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Limited evidence for the impact of climate change on the recent range expansion of the malaria vector *Anopheles stephensi* in the Horn of AfricaDiana Erazo^{1,2,3,*} , Rosa Pietroiusti⁴ , Guillaume Ghisbain⁵ , Felipe J Colón-González⁶ , Samuel Pironon^{7,8} , Wim Van Bortel^{9,10} , Matthias Mengel¹¹ , Katja Frieler¹¹ , Wim Thiery⁴ and Simon Dellicour^{1,12,13,*} ¹ Spatial Epidemiology Lab (SpELL), Université Libre de Bruxelles, Brussels, Belgium² Division of Invertebrates, Department of Biology, Royal Museum for Central Africa, Tervuren, Belgium³ Evolutionary Ecology group, University of Antwerp, Antwerpen, Belgium⁴ Department of Water and Climate, Vrije Universiteit Brussel, Brussels, Belgium⁵ Laboratory of Zoology, Research Institute for Biosciences, University of Mons, Mons, Belgium⁶ Data for Science and Health, Wellcome Trust, London, United Kingdom⁷ School of Biological and Behavioural Sciences, Queen Mary University of London, London, United Kingdom⁸ Royal Botanic Gardens, Kew, Richmond TW9 3AE, United Kingdom⁹ Unit Entomology, Department of Biomedical Sciences, Institute of Tropical Medicine, Antwerp, Belgium¹⁰ Outbreak Research team, Department of Biomedical Sciences, Institute of Tropical Medicine, Antwerp, Belgium¹¹ Department Transformation Pathways, Potsdam Institute for Climate Impact Research (PIK), Potsdam, Germany¹² Department of Microbiology, Immunology and Transplantation, Rega Institute, Laboratory for Clinical and Epidemiological Virology, KU Leuven, Leuven, Belgium¹³ Interuniversity Institute of Bioinformatics in Brussels, Université Libre de Bruxelles, Vrije Universiteit Brussel, Brussels, Belgium

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E-mail: diana.erazo.quintero@ulb.be and simon.dellicour@ulb.be**Keywords:** malaria, *Anopheles stephensi*, Horn of Africa, range expansion, climate change, climate attributionSupplementary material for this article is available [online](#)**Abstract**

During the last decade, the Horn of Africa has experienced an unexpected surge in urban malaria cases, with annual outbreaks intensifying each year in some countries. The trend began in 2012 in Djibouti City, followed by outbreaks in 2016 in Ethiopia and Sudan. Research involving mosquito surveillance revealed the presence of *Anopheles stephensi*, a species originating in Asia and well-adapted to urban environments. The World Health Organisation subsequently issued a vector alert, urging increased mosquito surveillance in the affected areas. Here, we analysed a database of geo-referenced records of *An. stephensi* collected across its native range to explore whether the recent range expansion of this vector in the Horn of Africa could be attributed to climate change. To this end, we implemented a boosted regression tree approach to train ecological niche models and investigated changes in the distribution of areas ecologically suitable for *An. stephensi*. We compare estimates derived from climate data spanning 1901–2019 with those from a counterfactual baseline in which climate trends were removed for the same period. Overall, our results indicated that factors other than climate change likely contributed to the expansion range of *An. stephensi* on the African continent. The association between lower pasture density and higher ecological suitability points to a potential link with expanding urban environments, where this vector is known to thrive. These findings highlight the need for further investigation into the ecological and anthropogenic drivers shaping the spread of *An. stephensi* to inform targeted and effective malaria control strategies.

1. Introduction

Malaria is a major public health concern in Africa, with the continent bearing over 90% of the global malaria burden (World Health Organization 2025). Traditionally, malaria transmission in Africa has been associated with rural settings, where dominant mosquito vector species, such as *Anopheles gambiae* sensu stricto, *An. coluzzii*, and *An. funestus* thrive in natural and human-made aquatic sites (Charlwood et al 1995, Robert et al 2003, Coetzee 2004, Sinka et al 2010). In contrast, urban areas in Africa have historically been considered less suitable for malaria transmission due to a combination of environmental conditions, vector ecology, and socioeconomic factors that limit mosquito production and human exposure (Hay et al 2005). However, in recent years, the epidemiology of malaria in Africa has begun to shift. The emergence of *Anopheles stephensi*, a malaria mosquito vector originating in Asia and largely adapted to urban environments, represents a significant challenge for malaria control and elimination efforts across the African continent (Sinka et al 2020, Taylor et al 2024).

During the last decade, the Horn of Africa has witnessed an increasing number of malaria outbreaks in urban centers, beginning in 2012 in Djibouti City (Faulde et al 2014), followed by outbreaks in 2016 in Ethiopia and Sudan (Carter et al 2018, Balkew et al 2020, Ahmed et al 2021). Entomological surveillance in Africa revealed the presence of *An. stephensi*, a species with a broad geographic range spanning South and Southeast Asia, the Arabian Peninsula and, more recently, Africa (Sinka et al 2020). Unlike endemic African *Anopheles* vectors, *An. stephensi* is well-suited to urban environments due to its ability to exploit artificial water storage systems such as household containers, cisterns, and rooftop tanks for larval development (Sinka et al 2010). Recognising the potential impact of *An. stephensi* on malaria transmission in Africa, the World Health Organisation issued a first vector alert in 2019, urging increased surveillance and vector control measures to curb its spread (World Health Organization 2023).

The mechanisms underlying the invasion of *An. stephensi* into Africa remain a topic of debate. Multiple hypotheses have been proposed to explain its introduction and expansion across the African continent. The most plausible explanation is human-mediated transport, a pathway consistent with the invasion patterns of other mosquito species such as *Aedes aegypti* and *Aedes albopictus* (Faulde et al 2014, Ahn et al 2023). *An. stephensi* was first detected in Djibouti, a major port city, suggesting that maritime trade routes likely facilitated its initial arrival (Faulde et al 2014). Windborne dispersal across the Red Sea has also been proposed as a possible mechanism, contributing to its range expansion from the Arabian Peninsula into the Horn of Africa, a

mechanism also documented for other mosquito species (Huestis et al 2019, Lehmann et al 2023). On the other hand, climate change has been suggested as a potential factor influencing the species' establishment and range expansion (Pecor et al 2023, Liu et al 2024). Rising temperatures, altered precipitation patterns, and changing humidity levels may impact vector distributions by modifying habitats and extending transmission seasons (Villena et al 2022, Ryan et al 2023). However, the extent to which climate change has contributed in the past and the present to the range expansion of *An. stephensi* in Africa remains unclear. The current study aims to assess whether Africa has long been climatically suitable for *An. stephensi*, thereby informing whether the recent expansion reflects increased introduction pressure rather than newly emerging ecological suitability.

The Working Group 2 of the Intergovernmental Panel on Climate Change (IPCC) has outlined a standardised framework for attributing observed changes in human, natural, and managed systems to climate change (O'Neill et al 2022). The impact attribution framework enables the distinction of climate-driven changes from other factors, such as anthropogenic activities. It requires available observed changes (here the range expansion of *An. stephensi*) and a model that can reproduce these observed changes given climate change and other drivers of change as input. Once model trust is established, the model can be used to produce counterfactual impacts by modeling the system in the absence of climate change while other drivers still evolve under historical conditions. The differences in model output between the factual simulation with climate change and the counterfactual simulation without climate change can then be attributed to climate change.

This IPCC impact attribution framework has been successfully applied for a number of impact categories (e.g. Grant et al 2021, Gudmundsson et al 2021, Burton et al 2024, Dimitrova et al 2024, Erazo et al 2024), often building on observationally based reanalysis climate datasets and respective counterfactual versions without climate change provided by the Inter-Sectoral Impact Model Intercomparison Project (ISIMIP) project (Mengel et al 2021, Frieler et al 2024). Counterfactual climate data, generated by removing long-term warming trends from historical climate records, provided a 'no-climate change' scenario, enabling a direct comparison with observed conditions (Mengel et al 2021). In particular, it has been used to assess the spatial expansion of West Nile virus in Europe (Erazo et al 2024) where reanalysis climate datasets based on historical and counterfactual scenarios were used to assess whether increasing ecological suitability for West Nile virus could be attributed to climate change. Such methodology offers valuable insights into the role of climate change in shaping

disease transmission patterns, yet they remain unexplored in the case of *An. stephensi* in Africa.

Here, we implement an ecological niche modelling framework based on a machine learning approach boosted regression trees (BRTs) combined with a comprehensive database of geo-referenced *An. stephensi* records spanning its extensive range across Asia, the Arabian Peninsula, and the Horn of Africa. By reconstructing the historical distribution of areas ecologically suitable for *An. stephensi* over the past century, we have assessed whether climate change has contributed to its recent range expansion into Africa. For this purpose, we leverage observational climate datasets alongside counterfactual climate datasets with climate change trends removed. This approach allows us to disentangle the influence of climate-driven changes from other factors, such as land-use changes, which could have facilitated the species' establishment in new regions. Given the increasing risk that *An. stephensi* poses to malaria control efforts, clarifying the role of climate change in its spread is essential for improving risk assessments, informing public health interventions, and guiding policy responses.

2. Results

Under factual and counterfactual climate conditions, as well as moving from 1901–1919 to 2000–2019, model simulations based on the GSWP3-W5E5 reanalysis dataset retrieved from ISIMIP display similar results of *An. stephensi* ecological suitability (figures 1 and S3). Ranging from 0 to 1, the ecological suitability can here be interpreted as a metric estimating to what extent the environmental condition in a given location could host the local occurrence of *An. stephensi*. Differences between factual and counterfactual scenarios for 2000–2019 showed an overall decrease in the ecological suitability of the species in Northeast India, Myanmar and Thailand, and the establishment of hotspots in southeast India, northwest China, Jordan and Syria (figure 1(C)). Overall, we did not find a clear difference in the distribution of ecologically suitable areas for *An. stephensi* across Africa, as obtained through the factual and counterfactual simulations. The same pattern was observed for the simulations using ecological niche models trained when considering three times more (figure S3) and six times more (figure S4) pseudo-absences than occurrence records, hereafter referred to as the 3X and 6X pseudo-absence sampling schemes. The lack of a clear difference between the factual and counterfactual simulations may be explained by the environmental covariates that most strongly influence the ecological niche models. Specifically, under the GSWP3-W5E5 reanalysis dataset and the 3X pseudo-absence sampling scheme, the two most

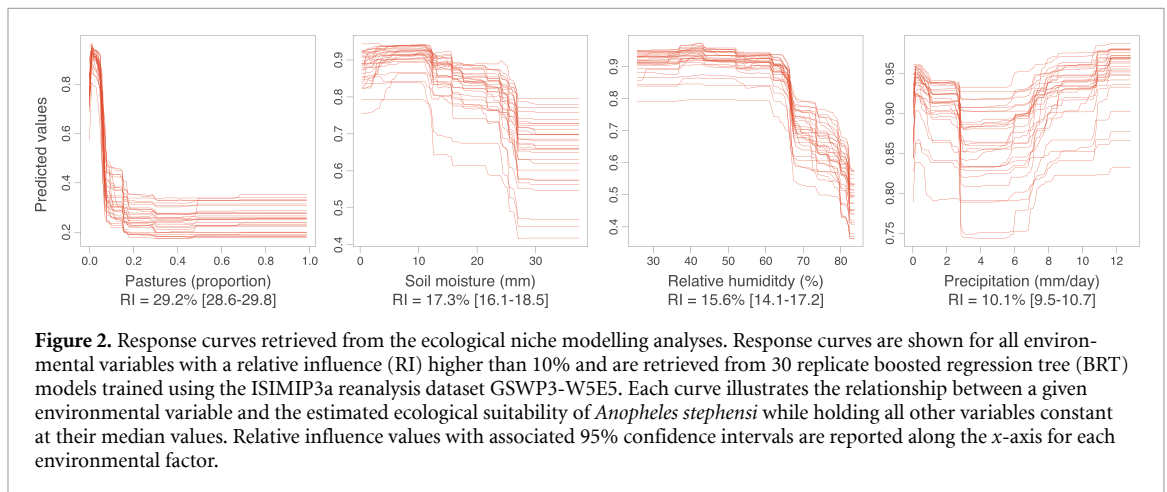
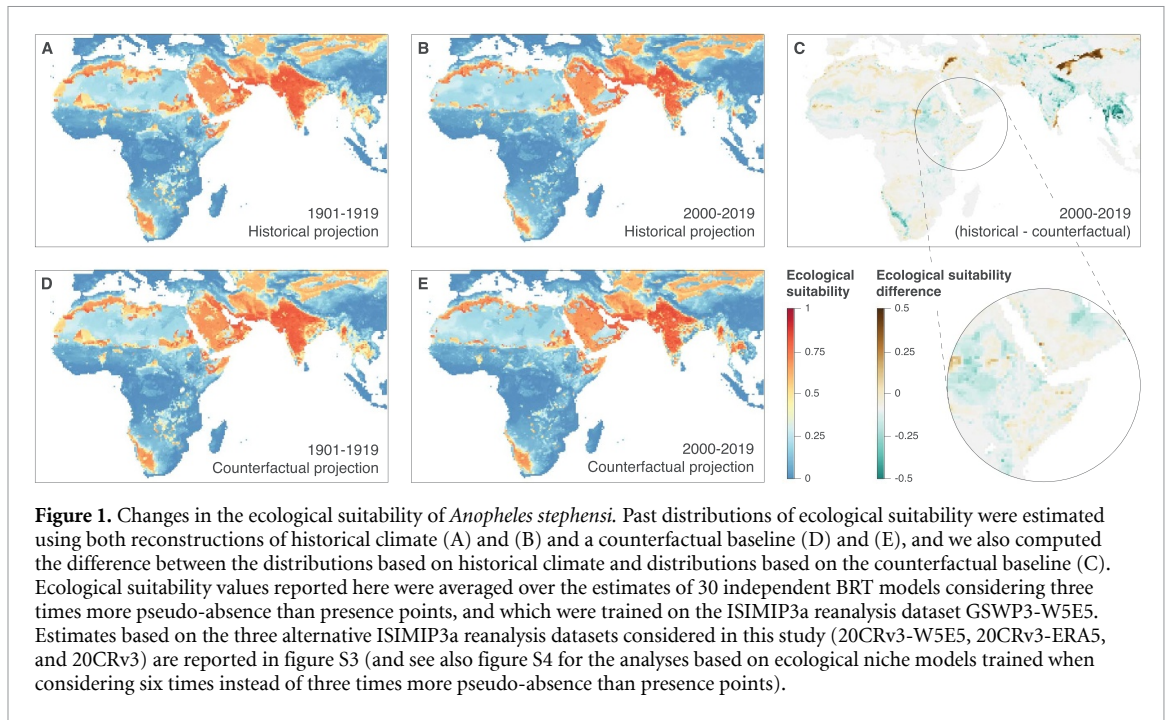
influential variables were pasture proportion (relative influence [RI] = 29.2% [28.6–29.8]) and soil moisture (RI = 17.3% [16.1–18.5]).

However, with a RI respectively equal to 15.6% [14.1–17.2] and 10.1% [9.5–10.7], relative humidity and precipitation were also identified as influential covariates in our ecological niche models (figure 2). These patterns are maintained when considering 6X instead of 3X pseudo-absences, as well as when considering all the reanalysis datasets (figures S5–S8) but Twentieth Century Reanalysis version 3 (20CRv3), in which the RI of temperature is comparatively high (RI = 16.7% [16–17.5]) when considering 3X pseudo-absences (figure S8).

To assess the relationship between the environmental factors and the estimated ecological suitability values, we plotted response curves showing how the estimated ecological suitability varies with the values of each environmental factor (figures 2 and S5–S8). For instance, with the 3X pseudo-absences sampling scheme, the precipitation displays a clear positive association with the ecological suitability estimated for *An. stephensi*, with precipitation above 6 mm d associated with a notable increase in ecological suitability (figures 2 and S5). Conversely, environmental variables such as proportion of managed pastures, soil moisture and relative humidity all present a negative association with the species' ecological suitability: the estimated ecological suitability displays a notable decrease for the proportion of pasture >10%, soil moisture >12 mm, and relative humidity >65% (figure 2). These patterns were also observed for the other reanalysis datasets (figures S6 and S7), except for 20CRv3. The ecological suitability values estimated with the ecological niche models trained with the 20CRv3 reanalysis dataset display a notable decrease for pasture proportion <5% and relative humidity >40%, and an increase for temperature >20 °C and precipitation >4 mm d (figure S8).

3. Discussion

We used factual and counterfactual climate data to assess whether the recent establishment of *An. stephensi* in the Horn of Africa can be attributed to climate change. Our ecological niche models, based on four reanalysis datasets, show no clear differences in ecologically suitable areas for *An. stephensi* between observed and counterfactual simulations. Consequently, our results indicate that there is no clear evidence that climate change was a main driver of the recent range expansion of *An. stephensi* into the Horn of Africa. At the regional scale, potential climate-driven changes in suitability at higher elevations are explicitly assessed through the comparison of factual and counterfactual climate simulations, and we did not observe a clear and systematic increase in



ecological suitability under factual conditions relative to the counterfactual baseline in Africa. Based on our analyses, the ecological niche suitability of *An. stephensi* across Africa has remained relatively stable over time, indicating that large areas of the continent have long been suitable for the species, and that its recent emergence likely reflects increased introduction pressure rather than new niche opportunities. In its native range, we observed a heterogeneous pattern: climatic suitability decreased in parts of northeast India, Myanmar, and Thailand, while localised ecological suitability hotspots emerged in Southeast India, Northwest China, Jordan, and Syria. However, the overall spatial extent of suitable areas in South and Southeast Asia did not expand markedly. Although ecological niche models remain valuable for forecasting potential future changes in the distribution of *An. stephensi* in response to climate and land-use changes, their utility depends on the mechanisms

being modelled. Mechanistic models have also proven to be useful for predicting future climate change scenarios (Villena *et al* 2022, Ryan *et al* 2023). Our findings highlight the importance of incorporating anthropogenic drivers, especially rapid urban expansion, into predictive frameworks.

Urban land conversion indeed plays a crucial role in shaping malaria dynamics, especially with the emergence of *An. stephensi* as a key malaria vector. Unlike endemic African malaria vectors, such as *An. arabiensis* and *An. gambiae* that primarily inhabit rural areas where larval habitats are omnipresent (Charlwood *et al* 1995, Robert *et al* 2003, Coetzee 2004), urban environments are largely suitable for *An. stephensi* (Sinka *et al* 2010). Its ability to thrive in water sources, such as household water storage tanks, cisterns, and other artificial containers, gives it a distinct advantage in densely populated areas (Sinka *et al* 2010). As urbanisation accelerates across

Africa, the spread of *An. stephensi* raises significant concerns about the potential expansion of malaria transmission beyond its traditional rural strongholds. Our findings indicate that lower pasture proportion is associated with increased ecological suitability for *An. stephensi*. At the 0.5° grid-cell scale, pasture proportion is a coarse indicator of land-use transitions and does not directly measure urbanisation, population density, or human mobility; the observed association may therefore reflect broader landscape change processes that can co-occur with urban expansion. However, we note that land-use change processes such as deforestation, pasture expansion, and urbanisation often co-occur and interact in complex ways. The observed negative correlation between pasture cover and suitability may therefore be consistent with a landscape shift where *An. stephensi* finds more favourable conditions in peri-urban and urban areas, rather than a simple causal pathway. Further work disentangling these overlapping land-use trends is needed to better understand their respective roles in shaping the distribution of this emerging vector.

Recent studies have shown that temperature, rather than precipitation, may be a reliable indicator of peak *An. stephensi* activity throughout the year (Miazgowiec *et al* 2020, Whittaker *et al* 2023). In our analyses, temperature is associated, but with a RI of less than 10% in the different ecological niche models trained to predict the areas ecologically suitable for the local occurrence of *An. stephensi*. Instead, soil moisture, relative humidity, and precipitation are associated with relatively higher RIs, regardless of the reanalysis dataset used to train the ecological niche models. In fact, literature indicates that relative humidity is a critical factor in thermal performance of mosquitoes and therefore, the spread of urban malaria (Santos-Vega *et al* 2022, Brown *et al* 2023, Huxley *et al* 2025). Although precipitation is positively associated with *An. stephensi* ecological suitability, both soil moisture and relative humidity show negative associations beyond certain thresholds. Notably, ecological suitability is highest at relative humidity levels between 30% and 68%, suggesting that *An. stephensi* may be better adapted to moderately dry conditions. This pattern is consistent with the species' success in urban environments, where larval habitats are less dependent on ambient moisture and primarily consist of artificial water containers. Our findings align with the known sensitivity of *Anopheles* eggs to desiccation: they typically lose viability within 48 h and rarely survive more than a week without moisture (Chalam 1927). Linking this to the transportation hypothesis, the environmental limitation restricts the mass transport of eggs necessary for successful establishment, known as 'propagule pressure' (Hawley *et al* 1987, Swan *et al* 2022). This process is well-documented in invasive *Aedes* mosquito species, whose desiccation-tolerant eggs can survive

long periods without moisture while being transported (Hawley *et al* 1987, Swan *et al* 2022). In contrast, immature *An. stephensi* would require stagnant freshwater aboard ships to survive maritime transport to new ports, along with adult mosquitoes (Ahn *et al* 2023).

Our study presents a series of analytical limitations. First, to align with available ISIMIP data that currently only extends until 2019, our models were trained on *An. stephensi* occurrence data reported up to the same year, excluding more recent records such as the first detections in West Africa (Nigeria in 2020, The Nigerian Institute of Medical Research 2022; Ghana in 2022, Afrane *et al* 2023) and new discoveries in 2020 in Somaliland (Ali *et al* 2022), 2021 in Yemen (Allan *et al* 2023), 2022 in Kenya (Ochomo *et al* 2023), and 2022 in Eritrea (<https://apps.who.int/malaria/maps/threats/>) (Taylor *et al* 2024). Second, potentially key environmental factors, such as the tasselled cap wetness (TCW, surface wetness mean and irrigation), could not be incorporated into our ecological niche modelling analysis because of data unavailability (Sinka *et al* 2020). Our necessary reliance on ISIMIP environmental data for historical simulations prevented us from including finer-scale land-use classes, such as peri-urban areas which may have improved model performance and detection of subtle shifts in suitability. In addition, the spatial resolution of the reanalysis data (0.5°) limits the representation of fine-scale urban microclimates, including potential urban heat-island effects in high-elevation cities. Moreover, intrinsic factors (e.g. adaptation and dispersal capacity) or missing environmental variables could also contribute to changes in suitability not captured by our approach. Third, it is also worth noting that *An. stephensi* taxonomy is not fully resolved. Indeed, the type form, associated with urban environments and identified as the one introduced into Africa, is distinct from other forms (Gholizadeh *et al* 2015, Mishra *et al* 2021, Walter Reed Biosystematics Unit 2025). This taxonomic complexity could affect species-level modelling and warrants consideration in future studies. Finally, our models assess ecological suitability based on presence/absence data, giving equal weight to all pixels with at least one confirmed record, regardless of the number of records per area.

In conclusion, we used factual and counterfactual reanalysis-derived climate data from the ISIMIP3a database to investigate the potential role of climate change in the range expansion of *An. stephensi* in the Horn of Africa. Our results suggest that climate change has not been a major driver of this expansion. Instead, the consistent ecological suitability across Africa over time points to the continent having long been suitable to the species. This recent range expansion is therefore likely linked to increased anthropogenic introduction pressure, rather than

emerging environmental conditions. Once introduced, *An. stephensi* establishment may be facilitated by rapid urbanisation and natural habitat loss. Nonetheless, as climate change continues to reshape ecosystems, understanding how future ecological suitability of *An. stephensi* may evolve remains crucial for informing surveillance and intervention strategies as literature suggests (Villena *et al* 2022, Ryan *et al* 2023).

4. Methods

4.1. Acquisition of occurrence records

Data on *An. stephensi* occurrences from 1985 to 2019 were obtained from the work of Sinka *et al* (2020), corresponding to data exploited during the HumBug Project, a database of global occurrence data for the dominant vector species of human malaria in Asia. The HumBug Project database was supplemented with the most recent reports of *An. stephensi* occurrences, including those in the Horn of Africa and Sri Lanka (<https://apps.who.int/malaria/maps/threats/>). All occurrence records were here treated as presence points in our ecological niche modelling analyses.

4.2. Sampling of pseudo-absence points

As detailed below, our ecological niche modelling analyses were based on both presence and absence data. Given the non-availability of the latter, we considered pseudo-absence points sampled from a 'background' area. This background area consisted of all locations reporting the presence of at least one anopheline species (except for *An. stephensi*) across Asia and Africa, as well as records of *Aedes* and *Culex* species. This approach ensured that background points were drawn from areas likely to have undergone some level of entomological surveillance (Phillips *et al* 2009). By constraining pseudo-absence sampling to locations with documented mosquito records, this approach reduces the risk of treating unsampled areas as absences. To ensure that this background area, thus used for the selection of pseudo-absence points, accurately represented the environmental space sampled for *An. stephensi*, we applied a systematic buffer approach following the procedure described by Sinka *et al* (2020). Specifically, we first constructed a minimum convex polygon encompassing all known *An. stephensi* occurrences and calculated the distance from its centroid to the most distant occurrence. This distance defined a buffer radius applied around each occurrence point and the union of these buffers formed the background area. To further refine this background area and reduce potential bias, we applied a 1° buffer around occurrence points to prevent the final selection of pseudo-absence points too close to presence locations. We generated 60 random datasets of pseudo-absence points sampled within the defined background area.

Half of these selections included three times more pseudo-absence points than the total number of presence points (the '3X' sampling scheme; figure S1(A)), while the other half considered six times more pseudo-absence points than the total number of presence points (the '6X' sampling scheme; figure S1(A)). This approach ensured a robust representation of the environmental space when training our ecological niche models. Previous studies have shown that increasing the number of pseudo-absence points can improve model performance up to a certain threshold, beyond which the benefit tends to plateau (Barbet-Massin *et al* 2012). By exploring both moderate and higher sampling ratios, we sought to ensure a robust and comprehensive representation of the environmental space captured by our models.

4.3. Environmental covariates

Climate, land-use, and human population data at a 0.5° spatial resolution (30 arc-min) for the period 1901–2019 were retrieved from the ISIMIP phase 3a (ISIMIP3a, www.isimip.org/protocol/3/) database. Human population data correspond to historical reconstructions available up to 2021, based on HYDE v3.3 (<https://data.isimip.org/10.48364/ISIMIP:822480.3>). ISIMIP prescribes protocols and provides datasets for modelling the impacts of climate change in various systems sensitive to climate and human management. In ISIMIP3a, modellers run historical impact simulations with four reanalysis datasets as input, which are global physically-consistent reconstructions of the historical climate that assimilate all available observations. These reanalysis datasets are GSWP3-W5E5, 20CRv3-W5E5, 20CRv3-ERA5, and 20CRv3, available at daily 0.5° spatial resolution (Frieler *et al* 2024). GSWP3-W5E5 and 20CRv3-W5E5 cover 1901–2019, while 20CRv3-ERA5 and 20CRv3 cover 1901–2021 and 1901–2015, respectively. For the period from 1979, the first two products use W5E5, while the third uses the latest version of the European Reanalysis (ERA5). W5E5 is a combination of WFDE5 v2.0 over land and ERA5 over the ocean, where WFDE5 is itself a bias-adjusted version of ERA5 using the WATCH forcing data methodology (Cucchi *et al* 2020). For the period 1901–1979, the products use one ensemble member of the 20CRv3 or the GSWP3 dataset, which is a dynamically downscaled and bias-adjusted version of 20CRv2. In each case, the data for the period 1901–1979 is homogenised to match the more recent 1979–2019/2015/2021 data using the ISIMIP2BASD v2.5 quantile mapping method based on the 1979–2004 reference period (Lange 2019, Lange *et al* 2022).

Importantly, ISIMIP additionally provides a counterfactual version of each of these reanalysis datasets, with the climate change signal removed (Mengel *et al* 2021), to enable an attribution of observed impacts to climate change. Counterfactual

datasets consist of stationary climate time series obtained from corresponding factual reanalysis daily data after having removed the long-term trend while preserving the internal day-to-day variability (Mengel *et al* 2021). Climate variables used in this study consist of daily gridded near-surface air temperature, surface precipitation, and relative humidity. In addition, gross primary productivity (GPP) and soil moisture were obtained from the ISIMIP simulation outputs generated by the JULES-ES model (version VN6P3). GPP, used here as a proxy for biomass productivity, captures seasonal variations in terrestrial ecosystem activity and serves as an ecologically relevant indicator of vegetation dynamics. Land-use data were retrieved from the Land Use Harmonisation project (version 2; LUH2), providing annual land-use states at a 0.5° spatial resolution. We applied conservative remapping to match the resolution of other climate variables. Land-use variables originated from two sources: croplands and urban areas were obtained from the ISIMIP3a dataset, which is based on LUH2-GCB2018 and held constant at 2018 values for the years 2019–2021 (<https://doi.org/10.48364/ISIMIP.571261.3>). In contrast, primary and secondary forest/non-forest areas and rangelands/pastures were taken from the updated LUH2-GCB2019 version, which includes improved historical land-use reconstructions (Chini *et al* 2021). The original LUH2 data framework is described by (Hurt *et al* 2020). Land-use categories included in our study were: primary forest areas, primary non-forest areas, secondary forest areas, secondary non-forest areas, croplands, rangelands/pastures, and urban areas.

4.4. Ecological niche modelling

We implemented a BRT approach to train the different ecological niche models for *An. stephensi*. BRT is a machine learning methodology that can be used to generate a collection of sequentially fitted regression trees optimising the predictive probability of occurrence given local environmental conditions. Such a predictive probability can be interpreted as a measure of ecological suitability, a value that ranges between 0 and 1. The interest of a BRT approach lies in its ability to model complex non-linear relationships between the response and various predictor variables. Additionally, a BRT approach does not require prior data transformation or elimination of outliers (Elith *et al* 2008). Of note, it has been shown that the BRT methodology has a superior predictive performance compared to alternative modelling methods, such as MaxEnt, BIOCLIM, GDM, among others (Elith *et al* 2006). For implementing a Bernoulli BRT approach, both presence and absence data are required. In the context of this study, 0.5° pixels presenting one or more *An. stephensi* occurrences were considered as 'presence' pixels. 'Pseudo-absence' points were selected following the above mentioned procedure and therefore if at least one pseudo-absence point fell

into a pixel it was considered a pseudo-absence pixel.

We used the BRT algorithm implemented in the R package 'dismo' (Hijmans *et al* 2011). To account for spatial autocorrelation and avoid related model overfitting, we implemented a spatial instead of a standard cross-validation procedure, the latter being known to frequently overestimate the ability of the model to make reliable predictions when occurrence data are spatially auto-correlated (Randin *et al* 2006). Specifically, we applied the spatial cross-validation procedure based on the blocks generation, described by Valavi *et al* (2019) and implemented in the R package 'blockCV' (Valavi *et al* 2019). Specifically, presence and pseudo-absence points were divided into five spatial folds following this method of block generation. BRT models were trained using the following parameter values: a tree complexity of 5, a learning rate of 0.005, and a step size of 10.

The predictive performance of each BRT model was first assessed by estimating the area under the receiver operating characteristic curve, also referred to as 'area under the curve'. Additionally, we computed a prevalence-pseudo absence-calibrated Sørensen's index (SI_{ppc}) to further assess the predictive performance of our ecological niche models. We computed a SI_{ppc} for each of the sixty independent ecological niche models (table S1). As detailed in table S1, all averaged SI_{ppc} values are higher than 0.80 with a mean of 0.90 [0.90–0.91]. For each trained ecological niche model, we also report the evolution of the SI_{ppc} according to the ecological suitability threshold value ranging from 0 to 1 (figure S2).

We trained 60 independent replicate BRT models (30 per pseudo-absence sampling scheme) using present-day climate data from the four ISIMIP3a reanalysis datasets. As outlined above, BRT models trained on the GSWP3-W5E5 reanalysis dataset were here emphasised over other reanalysis datasets since it is considered a priority forcing dataset in ISIMIP3a (Frieler *et al* 2024). Bias adjustments in ISIMIP3b are based on GSWP3-W5E5, and Mengel and colleagues also highlighted its use in evaluating factual and counterfactual climate datasets within the ATTRICI (ATTRIButing Climate Impacts) framework for generating counterfactual climate data (Mengel *et al* 2021). We simulated and averaged ecological niche models on past (1901–1999) and present-day (2000–2019) environmental conditions considering both a counterfactual baseline and the observed historical climate. The comparison between observed historical and counterfactual simulations allowed us to discuss if and to what extent the expansion of *An. stephensi* ecologically suitable areas across the Horn of Africa could be attributed to climate change. All analyses were performed using R (R Statistical Software version 4.02, R Foundation for Statistical Computing, www.r-project.org/).

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Data Availability Statement

R script and related files needed to run the ecological niche modelling and are all available at: <https://github.com/dieraz/anopheles>.

Figures S1-S8, Table S1 available at <https://doi.org/10.1088/1748-9326/ae51a7/data1>.

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