et al., 2023. Status of Acaricide Resistance and Detecting the Knockdown Resistance Mutation T2134a in the Cattle Tick *Rhipicephalus Microplus* (Acari: Ixodidae) From Northeastern Mexico. J. Am. Mosq. Control Assoc. 32 (2), 122–128. https://doi.org/10.2987/23-7113.

Koldasbayeva, D., Tregubova, P., Gasanov, M., Zaytsev, A., Petrovskaia, A. and Burnaev, E. 2023. Challenges in data-based geospatial modeling for environmental research and practice. ⟨http://arxiv.org/abs/2311.11057⟩.

Komac, B., Esteban, P., Trapero, L., Caritg, R., 2016. Modelization of the current and future habitat suitability of Rhododendron ferrugineum using potential snow accumulation. PLoS ONE 11 (1), 1–18. https://doi.org/10.1371/journal.pone.0147324.

Ledger, K.J., Beati, L., Wisely, S.M., 2021. Survey of ticks and tick-borne rickettsial and protozoan pathogens in Eswatini. Pathogens 10 (8), 1–25. https://doi.org/10.3390/pathogens10081043.

Léger, E., Vourc'h, G., Vial, L., Chevillon, C., McCoy, K.D., 2013. Changing distributions of ticks: Causes and consequences. Exp. Appl. Acarol. 59 (1–2), 219–244. https://doi.org/10.1007/s10493-012-9615-0.

Makwarela, T.G., Djikeng, A., Masebe, T.M., Nkululeko, N., Nesengani, L.T., Mapholi, N. O., 2024. Vector abundance and associated abiotic factors that influence the distribution of ticks in six provinces of South Africa. Vet. World 17 (8), 1765–1777. https://doi.org/10.14202/vetworld.2024.1765-1777.

Makwarela, T.G., Nyangiwe, N., Masebe, T., Mbizeni, S., Nesengani, L.T., Djikeng, A., Mapholi, N.O., 2023. Tick Diversity and Distribution of Hard (Ixodidae) Cattle Ticks in South Africa. Microbiol. Res. 14 (1), 42–59. https://doi.org/10.3390/microbiolres14010004.

Maldonado, C., Molina, C.I., Zizka, A., Persson, C., Taylor, C.M., Albán, J., Chilquillo, E., Rønsted, N., Antonelli, A., 2015. Estimating species diversity and distribution in the era of B ig D ata: to what extent can we trust public databases? pp.973-984 Glob. Ecol. Biogeogr. 24 (8), 973–984. https://doi.org/10.1111/geb.12326.

Mapholi, N.O., Banga, C., Dzama, K., Matika, O., Riggio, V., Nyangiwe, N., Maiwashe, A., 2022. Prevalence and tick loads in Nguni cattle reared in different environmental conditions across four provinces of South Africa. Veterinary. World 15 (8), 1943–1953. https://doi.org/10.14202/vetworld.2022.1943-1953.

Marquaridt, D.W., 1970. Generalized inverses, ridge regression, biased linear estimation, and nonlinear estimation. Technometrics 12 (3), 591–612. https://doi.org/10.1080/00401706.1970.10488699.

Mohammadi, S., Ebrahimi, E., Moghadam, M.S., Bosso, L., Ebrahimi, E., Moghadam, M. S., 2019. Modelling current and future potential distributions of two desert jerboas under climate change in Iran. Ecol. Inform. 52, 7–13. https://doi.org/10.1016/j.ecoinf.2019.04.003.

Mtambo, J., Madder, M., Van Bortel, W., Berkvens, D., Backeljau, T., 2007. *Rhipicephalus appendiculatus* and *R. zambeziensis* (Acari: Ixodidae) from Zambia: A molecular reassessment of their species status and identification. Exp. Appl. Acarol. 41 (1–2), 115–128. https://doi.org/10.1007/s10493-006-9037-y.

Naimi, B., Araújo, M.B., 2016. Sdm: A reproducible and extensible R platform for species distribution modelling. Ecography 39 (4), 368–375. https://doi.org/10.1111/ecog.01881.

Ncube, B., Shekede, M.D., Gwitira, I., Dube, T., 2020. Spatial modelling the effects of climate change on the distribution of Lantana camara in Southern Zimbabwe. Appl. Geogr. 117 (September 2019), 102172. https://doi.org/10.1016/j.apgeog.2020.102172.

Ndaimani, H., Tagwireyi, P., Sebele, L., Madzikanda, H., 2016. An ecological paradox: The African wild dog (Lycaon pictus) is not attracted to water points when water is scarce in Hwange National Park, Zimbabwe. PLoS ONE 11 (1), 1–14. https://doi.org/10.1371/journal.pone.0146263.

Nejash, A., 2016. Review of important cattle tick and its control in Ethiopia. Open Access. Libr. J. 3 (03), 1.

Norval, R.A.I., Horak, I.G., 2004. Vectors: Ticks. In: Coetzer, J.W.A., Tustin, R.C. (Eds.), Infectious diseases of livestock, 2nd ed. Oxford University Press, Cape Town, South Africa, pp. 3–42.

Nuttall, P.A., 2022. Climate change impacts on ticks and tick-borne infections. Biologia 1–10.
Nyangiwe, N., et al., 2017. Range expansion of the economically important Asiatic blue tick, *Rhipicephalus microplus*, in South Africa. J. South Afr. Vet. Assoc. 88 (0), 1–7.
Nyangiwe, N., Harrison, A., Horak, I.G., 2013. Displacement of *Rhipicephalus decoloratus* by *Rhipicephalus microplus* (Acari: Ixodidae) in the Eastern Cape Province, South Africa. Exp. Appl. Acarol. 61 (3), 371–382. https://doi.org/10.1007/s10493-013-9705-7.
Nyangiwe, N., Yawa, M., Muchenje, V., 2018. Driving forces for changes in geographic range of cattle ticks (Acari: Ixodidae) in Africa: A review. South Afr. J. Anim. Sci. 48 (5), 829–840. https://doi.org/10.4314/sajas.v48i5.4.
Obaid, M.K., Islam, N., Alouffi, A., Khan, A.Z., da Silva Vaz, I., Tanaka, T., Ali, A., 2022. Acaricides Resistance in Ticks: Selection, Diagnosis, Mechanisms, and Mitigation (July). Front. Cell. Infect. Microbiol. 12, 1–20. https://doi.org/10.3389/fcimb.2022.941831.
Ogden, N.H., Ben Beard, C., Ginsberg, H.S., Tsao, J.I., 2021. Possible Effects of Climate Change on Ixodid Ticks and the Pathogens They Transmit: Predictions and Observations. J. Med. Entomol. 58 (4), 1536–1545. https://doi.org/10.1093/jme/tjaa220.
Ogden, N.H., Radojević, M., Wu, X., Duvvuri, V.R., Leighton, P.A., Wu, J., 2014. Estimated effects of projected climate change on the basic reproductive number of the lyme disease vector *Ixodes scapularis*. Environ. Health Perspect. 122 (6), 631–638. https://doi.org/10.1289/ehp.1307799.
Petrosyan, V., Dinets, V., Osipov, F., Dergunova, N., Khlyap, L., 2023. Range Dynamics of Striped Field Mouse (*Apodemus agrarius*) in Northern Eurasia under Global Climate Change Based on Ensemble Species Distribution Models. Biology 12 (7). https://doi.org/10.3390/biology12071034.
Pfäffle, M., Littwin, N., Muders, S.V., Petney, T.N., 2013. The ecology of tick-borne diseases. Int. J. Parasitol. 43 (12–13), 1059–1077. https://doi.org/10.1016/j.ijpara.2013.06.009.
Pham, M.-P., Hoang, T.T.T., Pham, V.D., Pham, T.T., Vu, D.D., 2025. Global range extension of bioclimatic zone of *Bruguiera hainesii* C.G. Rogers 1919 (Rhizophoraceae). One Ecosyst. 10, e142064. https://doi.org/10.3897/oneeco.10.e142064.
Phillips, S.J., Dudík, M., Elith, J., Graham, C.H., Lehmann, A., Leathwick, J., Ferrier, S., 2009. Sample selection bias and presence-only distribution models: implications for background and pseudo-absence data. Ecol. Appl. 19 (1), 181–197. https://doi.org/10.1890/07-2153.1.
Pillay, A., Manyangadze, T., Mukaratirwa, S., 2022. Ticks and Tick-borne Diseases Prevalence of *Rickettsia africae* in tick vectors collected from mammalian hosts in sub-Saharan Africa: A systematic review and meta-analysis. Ticks Tick. borne Dis. 13 (4), 101960. https://doi.org/10.1016/j.ttbdis.2022.101960.
Polo, G., Gamarra, J., Robayo-Sánchez, L.N., Cortés-Vecino, J.A., Ramírez-Hernández, A., 2024. Impact of climate change on the geographical distribution of ticks of public health significance in Colombia: *Amblyomma ovale* (Ixodida: Ixodidae), the *Amblyomma maculatum* (Ixodida: Ixodidae) complex and the *Amblyomma cajennense* (Ixodida: Ixodidae) complex. J. Med. Entomol. (Xx) 1–12. https://doi.org/10.1093/jme/tjae100.
R Core Team. 2025. R: A Language and Environment for Statistical Computing: Vienna, Austria, 2025.
Ranc, N., Santini, L., Rondinini, C., Boitani, L., Poitevin, F., Angerbjörn, A., Maiorano, L., 2017. Performance trade-offs in target-group bias correction for species distribution models. Ecography 40 (9), 1076–1087. https://doi.org/10.1111/ecog.02414.
Ribeiro, R., Eze, J.I., Gilbert, L., Wint, G.W., Gunn, G., Macrae, A., Medlock, J.M., Auty, H., 2019. Using imperfect data in predictive mapping of vectors: a regional example of *Ixodes ricinus* distribution. Parasites Vectors 12 (1), 1–14. https://doi.org/10.1186/s13071-019-3784-1.
Robertson, T., Döring, M., Guralnick, R., Bloom, D., Wieczorek, J., Braak, K., Otegui, J., Russell, L., Desmet, P., 2014. The GBIF integrated publishing toolkit: facilitating the efficient publishing of biodiversity data on the internet. PloS One 9 (8), 1–7. https://doi.org/10.1371/journal.pone.0102623.
Robertson, M.P., Visser, V., Hui, C., 2016. Biogeo: an R package for assessing and improving data quality of occurrence record datasets. Ecography 39 (4), 394–401. https://doi.org/10.1111/ecog.02118.
Rochlin, I., Toledo, A., 2020. Emerging tick-borne pathogens of public health importance: a mini-review. J. Med. Microbiol. 69 (6), 781.
Rodriguez-Vivas, R.I., Jonsson, N.N., Bhushan, C., 2018. Strategies for the control of *Rhipicephalus microplus* ticks in a world of conventional acaricide and macrocyclic lactone resistance. Parasitol. Res. 117 (1), 3–29. https://doi.org/10.1007/s00436-017-5677-6.
Roffe, S.J., Fitchett, J.M., Curtis, C.J., 2021. Quantifying rainfall seasonality across South Africa on the basis of the relationship between rainfall and temperature. Clim. Dyn. 56 (7–8), 2431–2450. https://doi.org/10.1007/s00382-020-05597-5.
Rousseau, R., McGrath, G., McMahon, B.J., Vanwambeke, S.O., 2017. Multi-criteria Decision Analysis to Model *Ixodes ricinus* Habitat Suitability. EcoHealth 14 (3), 591–602. https://doi.org/10.1007/s10393-017-1247-8.
Samish, M., Rehacek, J., 1999. Pathogens and predators of ticks and their potential in biological control (December). Annu. Rev. Entomol. 44, 159–182. https://doi.org/10.1146/annurev.ento.44.1.159.
Sili, G., Byaruhanga, C., Horak, I., Steyn, H., Chaisi, M., Oosthuizen, M.C., Neves, L., 2021. Ticks and tick-borne pathogens infecting livestock and dogs in Tchicala-Tcholoanga, Huambo Province, Angola. Parasitol. Res. 120 (3), 1097–1102. https://doi.org/10.1007/s00436-020-07009-3.
Sillero, N., et al., 2021. Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. Ecol. Model. 456, 109671.
Soley-Guardia, M., Alvarado-Serrano, D.F., Anderson, R.P., 2024. Top ten hazards to avoid when modeling species distributions: a didactic guide of assumptions, problems, and recommendations. Ecography 2024 (4), 1–21. https://doi.org/10.1111/ecog.06852.
Song, Y., Xu, X., Zhang, S., Chi, X., 2024. Uncertainty Assessment of Species Distribution Prediction Using Multiple Global Climate Models on the Tibetan Plateau: A Case Study of *Gentiana yunnanensis* and *Gentiana siphonantha*. Land 13 (9), 1376. https://doi.org/10.3390/land13091376.
Spickett, A.M., Heyne, I.H., Williams, R., 2011. Survey of the livestock ticks of the North West province, South Africa. Onderstepoort J. Vet. Res. 78 (1), 1–12. https://doi.org/10.4102/ojvr.v78i1.305.
Statista (2023) South Africa: Total Population 2018 to 2028. Statista. Available at: ⟨https://www.statista.com/statistics/1117642/south-africa-total-population/⟩ (Accessed: 9 December 2024).
Sungirai, M., Moyo, D.Z., P, D.C., Madder, M., Vanwambeke, S.O., M, D.C.E., 2018. Modelling the distribution of Rhipicephalus microplus and R. decoloratus in Zimbabwe. Vet. Parasitol. Reg. Stud. Rep. 14 (April), 41–49. https://doi.org/10.1016/j.vprsr.2018.08.006.
Tagwireyi, P., Ndebele, M., Chikurunhe, W., 2022. Climate change diminishes the potential habitat of the bont tick (*Amblyomma hebraeum*): evidence from Mashonaland Central Province (Available at). Zimb. Parasites Vectors 15 (1), 1–9. https://doi.org/10.1186/s13071-022-05346-z.
Tawana, M., Onyiche, T.E., Ramatla, T., Mtshali, S., Thekisoe, O., 2022. Epidemiology of ticks and tick-borne pathogens in domestic ruminants across Southern African Development Community (SADC) Region from 1980 until 2021: A systematic review and meta-analysis. Pathogens 11 (8), 1–21. https://doi.org/10.3390/pathogens11080929.
Thuiller, W., Lafourcade, B., Engler, R., Araújo, M.B., 2009. BIOMOD–a platform for ensemble forecasting of species distributions. Ecography 32 (3), 369–373. https://doi.org/10.1111/j.1600-0587.2008.05742.x.
Tønnesen, M.H., Penzhorn, B.L., Bryson, N.R., Stoltsz, W.H., Masibigiri, T., 2004. Displacement of *Boophilus decoloratus* by *Boophilus microplus* in the Soutpansberg region, Limpopo Province, South Africa. Exp. Appl. Acarol. 32 (3), 199–208. https://doi.org/10.1023/B:APPA.0000021789.44411.b5.
von Maltitz, G., Midgley, G.F., Veitch, J., Brummer, C., Rotter, R.P., Viehberg, F.A., Veste, M., 2024. Sustain. South. Afr. Ecosyst. Glob. Change. https://doi.org/10.17159/caj/2024/34/1.18950.
Wisz, M.S., Hijmans, R.J., Li, J., Peterson, A.T., Graham, C.H., Guisan, A., NCEAS Predicting Species Distributions Working Group, 2008. Effects of sample size on the performance of species distribution models. Divers. Distrib. 14 (5), 763–773. https://doi.org/10.1111/j.1472-4642.2008.00482.x.
Worton, B.J., 1989. Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70 (1), 164–168. https://doi.org/10.2307/1938423.
Wright, C.Y., Kapwata, T., du Preez, D.J., Wernecke, B., Garland, R.M., Nkosi, V., Landman, W.A., Dyson, L., Norval, M., 2021. Major climate change-induced risks to human health in South Africa. Environ. Res. 196, 1–11.
Xu, Q., Wang, X., Yi, J., Wang, Y., 2024. Bias correction in species distribution models based on geographic and environmental characteristics. Ecol. Inform. 81, 1–14. https://doi.org/10.1016/j.ecoinf.2024.102604.
Zannou, O.M., Ouedraogo, A.S., Biguezoton, A.S., Abatih, E., Coral-Almeida, M., Farougou, S., Yao, K.P., Lempereur, L., Saegerman, C., 2021. Models for studying the distribution of ticks and tick-borne diseases in animals: a systematic review and a meta-analysis with a focus on Africa. Pathogens 10 (7), 1–31. https://doi.org/10.3390/pathogens10070893.