

RESEARCH ARTICLE

Climate change could fuel urinary schistosomiasis transmission in Africa and Europe

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Abstract

The freshwater snail *Bulinus truncatus* is an important intermediate host for trematode parasites causing urogenital schistosomiasis, a tropical disease affecting over 150 million people. Despite its medical importance, uncertainty remains about its global distribution and the potential impacts of climate change on its future spread. Here, we investigate the distribution of *B. truncatus*, combining the outputs of correlative and mechanistic modelling methods to fully capitalize on both experimental and occurrence data of the species and to create a more reliable distribution forecast than ever constructed. We constructed ensemble correlative species distribution models using 273 occurrence points collected from different sources and a combination of climatic and (bio)physical environmental variables. Additionally, a mechanistic thermal suitability model was constructed, parameterized by recent life-history data obtained through extensive lab-based snail-temperature experiments and supplemented with an extensive literature review. Our findings reveal that the current suitable habitat for *B. truncatus* encompasses the Sahel region, the Middle East, and the Mediterranean segment of Africa, stretching from Southern Europe to Mozambique. Regions identified as suitable by both methods generally coincide with areas exhibiting high urogenital schistosomiasis prevalence. Model projections into the future suggest an overall net increase in suitable area of up to 17%. New suitable habitat is in Southern Europe, the Middle East, and large parts of Central Africa, while suitable habitat will be lost in the Sahel region. The change in snail habitat suitability may substantially increase the risk of urogenital schistosomiasis transmission in parts of Africa and Southern Europe while reducing it in the Sahel region.

KEYWORDS

Bulinus truncatus, climate change, One Health, schistosomiasis, snail-borne disease, species distribution modelling, thermal niche, trematode, vector-borne disease

Tiem van der Deure and Tim Maes should be considered joint first author.

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1 | INTRODUCTION

Schistosomiasis is a tropical disease affecting over 150 million people worldwide, 80% of whom live in Africa (Abate et al., 2018). Although it is mainly a chronic, non-lethal disease, it has a huge economic burden with between 1 and 2 million years of healthy life lost due to disability (Abate et al., 2018). The disease is caused by parasitic flatworms of the genus *Schistosoma*, which are transmitted through freshwater intermediate host snails, primarily of the genera *Bulinus* and *Biomphalaria*.

Bulinus truncatus is an important host snail for *Schistosoma haematobium* (causing urogenital schistosomiasis) and *Schistosoma bovis* (causing bovine schistosomiasis). It is a generalist species with wide tolerance limits to environmental factors, capable of aestivating in mud when environmental factors become unsuitable (Appleton, 1978). Furthermore, it is an efficient colonist as it can be transported by birds (Pfenninger et al., 2011), reproduces rapidly (Klumpp et al., 1985), and is capable of self-fertilizing (Brown, 1994; Viard et al., 1997). The combination of these traits results in the widest presumptive distribution of all schistosome intermediate host snails, spanning across Africa, Southern Europe, and the Middle East (Brown, 1994).

Climate change is expected to affect the distribution of disease vectors and the associated diseases (Kim et al., 2014). A recent outbreak of urogenital schistosomiasis and the subsequent establishment of the disease in Corsica, France (Berry et al., 2016; Mulero et al., 2019), and the emergence of the disease in new areas at higher altitudes in Uganda (Kabatereine et al., 2004; Rubaihayo et al., 2008) indicate that climate change may already have an impact on schistosomiasis epidemiology. However, it remains unclear exactly how geographical patterns of schistosomiasis transmission will be affected in the future (De Leo et al., 2020; Stensgaard et al., 2019).

The distribution of schistosome parasites is determined by the occurrence of a suitable intermediate snail host, with the parasites having broader tolerance limits than the snails (Mulero et al., 2019). Moreover, predicting shifts in vector distributions is a priority to prepare for disease control (Nørgaard et al., 2022). Therefore, a better understanding of the potentially changing distribution of *Bulinus* snails is important to elucidate the effects of climate change on schistosomiasis transmission. *B. truncatus* is implicated in transmission in relatively cold (such as Corsica, Mulero et al., 2019) as well as in hot and dry environments (such as Mali, Tandina et al., 2016). This species is therefore key to understanding the effects of climate change on schistosomiasis transmission.

In this study, we combine the outputs of correlative and mechanistic models to predict the current and future suitable range for *B. truncatus*. Previous studies have used correlative modelling to estimate the distribution of intermediate host snails of schistosome parasites (Manyangadze et al., 2021; Palasio et al., 2021; Stensgaard et al., 2013) while mechanistic models on schistosomiasis prevalence (McCreesh et al., 2015; Yang et al., 2006) or

the host snails (Remais et al., 2007) are notably scarce. The lack of reliable life history data on the snails is a major restriction on the use of mechanistic models (Maes et al., 2021). Furthermore, only a handful of studies combine the two approaches (Stensgaard et al., 2016). Since correlative and mechanistic models have different strengths and weaknesses—correlative models excel at predicting species distributions in current-day climates while mechanistic models are better transferable to the future—combining the output of both models could improve our understanding of the future distribution of *B. truncatus*.

This is the first time that the effects of climate change on the distribution of *B. truncatus* have been investigated on an inter-continental scale. Furthermore, we take advantage of newly acquired, experimental data from extensive snail-temperature experiments (Maes et al., 2024). Finally, we compare the outputs of the snail models to empirical urogenital schistosomiasis prevalence data to assess the implications of potential *B. truncatus* range shifts for schistosomiasis transmission.

2 | MATERIALS AND METHODS

2.1 | Mechanistic model

To mechanistically estimate the distribution limits of *B. truncatus*, we calculated the intrinsic growth rate of *B. truncatus* using five key life history traits.

2.1.1 | Life history traits

Thermal performance curves for five important life history traits (lifespan, maturation time, hatching time, egg laying rate and egg hatching success) were estimated using Bayesian modelling. Experimental data were extracted from the literature (Maes et al., 2021) in addition to raw data from a recently conducted experiment with over 2000 snails (Maes et al., 2024) (Table S1).

To estimate egg-laying rate and lifespan, a hierarchical Bayesian model was used, with parameters allowed to vary between snail populations (i.e., different experiments or different populations within the same experiment, see Supporting Information). The models were implemented in JAGS and run through the R package 'R2Jags' (Plummer, 2003). The death rate of eggs was assumed to follow a uniform distribution with bounds 0.1–0.3 per week, as experimental data to estimate this trait was lacking.

2.1.2 | Model description

We developed a thermal suitability metric based on the intrinsic rate of increase of a snail population given no restrictions imposed by competition. The intrinsic rate of increase, given by

recruitment minus deaths, is a fundamental characteristic of a population.

Here, we consider a three-stage life cycle model, where mature snails lay eggs, eggs hatch to become juveniles, and juveniles eventually develop into mature snails (Figure 1). The proportion of newly laid eggs that will survive to become mature snails is given by

$$S(T) = \text{EHR} \times e^{-(\text{MT}(T) \cdot \text{DR}(T) + \text{HT}(T) \cdot \text{EDR})}, \quad (1)$$

where EHR is the share of viable eggs, MT(T) the maturation time for newly hatched snails, DR(T) the snail death rate (the reciprocal of the lifespan), HT(T) the hatching time, EDR the egg death rate, and S(T) the proportion of eggs that survives to maturity. Juvenile and adult snails share the same death rate DR(T). Following Amarasekare and Savage (2012), the relative change in the population of mature snails, or the intrinsic rate of increase, is then given by

$$r_m(T) = \frac{1}{\alpha(T)} \times W(\text{ELR}(T) \times \alpha(T) \times S(T) \times e^{\text{DR}(T) \times \alpha(T)}) - \text{DR}(T), \quad (2)$$

where ELR(T) is the egg-laying rate, $\alpha(T)$ the time for a newly hatched egg to reach maturity [equal to MT(T) + HT(T)], and $r_m(T)$ the population growth rate at any temperature T. W is the principal branch of the Lambert W function.

To calculate the habitat suitability, the rate of increase was calculated for each month, averaged, and normalized by dividing by the maximum growth rate. In this model, a location is within the thermal niche of *B. truncatus* if and only if the recruitment rate is on average greater than the death rate and thus if the suitability is above zero (Gvoždík, 2018).

All mechanistic modelling was done in Julia v1.9 (Bezanson et al., 2017) and the maximum growth rate was found using the 'Optim.jl' package (Mogensen & Riseth, 2018).

2.1.3 | Climatic data

Freshwater snails occupy a variety of habitats, which could have very different temperature profiles. We tried several approaches

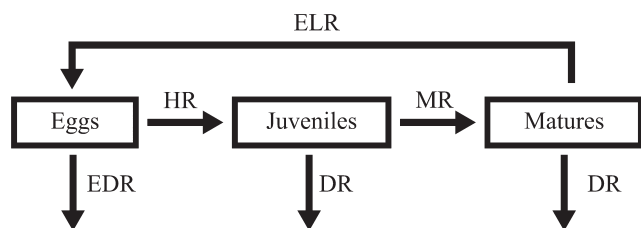


FIGURE 1 Schematic representation of the mechanistic model. In this model, snails are divided into three life stages: Eggs, juveniles, and matures. Matures produce eggs, which either hatch or die, and juveniles either mature or die. The model (Equation 2) gives the relative change in the number of mature snails under constant temperature and unlimited carrying capacity. DR, death rate; EDR, egg death rate; ELR, egg-laying rate; HR, hatching rate; MR, maturation rate.

to approximate temperature conditions experienced by snails and tested them on the occurrence data (see Supporting Information). We selected the best approach based on their performance.

2.2 | Correlative model

2.2.1 | Snail occurrence data

A systematic search on Web of Science using the keywords *B. truncatus* and the junior synonym *B. rohlfsi* was carried out on 03/02/2023 to identify all papers that reported on *B. truncatus*. Coordinates of presence locations were extracted either directly from the papers or through georeferencing using Google Earth and GeoNames.org. All occurrence data on *B. truncatus* from the Global Biodiversity Information Facility (GBIF) was downloaded on 28/09/2021 (10.15468/dl.xga6ck). Additional occurrence data were obtained through the museum collections of the AfricaMuseum, Belgium and the collections of the Natural History Museum of Denmark (the Mandahl-Barth mollusc collection from the former Danish Bilharziasis Laboratory). Observations with no geographical reference or a spatial resolution of less than 5 km were deleted, and all remaining observations were cleaned with the R package 'CoordinateCleaner' (Zizka et al., 2019) and visually verified in Qgis v3.16.10 (QGIS Development Team). Duplicated observations were deleted, and the density of sampling points was reduced to one observation per pixel using the R (R Core Team) package 'spThin' (Aiello-Lammens et al., 2015) (Figure S1). A target-group background selection approach was used to account for the effects of sampling bias (see Supporting Information).

2.2.2 | Environmental layers

The study area was restricted to currently endemic areas in Africa, the Middle East and Southern Europe. The northern limits were delineated by natural dispersal borders like the Pyrenees and the Alps (Figure S1). A range of bioclimatic variables that were considered relevant for the global distribution of freshwater snails (Appleton, 1978; Brown, 1994; Maes et al., 2021) was collected from different sources (see Table S2) and clipped to the same spatial extent of the study area. All layers were bilinearly resampled to a 2.5 arcminute resolution (approx. 5 km at the equator). The correlation between the different clipped variables was checked using the Pearson correlation coefficient and only one of each of the highly correlated variables ($r > .70$, Figure S4) was retained based on ecological knowledge of the species and a principal component analysis (PCA) to identify the most relevant variables that best explain the separation of the presence points from the background points (Figure S5).

2.2.3 | Correlative model building

Using the R package 'Biomod2' (Thuiller et al., 2023), we fit the occurrence data using four algorithms: Maxent, generalized linear models, generalized additive models, and gradient boosted models (Elith & Graham, 2009; Phillips et al., 2006). Each model was run 100 times and evaluated via the random test percentage using 70% of the presence dataset as training data and 30% of the data for evaluation. Variable importance was assessed through a randomization method (Thuiller et al., 2023) and the area under the curve (AUC), the true skill statistic (TSS), and Continuous Boyce Index (CBI, see Boyce et al., 2002; Márcia Barbosa et al., 2013) values were used to assess model performance. Model parameters were tuned for optimal performance (for more details on the model building procedure and algorithm settings see [Supporting Information](#)) and an ensemble model was constructed from the four algorithm outputs to produce more reliable forecasts (Araújo & New, 2007).

2.3 | Projections

For future climatic predictions, seven global circulation models (GCMs; ACCESS-CM2, CMCC-ESM2, GISS-E2, IPSL-CM6A-LR, MIROC6, MPI-ESM1-2-HR, and MRI-ESM2-0) were selected based on their performance to predict the African climate (Thuiller et al., 2019) and downloaded from the WorldClim database. We used two different Shared Socioeconomic Pathways used by the Coupled Model Intercomparison Project Phase 6 (CMIP6) (SSP126 and SSP370) for 2050 (average 2041–2060) and 2090 (average 2081–2100). The SSP126 is an optimistic scenario simulating a development that is compatible with the 2°C warming target set by the Paris Agreement in 2015 while the SSP370 represents the upper-middle part of the full range of scenarios and is more like the current warming rate (IPCC, 2022).

The models were projected to each combination of GCM, socioeconomic pathway, and time. For the correlative model, regions of strict extrapolation between the calibration dataset and transfer regions were identified through a multi-oriented parity analysis using the R package 'mop' (Cobos et al., 2023). For the mechanistic model, 5000 iterations were run for each climate change scenario and the current climate. The mean across projections and replications was used for future distribution for each period and SSP scenario.

To assess range shifts, a binary map was constructed for both the present and the future scenarios. The threshold to distinguish presence from absence was set to the tenth percentile training presence for the correlative model (Guillera-Arroita et al., 2015) and to 0 for the mechanistic model.

2.4 | Schistosomiasis data

To investigate the significance of possible future range shifts of *B. truncatus* with respect to schistosomiasis transmission, we compared

our model outputs to the reported prevalence of *S. haematobium* in Africa (Hürlimann et al., 2011; Schur et al., 2011). The posterior predictive median *S. haematobium* prevalence in 2000–2010 was estimated using 200 draws from the posterior of the model described in (Kokaliaris et al., 2021). The study did not estimate prevalence in Madagascar, Western Sahara, or any of the North African countries bordering the Mediterranean Sea. We used the estimated prevalence in the period 2000–2010 as reported by Kokaliaris et al. (2021) to identify high-risk areas, since mass drug administration after this period caused a sharp drop in schistosomiasis prevalence in many areas. Following the cut-off used by Kokaliaris et al. (2021), areas with a predicted prevalence of 10% or higher were considered sustained moderate to high transmission areas.

3 | RESULTS

3.1 | Mechanistic snail model

The posterior distributions for each investigated life history trait are shown in [Figure 2a–f](#) and [Table S3](#). A relationship with temperature was evident for all life history traits except for egg hatching success, where the data were fit to a constant. The population growth rate peaked at 26.6°C (95% CI 25.3–28.1°C) but was positive between 13.5°C (95% CI 11.3–14.7°C) and 31.3°C (95% CI 29.8–33.4°C), indicating *B. truncatus* can tolerate a large range of temperatures. Based on model performance, we assumed that water temperature is 3°C below air temperature ([Table S4](#)).

[Figure 3a](#) shows the current thermal suitability for *B. truncatus*. Almost all of Africa as well as major parts of the Middle East are within the thermal niche of *B. truncatus*, with optimal temperatures in the equatorial regions.

3.2 | Correlative models

The systematic literature search identified 314 papers mentioning *B. truncatus* or *B. rohlfsi* but only 69 contained the geographical coordinates of the collection sites or had sites that could be retrospectively georeferenced using Google Earth or [geonames.org](#). A total of 416 presence points could be extracted from the papers, which were complemented by 89 presence points from the AfricaMuseum and the Natural History Museum of Denmark snail collections, and 3078 occurrences from GBIF. After removing duplicated observations and applying spatial filtering, 273 occurrences could be used for species distribution modelling ([Figure S1](#)).

After removing highly correlated variables (correlation analysis, see [Figure S4](#); and PCA, see [Figure S5](#)), we built two candidate models using either bioclimatic (e.g., annual mean temperature, max temperature of the warmest month, etc.) variables only or bioclimatic as well as physical (e.g., elevation, slope, and soil temperature) variables. Based on the variable importance and performance of both models (see [Tables S5](#) and [S6](#)), the model with bioclimatic variables

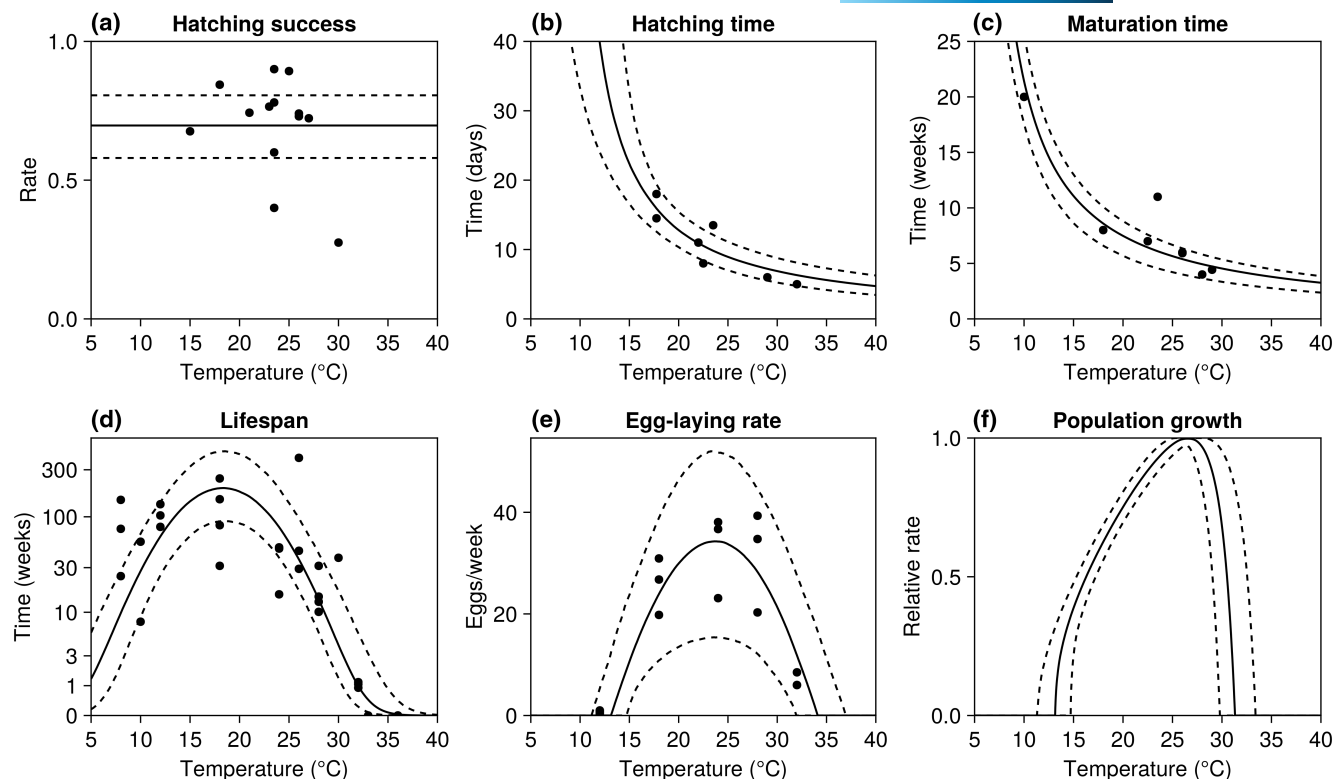


FIGURE 2 Posterior estimates of *Bulinus truncatus* life history traits. Mean estimates and 2.5% and 97.5% credible intervals of curve fits are shown, as well as input data (where applicable, mean values are shown). (a) Hatching success, (b) hatching time, (c) maturation time, (d) lifespan, (e) egg-laying rate, and (f) population growth rate as derived from other life history traits using Equation (2).

B. truncatus suitability and *S. haematobium* prevalence

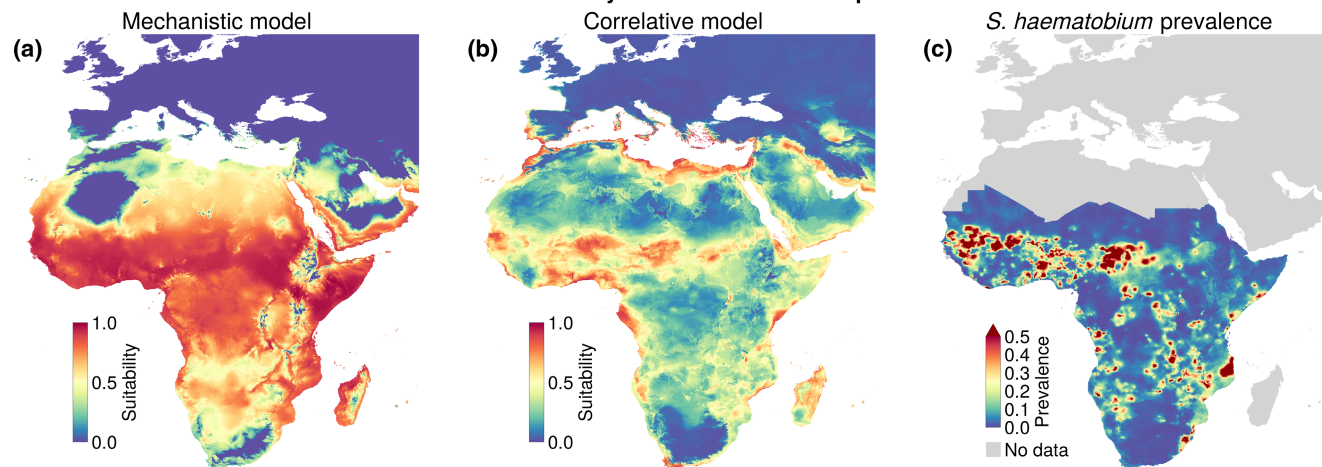


FIGURE 3 Predicted current suitability of *Bulinus truncatus* and *Schistosoma haematobium* prevalence. (a) Thermal suitability for *B. truncatus* predicted by the mechanistic model. (b) Habitat suitability for *B. truncatus* predicted by the correlative model (set 2; bioclimatic variables only). (c) Prevalence of *S. haematobium* infection, 2000–2010 (data from Kokaliaris et al., 2021).

only was selected. The ensemble model showed a high performance with an AUC of 0.878, a TSS of 0.590, and CBI of 0.826 with the mean temperature of the driest quarter, the annual mean temperature and the minimum temperature of the coldest month as the highest contributing variables. The response curves for all variables are given in Figure S6.

The model predicted high habitat suitability in the Sahel region, Northern Africa and in the Middle East, whereas tropical regions in Central Africa are deemed largely unsuitable (Figure 3b). The outcome of the model algorithm for each period and climate change scenario is given in Figure S7, while the variation in model predictions is depicted in Figure S8.

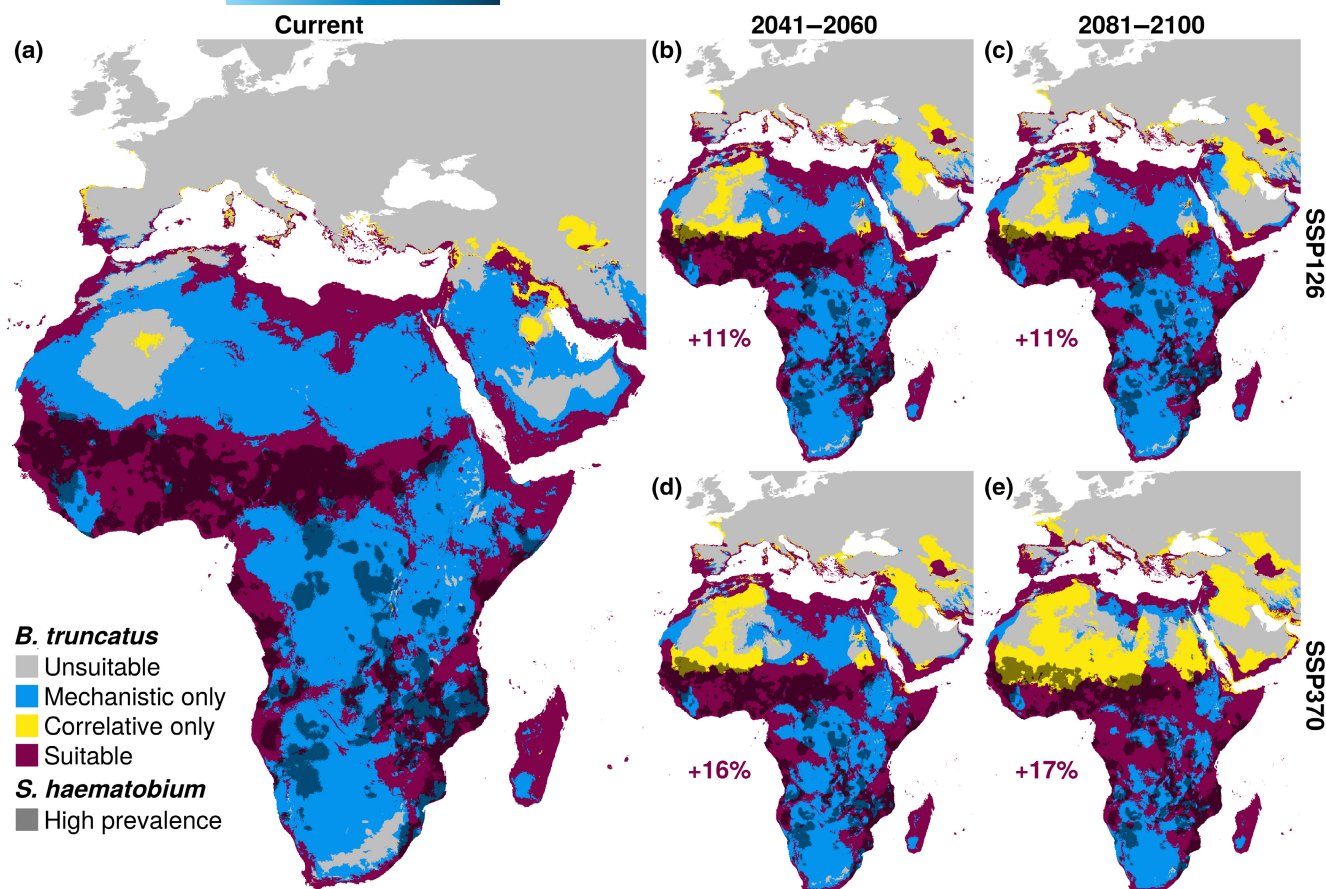


FIGURE 4 Super-imposed predictions of *Bulinus truncatus* habitat suitability by the mechanistic and correlative model under current and future climatic scenarios. Blue and yellow areas are predicted to be suitable by the mechanistic or the correlative, respectively, model only. Dark red areas are predicted to be suitable for *B. truncatus* by both models. Shaded areas are areas with currently a high urogenital schistosomiasis prevalence. (a) Current climate, (b) SSP126 low emission scenario predictions for 2041–2060, (c) SSP126 low emission scenario predictions for 2081–2100, (d) SSP370 high emission scenario predictions for 2041–2060, and (e) SSP370 high emission scenario predictions for 2081–2100. The overall area predicted to be suitable by both models increases by up to 17% in this scenario. However, some areas that are currently suitable might no longer be suitable by the end of the century.

3.3 | Superimposition of model outputs

Figure 4a shows the habitat suitability from the correlative model and thermal suitability from the mechanistic model, as well as previously reported areas with high *S. haematobium* prevalence (Kokaliaris et al., 2021). Areas with a high suitability according to both models are mainly situated in West and East Africa. These areas also contain many hotspots of *S. haematobium* and many previously reported instances of schistosomiasis transmission by *B. truncatus* (Njiokou et al., 2004; Pennance et al., 2020; Sène et al., 2002; Southgate et al., 2000; Webster & Southgate, 2003). Central Africa has close to optimal temperatures according to the thermal suitability model but is largely unsuitable according to the correlative model.

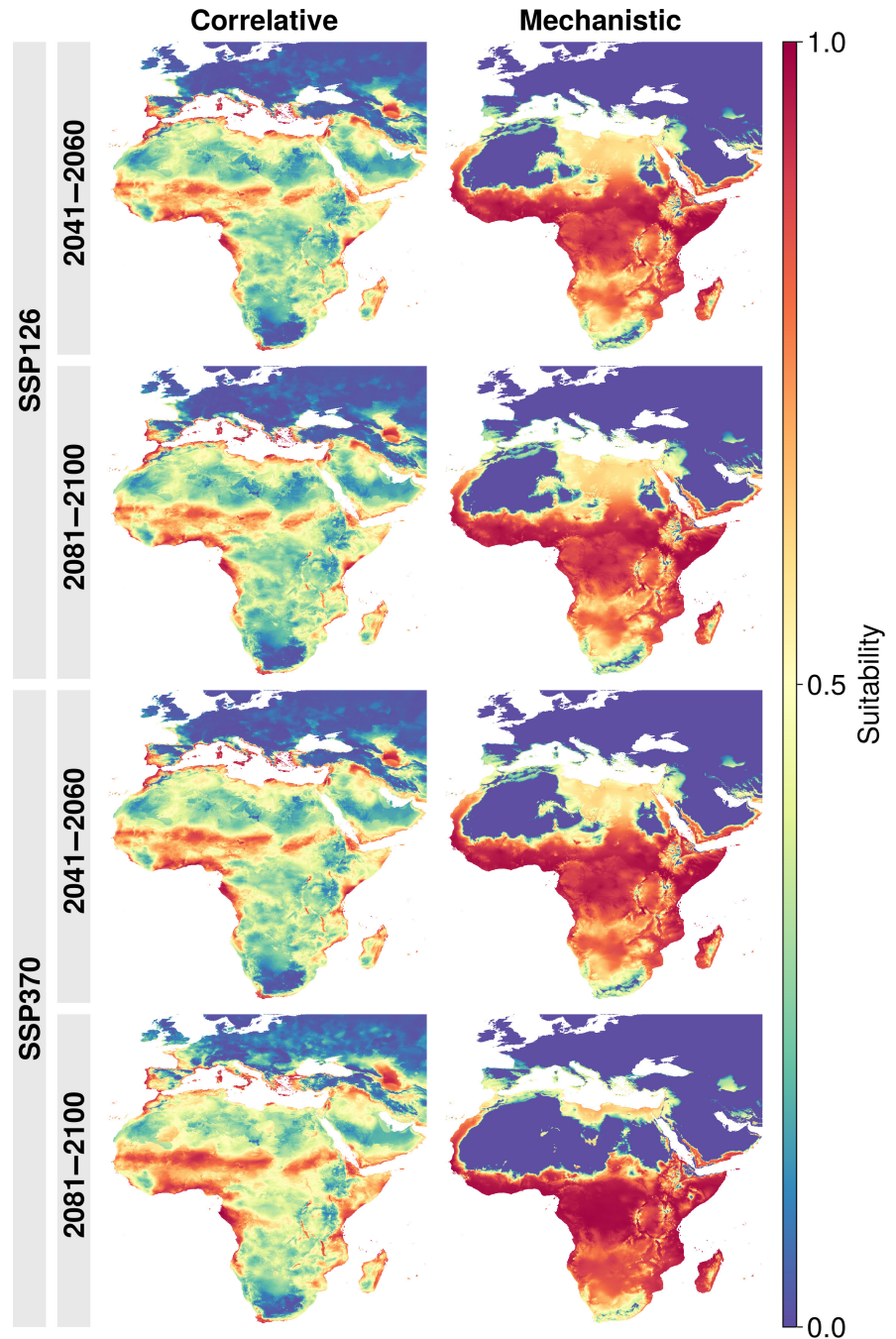
3.3.1 | Future distribution of *B. truncatus*

Under future climate scenarios, both models predict major shifts in the suitable area of *B. truncatus* (Figures 4b–e and 5). In Southern

Europe, both models predict a northwards expansion of the suitable area, with much of Italy, Spain, and southern France predicted as suitable by the end of the century under the SSP370 scenario of moderately high warming. The projected distribution under each scenario and GCM for the correlative and mechanistic models are given in Figures S10 and S11, respectively. The standard deviation between the GCMs is given in Figure S12.

In the Sahel and Sahara regions, the models make opposing predictions. The mechanistic model predicts a decrease in suitable area, with areas in Mauritania, Mali, and Senegal where *S. haematobium* is currently endemic predicted to be unsuitable for *B. truncatus* by the end of the century, especially under the SSP370 scenario. The correlative model, on the other hand, predicts that these areas will stay suitable and indicates a further increase in suitable area in parts of Niger, Mali, and Mauritania. However, these are also the areas of strict extrapolation as shown by the mop analysis (Figure S9). Additionally, both models predict increasing suitability in large parts of Central Africa (Figures 4b–e and 5).

FIGURE 5 Maps showing future suitable areas for *Bulinus truncatus* according to the correlative and mechanistic model under the different climate change (SSP) scenarios and time periods. Red areas have a high predicted habitat suitability; blue areas are predicted as not suitable.



In all, under the SSP370 model, the total area predicted as suitable by both models will increase by 17% (from 14.0 million km² today to 16.4 million km² by the end of the century, Figure 4e). However, a major shift in the suitable area means that an area of 4.2 million km² projected as suitable today will no longer be suitable by the end of the century. In contrast, 6.7 million km² predicted to be unsuitable today will become suitable. Of the 4.4 million km² that is currently both suitable for *B. truncatus* and has a high prevalence of schistosomiasis, 30% will no longer be suitable by the end of the century.

The difference between the two socioeconomic pathways investigated becomes most apparent after the middle of the century. Under the SSP370 scenario, the predicted range shift will accelerate after the 2050s until the end of the century. Under the SSP126

scenario, on the other hand, predicted suitability similarly changes until the middle of the century, but then almost no further changes are predicted until the end of the century.

4 | DISCUSSION

Here, we report on the current and future suitable area for *B. truncatus*, intermediate host snail for *S. haematobium* and *S. bovis*. Our study is the first to use reliable life-history data on *B. truncatus*, obtained from the literature and newly conducted experiments (Maes et al., 2024) to construct mechanistic niche models for this species. Combining the output of mechanistic and correlative modelling

improves the reliability of model projections considerably. We found an overlap between areas with high habitat suitability in both models and regions that are endemic for urogenital schistosomiasis (data from Kokaliaris et al., 2021). This finding aligns with earlier research conducted on a local scale, where the presence of suitable snail habitats proved to be a reliable indicator of schistosomiasis risk (Rohr et al., 2023; Wood et al., 2019).

Climate change is predicted to have different effects on *B. truncatus* habitat suitability in different regions. Our models show a net increase in the total area of suitable habitat by up to 17%, mainly in Central Africa and Southern Europe with the biggest expansion under the SSP370 scenario by the end of the century. In these regions, urogenital schistosomiasis is currently absent or has a low prevalence. Thus, the expansion of *B. truncatus* has the potential to put new populations at risk for urogenital schistosomiasis transmission, although a large part of the expansion can still be prevented by limiting climate change. In contrast, our results indicate that the Sahel region, presently characterized by a high *S. haematobium* prevalence (Figure 3c), is predicted to become unsuitable for *B. truncatus* from the middle of the century onwards. Under the SSP370 scenario, a total of 30% of the high schistosomiasis transmission areas currently suitable for *B. truncatus* will be unsuitable by the end of the century. Given that *B. truncatus* lives near its thermal tolerance limits in the Sahel region, it is unlikely that the species will persist there despite its local adaptation capacity (Konan et al., 2022; Maes et al., 2024). The potential loss of this intermediate host snail might lead to a reduction in urogenital schistosomiasis risk in that region.

Our results align with the predictions made by Yang and Bergquist (2018), who predict a decrease in urogenital schistosomiasis prevalence in the Sahel region and an increase in Europe by 2090 based on a growing degree day model of an unspecified *Bulinus* species and *S. haematobium*. However, previous studies on the future distributions of other snail hosts have primarily predicted a decreasing global habitat suitability. For instance, a correlative modelling study by Stensgaard et al. (2013) projects a potential decrease of up to 43% in the total suitable area for *Biomphalaria pfeifferi* by 2080, while the suitable area for *Biomphalaria sudanica* is predicted to increase by up to 14% by the same year (both under a high emission scenario). Similarly, Pedersen et al. (2014) anticipate a decrease in suitable area for both *Bulinus globosus* and *Bi. pfeifferi* in Zimbabwe by 2090. However, these studies were carried out on other snail species with different tolerance limits, using only correlative modelling approaches.

The presence of *B. truncatus* is just one of many factors governing *S. haematobium* transmission. *S. haematobium* is also compatible with other *Bulinus* species, such as *B. globosus* and *B. senegalensis* (Southgate et al., 2000). Moreover, factors such as vector competence; variable snail infection prevalences in natural populations; snail population structure; fluctuating seasonal snail densities; water, sanitation, and hygiene (WASH) practices; and access to healthcare also play significant roles in affecting human schistosomiasis prevalence rates. Due to the complex interplay of these factors impacting

S. haematobium transmission, this study refrains from providing a quantification of schistosomiasis risk.

Because of the factors mentioned above, the degree to which the increase in suitable area for *B. truncatus* will translate into an actual increase in schistosomiasis risk will vary across regions. In Europe, where adequate WASH practices are in place and health systems well-developed, establishment of widespread autochthonous schistosomiasis transmission is improbable, despite the presence of the intermediate snail host (Grimes et al., 2015). Conversely, in Central Africa, there is a projected increase in habitat suitability for *B. truncatus* in countries like the Democratic Republic of the Congo, South Sudan, Uganda, and Zambia where WASH infrastructure and measures are not equally available and even absent in some areas. Particularly in these areas, the projected expansion of *B. truncatus* represents a significant health hazard that should not be ignored (Allan et al., 2020; Díaz et al., 2023).

Our combined approach, comparing the outputs of both correlative and mechanistic models, offers significant strengths and advantages compared to the individual methods. Firstly, the two types of models estimate different niches; the correlative model approaches the realized ecological niche, while the mechanistic model estimates the fundamental niche. Secondly, while correlative models are excellent at predicting habitat suitability in known environments, a well-known limitation is their weak extrapolation capacity to novel environments, including a warmer climate (Higgins et al., 2020). Indeed, the mop analysis (Figure S9) reveals strict extrapolation in the Sahel and Sahara regions, where the correlative models predict a substantial increase in habitat suitability, making these predictions highly unreliable (Owens et al., 2013). In contrast, a key strength of mechanistic models is that they project into novel environments relying on experimentally derived responses to environmental triggers without extrapolation (Kearney & Porter, 2009). Consequently, the mechanistic model's prediction of a decrease in suitability in the Sahel region is likely a better indication of future suitability for *B. truncatus* than the prediction of the correlative model.

Despite the strengths of our approach, there are still some limitations to our models. For one, since our models are built on a continental scale, using a resolution of 2.5 arcminutes (approx. 5 km²), we may overlook fine-scale patterns resulting from micro- and mesoclimatic variations. For instance, both models predict low suitability in Corsica, even though snails are present in favorable microclimates in warmer pools along some rivers (Boissier et al., 2016). There is a lack of data on freshwater temperature conditions, which is why we assumed that water temperature is 3°C below air temperature. Tools to generate microclimatic conditions in freshwater habitats, such as exist for terrestrial and subterranean habitats (Kearney et al., 2014), could improve mechanistic modelling of freshwater snails.

Our results indicate that snail distribution modelling could provide a reliable estimate of schistosomiasis risk. Nevertheless, this study focuses only on *B. truncatus*. To better understand the connection between snail distributions and schistosomiasis risk, it is essential to model the distribution of all schistosome snail hosts. However, the scarcity of ecological data on most snail

species presents a major obstacle, making the construction of reliable mechanistic models for a broader range of snail species a real challenge.

5 | CONCLUSION

The present study capitalizes on the complementary value of mechanistic and correlative modelling to predict the impacts of climate change on an important host snail of schistosome parasites. The correlative modelling approach allows us to take full advantage of existing empirical occurrence data and explains the current distribution of *B. truncatus* well. The mechanistic models on the other hand, allowed us to take advantage of newly available experimental data, and were particularly instrumental in predicting the potential future distribution, since it identified areas outside of the thermal niche, which the correlative model predicted as suitable. Therefore, relying on just one of the models could result in biased conclusions. For this reason, we conclude that using both mechanistic and correlative approaches is a promising way to increase the robustness of species distribution predictions.

Our projections indicate that a large part of the Sahel region will be outside of the thermal niche of *B. truncatus* due to climate change, potentially leading to a decrease in schistosomiasis prevalence. In contrast, both models indicate that other areas, including in Southern Europe and Central Africa, might become suitable, thus potentially increasing the risk of schistosomiasis transmission. As such, monitoring and adaptive strategies are crucial for addressing the dynamic landscape of schistosomiasis transmission.

AUTHOR CONTRIBUTIONS

Tiem van der Deure: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; software; visualization; writing – original draft. **Anna-Sofie Stensgaard:** Conceptualization; funding acquisition; supervision; writing – review and editing. **Tim Maes:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; visualization; writing – original draft. **Tine Huyse:** Supervision; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

The model outputs and original model inputs (occurrence and life history data) are available on Dryad at <https://doi.org/10.5061/dryad.98sf7m0s9>. All model and plotting code is archived from GitHub at https://github.com/tiemvanderdeure/bulinus_truncatus_models and available on Zenodo at <https://zenodo.org/doi/10.5281/zenodo.12698361>. Historical and future climate and elevation data is provided by WorldClim and available at <https://www.worldclim.org/>.

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DATA SOURCES

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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