nature climate change

LETTERS

PUBLISHED ONLINE: 18 JULY 2016 | DOI: 10.1038/NCLIMATE3085

Climate change unlikely to increase malaria burden in West Africa

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The impact of climate change on malaria transmission has been hotly debated. Recent conclusions have been drawn using relatively simple biological models[1,2] and statistical approaches[3–5], with inconsistent predictions. Consequently, the Intergovernmental Panel on Climate Change Fifth Assessment Report (IPCC AR5) echoes this uncertainty, with no clear guidance for the impacts of climate change on malaria transmission, yet recognizing a strong association between local climate and malaria[6,7]. Here, we present results from a decade-long study involving field observations and a sophisticated model simulating village-scale transmission. We drive the malaria model using select climate models that correctly reproduce historical West African climate, and project reduced malaria burden in a western sub-region and insignificant impact in an eastern sub-region. Projected impacts of climate change on malaria transmission in this region are not of serious concern.

Climate is known to affect malaria transmission through multiple pathways[8–11], therefore the future of the disease in a warmer world is a question of great public health concern. Model forecast discrepancy has been attributed to differences in modelling approaches[12], as some studies use relatively simplistic biological models that do not capture the complex nonlinear relationships between environmental determinants and malaria[1,2], while others employ statistical regressions that similarly bypass important intermediate processes[3–5]. Thus far, very few studies have incorporated climate-driven hydrology as a determinant of mosquito populations and malaria transmission[13], and no models have moved beyond simple coarse surface hydrology parameterization as an intermediate link between climate and malaria. We address this shortcoming using a sophisticated high-resolution model to simulate future malaria transmission for West Africa at spatial and temporal scales that match village-scale transmission dynamics. In an earlier study[14], we assessed the changes in mean environmental suitability for malaria transmission corresponding to the most extreme predictions of future rainfall and temperature from an ensemble of global climate models. Here, we extend this analysis by predicting changes to the frequency of malaria outbreaks and seasonal malaria prevalence rates using the most credible climate predictions for this region.

West Africa is a hotspot for malaria transmission, as the region currently has the highest rates of malaria infections and deaths in the world[15]. Transmission is dominated by *Anopheles gambiae sensu lato* mosquitoes that develop in the numerous small, turbid pools that form following rainfall. *Anopheles funestus* mosquitoes, which prefer larger bodies of water, are also efficient malaria vectors where suitable developmental habitat exists. In many parts of West Africa, rainwater pools are quickly emptied by evapotranspiration and infiltration, and become productive developmental habitat only if they persist for the duration of the aquatic, subadult stage of mosquitoes. The persistence of such pools depends on rainfall amount and temporal patterns of rainfall[16], but local micro-topography will yield a wide range of pool sizes with variable persistence. Moreover, spatial relationships of developmental habitat with human habitation can be very important[17]. As a result, the relationship between rainfall and malaria is highly nonlinear and difficult to parameterize without resorting to a fully mechanistic representation of hydrological processes and mosquito population dynamics. Mosquito survival is a function of temperature, with maximum longevity between 15 and 30 °C, and severe mortality at temperatures below 10 °C and above 35 °C[18]. Temperature also affects the development rates of the aquatic-stage mosquito, as well as the incubation period of the parasite within the mosquito. Supplementary Fig. 1 shows the primary relationships linking climate to malaria transmission.

Extensive field work in two villages in Niger (Fig. 1 and Supplementary Fig. 2) led to the development of the Hydrology, Entomology, and Malaria Transmission Simulator (HYDREMATS), a mechanistic model of malaria transmission incorporating spatially explicit hydrology representation and agent-based mosquito population dynamics[19,20]. All of the major processes linking environmental variables to malaria infections in human populations are explicitly simulated with high spatial and temporal resolution, including the geophysical processes dominating the formation of water pools, spatially distributed agent-based simulation of individual mosquitoes and their interaction with developmental habitat and human populations, and human physiological processes of infection, recovery, and gradual acquisition of immunity (Fig. 2a). Model parameter settings were adjusted for *Plasmodium falciparum*, the dominant malaria parasite in West Africa[15].

Data collected from our field campaigns in Niger were previously used to calibrate and test the ability of HYDREMATS to represent soil moisture, water pool location, pool depth, water temperature and adult mosquito population dynamics accurately in this semi-arid climate region[21]. Previous work has also evaluated the uncertainty in the deterministic model forecasts[19,20]. In this study, our objective is to assess the impacts of climate change not only on the basic reproduction number (R_0, the expected number of secondary infections resulting from an initial case), but also on the frequency and severity of malaria outbreaks throughout the region. These outbreaks may take the form of malaria epidemics in the northernmost locations in the desert fringe, and they may involve transmission intensification in the endemic regions of the Sahel and Sudano-Sahel. To this end, we simulate entomological

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NATURE CLIMATE CHANGE DOI: 10.1038/NCLIMATE3085

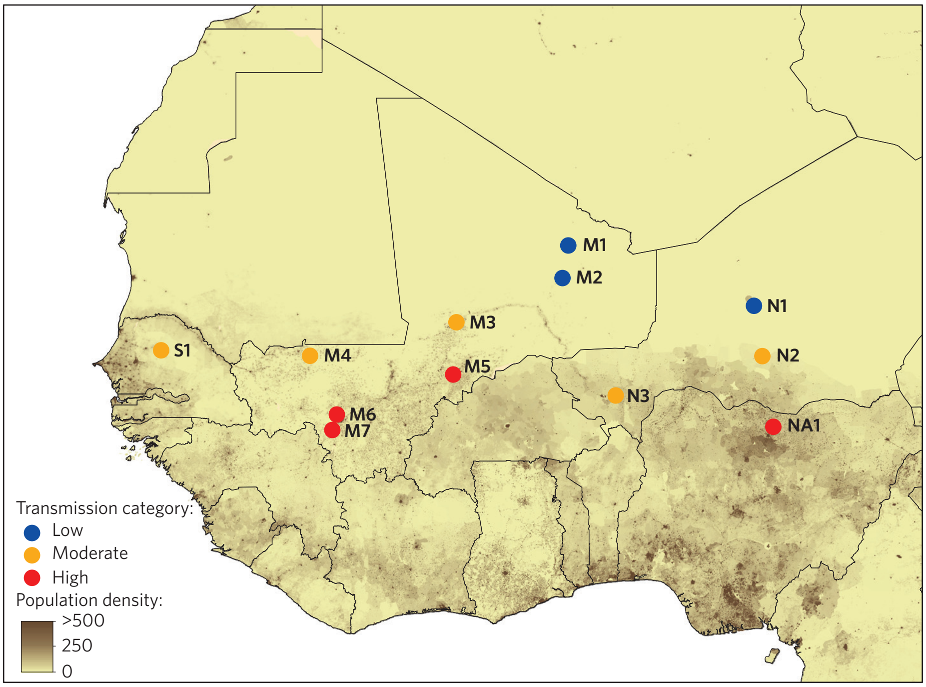

Figure 1 | Study location. Simulations are conducted for each of the 12 locations indicated on the map. The study field locations at Banizoumbou and Zindarou villages in Niger are located at the N3 marker. The model is tested against observations from the Garki district, located at maker NA1. The background image shows estimated persons per 0.0083° grid cell (roughly 1 km^2) in 2010 from the WorldPop database[28].

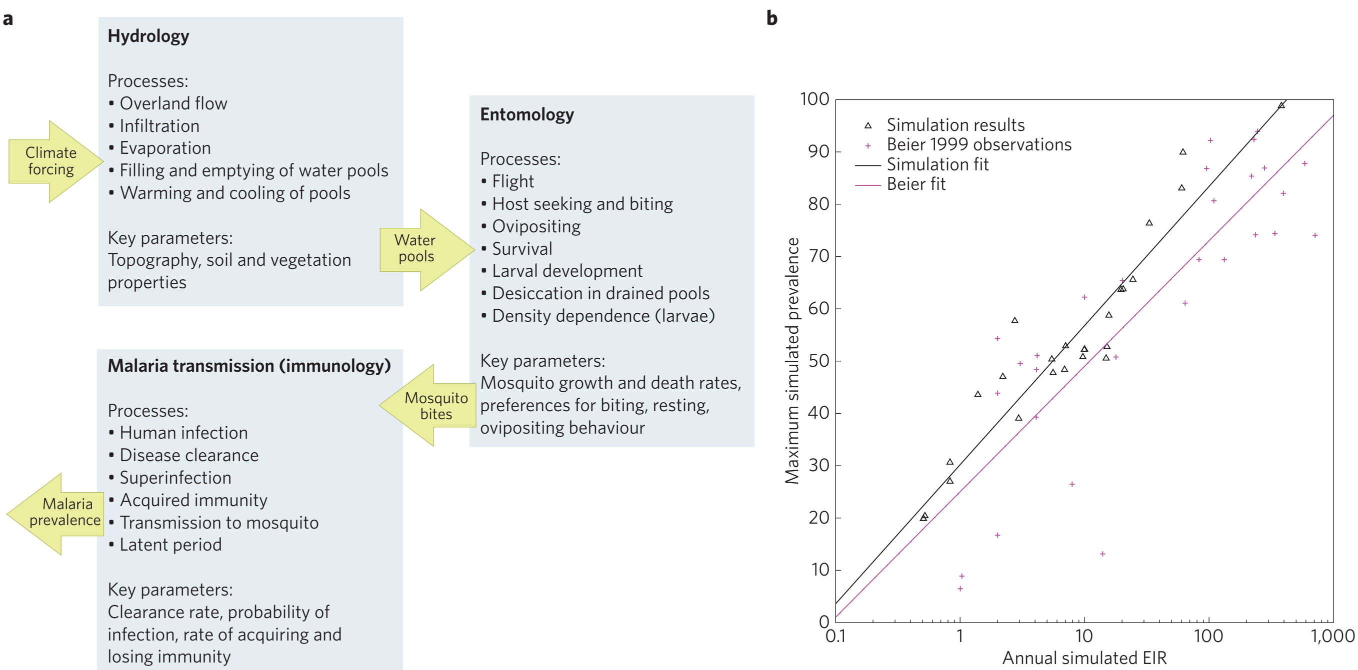

Figure 2 | HYDREMATS model. a, Schematic of the three model components of HYDREMATS. **b**, Relationship between the entomological inoculation rate (EIR) and malaria prevalence in observational data reported by Beier *et al.*[24] (pink) and simulated by HYDREMATS (black).

conditions and malaria prevalence and compare them to various observational data sets from multiple climate zones in West Africa to explore the model's credibility in simulating these variables. In the Supplementary Methods, we show the results of these comparisons, including malaria prevalence estimates from the Malaria Atlas Project (Supplementary Fig. 3)[22] and entomology and malaria prevalence data from the Garki district in Nigeria (Supplementary Figs 4 and 5)[23]. Figure 2b compares the simulated and observed relationship between malaria prevalence and the entomological inoculation rate (EIR), a measure of force of infection that combines mosquito population dynamics and parasite presence to represent the number of infectious bites per person per day. Beier *et al.*[24] established a log-linear relationship between prevalence and EIR that persisted when data were stratified by ecological zone as well as between East and West Africa, indicating that this is a fundamental relationship and independent of climate. HYDREMATS simulates

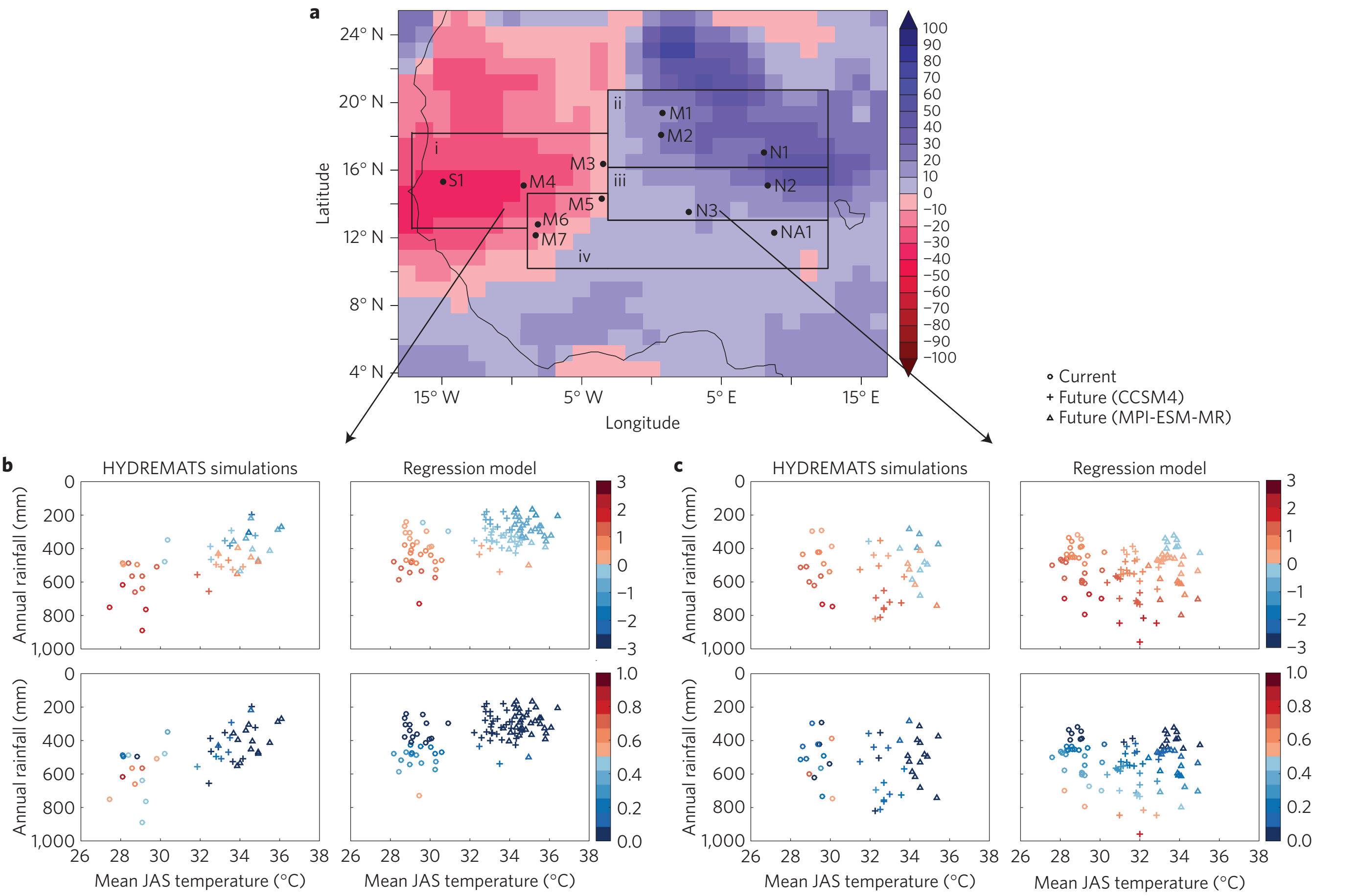

Figure 3 | Projected changes in rainfall, basic reproduction number and malaria prevalence. a, Projected change in annual rainfall by 2070–2100 as a percentage of 1975–2005 mean rainfall under RCP8.5, averaged between CCSM4 and MPI-ESM-MR. The labelled rectangles group the study area by response to climate change. **b**,**c**, Detailed simulation results are shown for two sites, M4 (**b**) and N3 (**c**), with current climate (circles), CCSM4-projected future (crosses) and MPI-ESM-MR-projected future (triangles). The top rows show $\log_{10}$ (R_0) and the bottom row shows mean prevalence in children aged 2–10. The left-hand panels are modelling results from the detailed HYDREMATS simulations. The right-hand panels apply a regression relationship to annual rainfall and mean wet season temperature data. JAS: July–August–September.

a very similar log-linear relationship (Fig. 2b), validating the model's ability to simulate the immune response to EIR (ref. 6). Immunological processes included in the model follow standard models in the literature, and are fully described in Yamana and colleagues[20]. Therefore, the validated disease transmission model is able to simulate the feedbacks between inoculations, immunity and infections for a wide range of malaria transmission levels.

We use the model to assess impacts of climate change on frequency and severity of malaria outbreaks in West Africa. However, in addition to the complexities in linking rainfall to malaria transmission under current climate conditions, climate models do not agree on the future rainfall of West Africa, adding additional uncertainty to malaria projections. We thus evaluate climate models' abilities to simulate historical climate to determine the most skilled models for use in the future climate change impact assessment (Methods and Supplementary Fig. 6). We identify two models, CCSM4 and MPI-ESM-MR, as being the most credible in this region. Under the Representative Concentration Pathway 8.5 (RCP8.5) scenario, these two models predict similar patterns of rainfall changes by the end of the twenty-first century: drier conditions in the western sub-region of West Africa, and wetter conditions in the east (Methods and Supplementary Figs 7 and 8). This pattern of change is consistent with the majority of CMIP5 models, as well as the CMIP3 and CMIP5 ensemble means[25,26]. We simulate malaria transmission using these projections of future climate at each of twelve locations across West African climate zones. We report the expected change in frequency of malaria outbreaks as determined by the fraction of years with $R_0 > 1$, and the severity of these outbreaks as determined by the disease prevalence in the simulated population at the peak of the transmission season. While there are a number of factors besides the basic reproduction number that determine whether a malaria outbreak will occur in a given year, the $R_0 > 1$ criterion provides a necessary condition that must be met in order for the disease to spread.

The results are categorized by geographical sub-region as shown in Fig. 3a, and expected response to climate change is shown in Fig. 3, Supplementary Fig. 9 and Supplementary Table 1. Current wet season temperatures throughout our study region currently approach or exceed the limits of mosquito survival, thus all future warming scenarios led to increased mosquito mortality. Overall changes are expected to be small in the northernmost locations (Sub-region ii) despite increases in rainfall. The hot and dry conditions severely limit mosquito breeding and survival, and thus do not sustain malaria transmission in either the current or the future climate. The southern locations (Sub-region iv), where recent climate is currently highly suitable for transmission, are also insensitive to changes in climate. In the simulations, future temperatures increase, but remain within the mosquito's survival limits. Projected long-term changes in rainfall are modest (±20%) and small compared to current inter-annual variability. As

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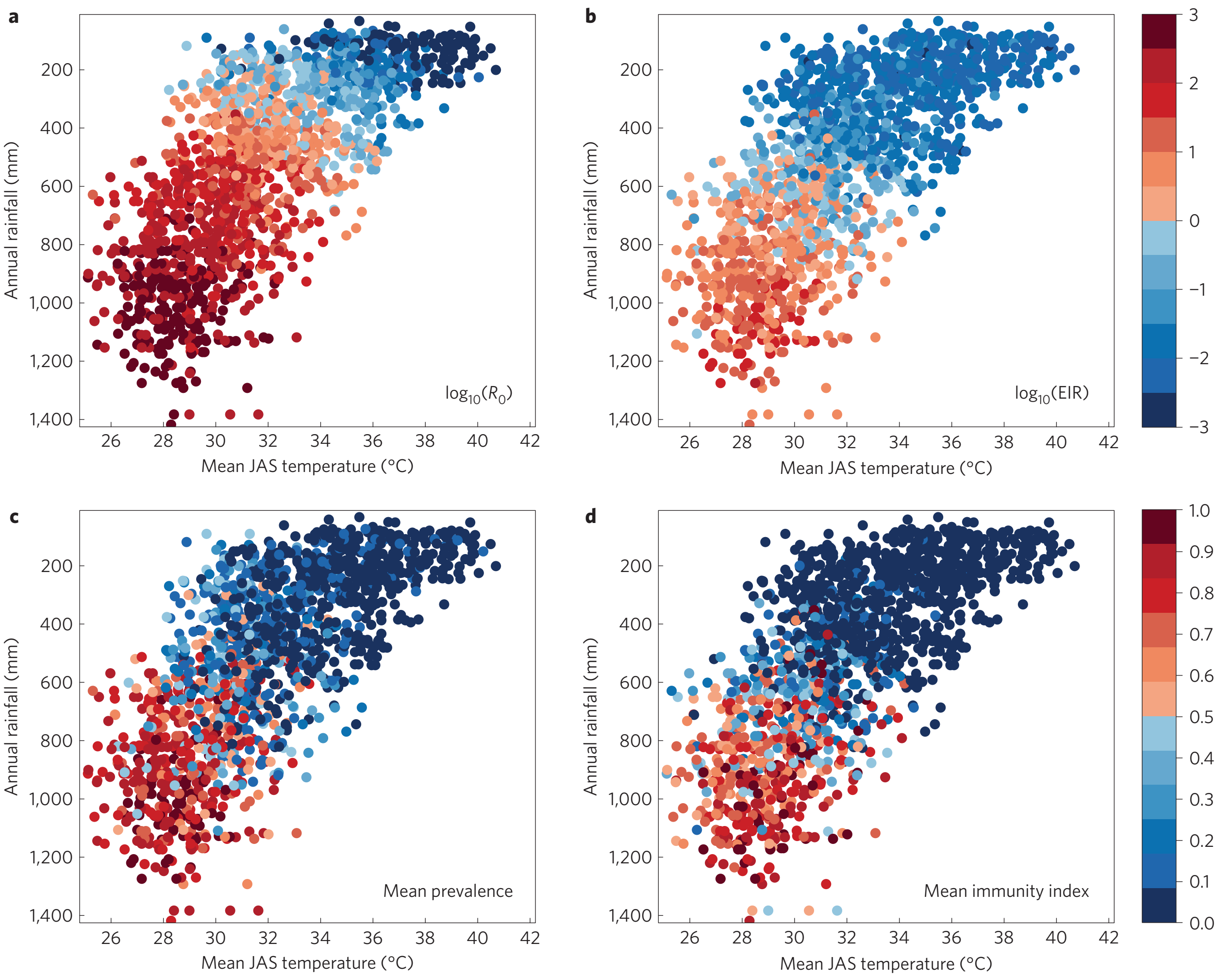

Figure 4 | Simulated relationships between environmental variables and malaria transmission indices. a–d, Simulated relationships between annual rainfall, July–August–September (JAS) temperature, and annual $\log_{10}(R_0)$ (**a**), annual $\log_{10}$(EIR) (**b**), mean wet season malaria prevalence in children aged 2–10 (**c**) and mean immunity index in the modelled population (**d**). **a**,**b** share the top colour bar and **c**,**d** share the lower colour bar.

a result, there is little expected change in malaria transmission in these locations.

Sub-region i, where both climate models predict decreased rainfall along with substantial increase in temperature, will see the most dramatic changes. Because this sub-region has R_0 values close to the threshold value for most years in the current climate, the hotter and drier future conditions lead to a higher proportion of years with $R_0 < 1$. The result is a projected significant decrease in frequency and severity of malaria outbreaks, as reflected in the simulated peak prevalence. Detailed results for village M4 in Southern Mali are shown in Fig. 3b.

Finally, Sub-region iii represents the most critical scenario, due to projected increase in rainfall and low levels of population immunity. In the current climate, these locations have low to moderate malaria transmission, with strong inter-annual variability. In our simulations, we find that the effects of future changes in rainfall (by increasing mosquito breeding) and temperature (by increasing mosquito mortality) are of similar magnitude, leading to small and uncertain changes in simulated R_0, and the associated frequency of malaria outbreaks.

Climate change in West Africa can lead to changes in both the mean conditions and inter-annual variability of malaria transmission. We extend our analysis beyond the 15-year period for which high-resolution temperature and precipitation data are available by using HYDREMATS to establish relationships between current climate and important indices of malaria transmission. We perform simulations for several locations throughout the region and present malaria metrics for individual years in multi-year simulations as points in rainfall–temperature space (Fig. 4 and Methods). For any given rainy season temperature and precipitation combination, the immunological indices (prevalence and immunity) show much greater variability than the entomological indices EIR and R_0, because the human immune system has a memory of past malaria exposure. Human immune response to malaria inoculation operates on the timescale of several years[27], as human agents slowly build immunity with each infectious bite received. Prevalence is influenced by mosquito population dynamics and immunity levels in the human population, as well as the recent history of malaria exposure within the population. During a multi-year simulation, the memory of human immunity therefore prevents immediate pronounced malaria response to a new, altered combination of temperature and precipitation in a subsequent year, resulting in the greater scatter of points shown in Fig. 4c,d. In contrast, clustering is observed in Fig. 4a,b, reflecting the more immediate response of EIR and R_0 to climate phenomena.

The simulated relationships of malaria indices to climate variables, shown in Fig. 4, are simplified using regression analysis. The resulting regression models are applied here to estimate the response of malaria transmission to climate change, for the same locations, using a longer period of climate forcing without the need to resort to detailed and computationally expensive modelling (see Supplementary discussion and Supplementary Tables 2 and 3). We apply this regression approach to determine the expected change in variability of R_0 and prevalence for a longer time period under current and future climate, shown in the right-hand panels of Fig. 3b and 3c, and compare with the results of direct HYDREMATS application. The results for the longer period compare favourably with the conclusions drawn from the shorter simulations.

Taken together, results presented here signal an impact of future climate change on West African malaria transmission that is negative at best, and positive but insignificant at worst. This analysis confirms that no major increases in the frequency or the severity of malaria outbreaks in West Africa are expected as a result of climate change.

Methods

Methods and any associated references are available in the online version of the paper.

Received 10 September 2015; accepted 14 June 2016; published online 18 July 2016

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Acknowledgements

This work was funded by the US National Science Foundation grants EAR-0946280 and EAR-0824398, and the US National Oceanic and Atmospheric Administration Oceans and Human Health Initiative. We thank the Centre de Recherche Médicale et Sanitaire (CERMES) of Niamey, Niger, for logistical support in the field, and J.-B. Duchemin for expert guidance and support in field entomology. We also thank the late A. Spielman and B. Jobin for their contributions to this interdisciplinary study. We thank J. Berta-Thompson for assistance in preparing figures.

Author contributions

A.B. led the model development and field campaign in Niger. T.K.Y. conducted the modelling study and climate change analysis and contributed to model development. E.A.B.E. conceived the study, and supervised the design and implementation of the research plan. All authors participated in writing and approved the final version of the manuscript.

Additional information

Supplementary information is available in the online version of the paper. Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to A.B.

Competing financial interests

The authors declare no competing financial interests.

Methods

HYDREMATS simulations. *HYDREMATS Model description.* The modelling tool used in this study is the Hydrology, Entomology and Malaria Transmission Simulator (HYDREMATS). A detailed description of the model has previously been reported[19,20]. In brief, the model consists of three coupled components: a physics-based hydrology model, an agent-based entomology model, and a spatially explicit malaria transmission model (Fig. 2a). The model has been developed for the village scale, with a spatial resolution of 10 m × 10 m and a 1 h time step. The hydrology component represents the partitioning of rainfall into infiltration and runoff, and subsequent water ponding in topographical low points leading to the small, turbid developmental habitats used by the *Anopheles gambiae s.l.* mosquitoes that dominate malaria transmission in West Africa. The model also simulates the physical processes by which the pools grow due to additional rainfall and shrink due to evaporation and infiltration for each time step. These processes are sensitive to the meteorological variables: precipitation, temperature, humidity, incoming solar radiation and wind. The temperature of each water pool, which is important for larval development, is computed by solving a system of energy balance and heat transfer equations.

The HYDREMATS entomology component simulates individual mosquito and human agents throughout the model domain. Mosquito agents respond probabilistically to their environment based on a set of rules governing dispersal and discrete events, including feeding, resting, egg-laying, and death. The aquatic stage of mosquitoes is simulated in water pools. Aquatic-stage mosquitoes develop at a temperature-dependent rate before emerging as adults. Aquatic-stage mosquitoes present in a pool that completely dries are killed in the model, as no surviving larvae were ever found in the rapidly drying mud of the study region. By this mechanism, the model represents nonlinearity in precipitation/mosquito connections derived from land-surface hydrological processes. Some studies have found that intense precipitation flushes larval mosquitoes from their developmental habitat, which can contribute to nonlinearity between precipitation and malaria transmission[29,30]. However, in our study sites, twice-weekly counts of larvae and pupae in water pools within and surrounding villages revealed that subadult populations are insensitive to intense precipitation. This process was therefore not modelled.

Daily mosquito survival is calculated as a function of temperature, according to the Martens equation[18].

The malaria transmission component of the model simulates the spread of the *Plasmodium* parasite through mosquito bites[20]. A mosquito biting an infected individual has a probability of acquiring the disease. After a temperature-dependent extrinsic incubation period[11], the mosquito becomes infectious to humans during subsequent blood meals. Humans with repeated malaria inoculations gradually build partial immunity to disease. This immunity reflects temporal and spatial heterogeneities in the entomological inoculation rate, both between different climates in West Africa, as well as localized differences within villages based on proximity to mosquito breeding sites. Partial immunity decreases the probability that a human acquires the disease after an inoculation, and also decreases the duration of infection in infected individuals.

Because *Anopheles gambiae s.l.* is dominant throughout the Sahel, and transmits malaria throughout most parts of the steep meridional climatic gradient that currently exists in the Sahel, we assume that mosquito behaviour will not change in response to climate. However, it is possible that, as the climate changes, individual mosquitoes in a particular population may begin to seek out and prefer microclimates, such as more time sheltered in the cool shade of houses or trees, that shield them from climatic extremes. This sort of behavioural response requires further research and we therefore do not include it in the model.

Design of numerical experiments. We selected 12 locations, shown in Fig. 1, from areas that currently have low to moderate levels of malaria transmission. For each location, we conducted a 15-year simulation, driven by environmental data from 1998 to 2012. The relatively long simulation length allowed simulation of the effects of inter-annual variability, particularly through the complex feedback processes between entomological inoculation rates (EIR), acquired immunity to malaria, and disease prevalence. Although simulation longer than 15 years would have been preferable, we were limited by the availability of environmental data with sufficient temporal resolution (hourly). Rainfall increases from north to south, both in the amount of rainfall per week and the number of weeks with rainfall. Wet season temperatures decrease from north to south. Environmental data sources used in the current-climate HYDREMATS simulations are described in the Supplementary Methods and summarized in Supplementary Table 4.

Selecting CMIP5 climate models. We examined historical temperature and rainfall data simulated by 23 global climate models (also called general circulation models; GCMs) and earth systems models (ESMs) from the Coupled Model Inter-comparison Project Phase 5 (CMIP5)[31]. The models analysed are listed in Supplementary Table 5, and their main features are described in the IPCC AR5[32].

Current global climate models are known to have biases in simulating the main characteristics of the West African Monsoon, which dominates rainfall in our study area[25,33,34]. This is believed to be the result of a warm sea surface temperature bias in the equatorial Atlantic, which affects the northward migration of the Intertropical Convergence Zone over the region[25,33]. In selecting our climate models, we make the assumption that the models that most accurately reproduce the seasonal cycle of rainfall and temperature, and hence are most accurate in simulating the West African monsoon, are therefore the reliable models to use in a climate impacts study.

We conducted an evaluation of CMIP5 models based on simulated temperature and rainfall, in our study region, as these are the variables most relevant to malaria transmission, and are required as inputs for HYDREMATS. The evaluation consisted of three stages: an analysis of the models' performance in simulating the seasonal cycles of rainfall and temperature in the study area; a literature search for known defects in the top climate models; the selected models were then ranked based on their ability to reproduce the spatial characteristics of historical climate.

We defined the region of interest as bounded by 18° W to 16° E, and 11° N and 21.5° N. This area was further divided into three sub-regions, corresponding roughly to the Sahelo-Sahara (Zone 1: 18–21.5° N), Sahel (Zone 2: 14.5–18° N), and Soudan (Zone 3: 11–14.5° N) eco-climate zones[35]. We compared output from the models' CMIP5 historical simulations[31] to data from the Climatic Research Unit Time-Series Version 3.21 (CRU TS 3.21). The CMIP5 family of historical simulations spans the period 1850 to 2005, forced by observed concentrations of greenhouse gases.

We calculated the average monthly observed rainfall and temperature from 1930 to 2005 using the CRU TS 3.21 data set and compared the observed seasonal cycles to simulated average monthly rainfall and temperature from each of the 21 climate models. We computed the sum of squared errors (SSE) for each model in each of six measurements: average monthly rainfall in Zones 1–3 and average monthly temperature in Zones 1–3. For each of six measures, we ranked the models from best to worst using the SSEs. We then assigned one point to the top six models for each measure, and subtracted one point for the bottom six models. The results of this analysis are shown in Supplementary Table 5. The highest scoring models were BNU-ESM (6 points), MIROC5 (5 points), MPI-ESM-MR (4 points), CCSM4 (3 points) and CanESM2 (3 points).

Next, we performed a literature search focusing on the top-scoring climate models to screen them based on already identified defects. The only model that stood out is BNU-ESM, which exhibits large errors in simulating the global atmospheric water balance, leading to a ghost source of precipitation and false latent cooling[36]. We deemed this non-stationary error to be sufficiently problematic to preclude the model's ability to simulate future rainfall, and thus excluded this model from the study.

The spatial characteristics of historical rainfall during the period 1930–2005 for the observational data set and the selected models are shown in Supplementary Fig. 6. The observations feature a north-to-south gradient in rainfall, while remaining relatively constant from east to west, with local maxima associated with orographic effects over the Fouta-Djallon region along the southwestern coast and over the Mount Cameroon region, the southeastern extent of our study area[37]. These features are generally well reproduced by CCSM4 and MPI-ESM-MR. While MIROC5 performed well in the area used for our initial analysis, it greatly overestimated rainfall in the southern half of West Africa, by as much as 1,000 mm yr^{-1}. CanESM2 also showed errors in the spatial distribution of rainfall, extending too far north into the Sahara desert, and its isohyets peaked between 5° W and 5° E, unlike the roughly latitudinal isohyets in the observations. As a result, we select CCSM4 and MPI-ESM-MR as the most credible models in this region.

Using projections of rainfall and temperature from CCSM4 and MPI-ESM-MR climate models, we simulated malaria transmission in 2070–2100 for each of the 12 locations to determine the changes in malaria transmission due to climate change. In addition, we present results using projections from MIROC5 and CanESM2 to show the sensitivity of our results to differences in climate projections (Supplementary discussion and Supplementary Fig. 10 and Supplementary Table 1).

Climate predictions for West Africa. We obtained monthly rainfall and temperature output for our selected climate models from the RCP8.5 scenario, which represents a future with high greenhouse gas concentrations, resulting in an increased radiative forcing of 8.5 W m^{-2} by 2100 relative to pre-industrial levels[31]. We computed monthly and annual average rainfall and mean temperature between July and September (JAS; the peak malaria transmission season) over the short-term (2030–2060) and long-term future climate (2070–2100), and compared to recent values (1975–2005). Predicted changes in rainfall are shown in Supplementary Fig. 7 and predicted changes in temperature are shown in Supplementary Fig. 8. The two models show a general pattern of drying in the western portion of our study area, and wetting in the eastern and southern areas.

The magnitude of these changes, as well as the extent of the area with predicted drying, varies somewhat by model. This pattern of rainfall change is consistent with 75% of the CMIP5 models analysed by Roehrig *et al.*[25], and is consistent with analyses of various subgroupings of CMIP5 models[26,38–40].

The overall precipitation signal is stronger in CCSM4 than in MPI-ESM-MR. As a result, the average of the two models more closely resembles the pattern predicted by CCSM4. Temperatures generally increase more in the west than in the east, consistent with the spatial extent of predicted changes in precipitation. MPI-ESM-MR predicts JAS temperature increases between 2.0 and 5.9 °C in 2070–2100, while CCSM4 predicts slightly less warming, between 0.5 and 2.8 °C in 2030–2060, and between 1.2 and 5.5 °C by 2070–2100.

Establishing regression relationships between climate and malaria transmission indices. Our initial simulation of twelve baseline locations yielded relationships between annual rainfall and temperature and the corresponding entomological and immunological values. To further explore these relationships, we performed additional realizations at each location using hypothetical combinations of annual rainfall and temperature inputs for a total of 1,600 realizations. Each of these additional simulations ran for 15 years at one of the twelve baseline locations.

We used the results of these simulations, shown plotted in rainfall–temperature space in Fig. 4, to fit linear regression models to predict R_0, EIR, immunity level and peak prevalence based on annual rainfall and July–September mean temperature. We correlated all four indices of malaria transmission with annual rainfall and July/August/September temperature (TJAS), as well as with each other. The coefficients of determination (R^2) are listed in Supplementary Table 2. The coefficients and R-squared values for these regression models are listed in Supplementary Table 3 in the form f(TJAS,rain) = a + b × TJAS + c/1,000 × rain.

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