HHS Public Access

Author manuscript

Curr Environ Health Rep. Author manuscript; available in PMC 2021 December 01.

Published in final edited form as:

Curr Environ Health Rep. 2020 December ; 7(4): 415–423. doi:10.1007/s40572-020-00290-5.

Mapping thermal physiology of vector-borne diseases in a changing climate: shifts in geographic and demographic risk of suitability

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Abstract

Purpose of Review: To describe a collection of recent work published on thermal suitability for vector-borne diseases, in which mapping approaches illustrated the geographic shifts, and spatial approaches describe the demographic impact anticipated with a changing climate.

Recent Findings: While climate change predictions of warming indicate an expansion in VBD suitability risk in some parts of the globe, while in others, optimal temperatures for transmission may be exceeded, as seen for malaria in Western Africa, resulting in declining risk. The thermal suitability of specific vector-pathogen pairs can have large impacts on geographic range of risk, and changes in human demography itself will intersect with this risk to create different vulnerability profiles over the coming century.

Summary: Using a physiological approach to describe the thermal suitability of transmission for vector-borne diseases allows us to illustrate the future risk as mapped information. This in turn can be coupled with demographic projections to anticipate changing risk, and even changing vulnerability within that population change.

In recent years, the thermal biology of transmission has been described for a series of vector-borne diseases following an initial publication by Mordecai et al. (1), which described the optimal temperature for malaria transmission by *Anopheles spp*. mosquitoes. Since then, the thermal bounds of transmission have been systematically characterized for eleven mosquito-transmitted diseases of humans (2–7). These methods were extended to a vector-borne plant pathogen, citrus greening, transmitted by a psyllid (8), and a livestock disease, bluetongue, transmitted by midges (9). The methodology of assessing the individual thermal traits of coupled vector-parasite life histories establishes a temperature-dependent transmission

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curve, describing R_0, the threshold of transmission, relative to its maximum. This provides a means to describe the temperature bounds of transmission, and to assess where thermal conditions are suitable to allow transmission to take place.

The equation for R_0 in these studies is modified from MacDonald's 1957 equations describing malaria transmission (10) as:

$$R_0 = \sqrt{\frac{a^2 bcmp^T}{(-\ln p)r}}$$

comprising mosquito biting rate (a), vector competence (b*c), vector density (m), vector survival (p), the parasite extrinsic incubation period, EIP (T), and r, the human recovery rate – all of which, except r, are temperature-sensitive parameters. All of these temperature sensitive traits have non-linear responses to temperature, and they must be measured from lab experimental data at constant temperatures to generate the curved responses used to parameterize the transmission equation. The resulting overall relationship for each trait is curvilinear with respect to temperature, which reveals an optimal temperature for transmission (see (1)).

Temperature is not the only factor that will determine, or constrain, transmission of vector-borne diseases on the landscape. For example, humidity, precipitation, availability of hosts, and the role of existing interventions will heavily influence the true transmission risk (11–13). This framing nonetheless presents a fundamental means to define areas on the landscape where temperature permits potential transmission. A key means to convey this information is to map the thermal transmission bounds to climate data products, demonstrating the implied geographic limits of these suitable conditions – i.e. where temperature allows for transmission. Using mean monthly temperature data at regional to global scales, this mapping approach appears in several descriptions of new thermal transmission curves, wherein lab-based measurements of life-history traits as functions of temperature were used in transmission equations, and mapped (6,8,9,14–18). These maps broadly illustrate the suitability of temperatures for transmission – in some cases, constrained by descriptions of sufficient moisture levels to support vector breeding (e.g. aridity bounds for malaria suitability mapping (15,16)).

Mapping approaches have also proven useful in communicating differential risk in emerging pathogens. The world's attention was brought into focus on *Aedes spp.* transmitted diseases as Chikungunya swept through the Americas, starting in 2013(19). Zika leapt onto the world stage in the following two years with its terrifying syndrome of microcephaly in the children of infected mothers (20–25). While dengue had consistently been causing an estimated 390 million cases a year across the world prior to this (26), the appearance of low mortality impacts left it largely second chair to the far more lethal malaria (27,28). When Zika emerged, a multitude of studies estimating its potential spatial distribution followed suit – maps of *Aedes* suitability, generated with species distribution modeling (SDM) or ecological niche modeling (ENM) approaches (29–32), maps of Zika case suitability (33,34), and a comparison of models of Zika and dengue case data niche models, suggesting that Zika was somehow different than dengue, bioclimatically (35). Mordecai et al. published thermal

suitability models for *Aedes aegypti* and *Aedes albopictus* transmission of flavivirus (lab strains of dengue), and validated these models with outbreak data for Chikungunya and Zika viruses to demonstrate the thermal suitability for transmission by these two vectors (4). Perhaps surprisingly, this revealed that optimal transmission by *Ae. aegypti* occurs at a higher temperature than by *Ae. albopictus* (Figure 1), underscoring the importance of the potential for different climate profiles of transmission for different vectors, even with the same human-disease causing pathogen.

When we think of *Aedes spp.* transmitted diseases, we are no longer constrained by the natural occurrence of moisture on the landscape – mosquitoes like *Ae. aegypti* are anthropophilic, urban adapted, container-breeding mosquitoes (36). Therefore, they can exploit human altered environments and will take advantage of almost any type of water storage to oviposit, regardless of broader scale environmental conditions (37,38). Thus, while some studies can identify precipitation cues for *Aedes aegypti* occurrence at a household level (39), with sufficient social-ecological conditions to promote larval habitat (e.g. containers, abandoned tires, other water catchment in the domestic landscape), any signals of precipitation can be drowned out (40). In 2019, Ryan et al. described risk of disease transmission exposure in terms of the number of thermally suitable months for dengue transmission by *Aedes aegypti* and *Aedes albopictus*, geographically overlaying a spatial projection of the thermal suitability model of Mordecai et al. (4) on demographic projections of population density (17). In this way, the number of people at risk (PAR) across the globe was calculated under the assumptions that where there are people there is water storage (i.e. available mosquito habitat), and only thermal bounds would functionally limit range expansions and establishment by these two vectors (Figure 2).

Climate Change Induced Shifts in Geographic Risk

Understanding the potential impact that climate change will have on the vector-borne disease risk discussed here requires projecting transmission suitability under future scenarios of climate patterns and human mediation actions. This is conceptually straightforward, but rapidly becomes complicated by the myriad of increasingly sophisticated climate model projections available (41). In 2015, Ryan et al. used the future climate scenario framework presented in the 2007 Intergovernmental Panel on Climate Change (IPCC) 4th Assessment Report (AR) to map the physiological suitability of malaria transmission under climate change (42), specifically using the SRES (Special Report on Emissions Scenarios (43)) A1B emission scenarios, downscaled using the delta method (44). The A1B scenario falls in the center of projections of anthropogenic emissions and makes a general assumption of continuing globalization (45), balancing across fossil and non-fossil energy sources. This choice of projected future trajectory for climate change was chosen to present a balanced view of the impact of climate change, without illustrating extremes. We projected the shifting geography of the malaria season (i.e. the number of months suitable for transmission) across the continent of Africa using projected mean monthly temperatures for three endpoints, 2020, 2050, and 2080. As part of the study, the temperature-dependent spatial model was overlaid onto UN generated population density data estimates for 2015 to illustrate demographic risk, using the number of months suitable for transmission multiplied by log-transformed population density to illustrate a shifting gradient of risk over time. This

revealed a transitioning zone of increased months of transmission suitability and high density population, where the highlighted zone of increased risk moves from West Africa across the center of the continent, and arrives over the Albertine Rift region of East Africa by 2080 (Figure 3)

Since that publication, the framing of climate change scenarios and the projection models used have shifted with IPCC iterations, presenting the need to update study results that rely on these mapped projections. This is particularly vital when describing population risk, where mapped products are used to facilitate communication to decision makers, such as USAID's President's Malaria Initiative (PMI) (46). In 2020, Ryan et al. published a new study that used updated underlying climate models to describe regional shifts and population risk changes for malaria in Africa, using policy language that aligned with decision-making frameworks for intervention planning (16). Part of this effort was to engage in conversations about definitions and assumptions of transmission season length, given models of intervention for epidemic, seasonal, and endemic malaria, and these were used to frame the discussion in a series of reports (46–48).

While broad geographic and demographic shifts remain similar – a shifting zone of longer seasons moving across the continent from West Africa to East Africa – the updated paper reflects both a shift towards aligning with the language of funding decisions, as well as newer climate models. These papers, published only 5 years apart, reflect the changing descriptions of climate change upon which estimates of future VBD risk are based. Updating our projected risk estimates not only improve how multiple climate groups' models can be incorporated into better understanding potential future climate dynamics, but also improve our own options and actions for mitigation. The Representative Concentration Pathways (RCPs), introduced with the AR5 IPCC assessment (49) describe futures in which the international community takes action of different magnitudes, at different time points, to mitigate climate change impacts. By linking the descriptions of malaria seasons to the intervention language – where seasonal and endemic risks had quantified lengths – and by using two pathways, RCP 4.5, a moderate trajectory, and RCP 8.5, the worst-case scenario, with ensembled climate models specifically created for the African continent (46), this paper cast the risk into decision-making frameworks. Figure 4, adapted from the study, exemplifies the differences between geographic risk (space on the landscape) and demographic risk (number of people impacted) involved in these projected shifts in suitability. The spatial risk decreases for both endemic (year-round) and seasonal (6-9 months) malaria transmission suitability (map panels), but the demographic risk is shifted dramatically (illustrated in right panels for endemic risk), as that suitability moves into high-density population areas.

Midtiple vectors, multiple pathogens, multiple futures

As stated previously, understanding risk of exposure to arboviral infections, particularly those spread by *Ae. aegypti* and *Ae. albopictus*, has become an urgent research priority in light of newly emerging pathogens. Like malaria, the potential geographic spread of emerging and re-emerging arboviruses is now of great interest to agencies tasked with communicating and preparing for risk (50). In order to project the future risk of *Aedes spp.* transmitted diseases with the new IPCC and RCP framework, in our 2019 paper, we were

faced with the task of communicating futures for two vectors with different thermal profiles, under a variety of possible scenarios, and across different time horizons (17). Several variable factors contribute to IPCC climate change scenarios, including a multitude of mitigation strategy pathways, products from multiple circulation models from different climate research units, and choices of endpoints (e.g. the years 2050, 2080, and even 2100) When communicating geographic information, spatial scale can also become a complicating factor. While global scale maps are visually pleasing, they complicate the succinct communication of quantitative information. In the paper in 2019, we used a combination of synoptic boxplots to demonstrate the range of results from different GCMs, under two RCPs, at two future endpoints (2050 and 2080), in context of the number of people at risk due to thermal transmission suitability, either year-round (i.e. suitable transmission for 12 months) or 1 or more months. For the *Aedes spp.* transmission models, we used a different descriptor of seasonality than for the malaria work; in the context of emerging diseases, the question of "any" risk (i.e. a month or more) is important to know, and at the other extreme, describing areas of year-round suitability risk – potential endemic areas – is of interest. Given that intervention for these arboviral diseases, dengue, chikungunya, and Zika, is limited to vector control, with low availability of effective vaccines – unlike Yellow Fever – understanding the potential for emergence, or the need for continuous surveillance and vector control, guides the decision frameworks, and thus our model illustrations.

While we were developing spatial and demographic risk approaches in 2018, for the two *Aedes spp.* vectors, results from lab studies examining the vector-pathogen thermal responses of *Aedes aegypti* infected with Zika virus revealed that the optimal temperature for transmission was similar to that for dengue, as previously assumed. However, at lower temperatures, the two curves (dengue and Zika) differed (6). Zika appeared to have a higher minimum temperature bound on transmission suitability, and when mapped onto climate in the Americas, this difference in the thermal performance curve revealed a rather smaller potential geographic range of transmission risk compared to what was predicted for dengue in the same *Aedes aegypti* vector (6). This difference in important vector-pathogen coupled thermal responses has large geographic (and demographic) implications (51), suggesting that despite the commonality of the vector *Aedes aegypti*, more of the world is at risk of dengue transmission than Zika transmission. This highlights the importance of understanding the biological mechanisms fundamental to describing temperature dependent transmission suitability for vector-borne diseases. Tightly coupled vector-pathogen life histories will yield idiosyncratic transmission cycles, each with their own unique outcomes in terms of spatial and demographic risk. This specific contrast between dengue and Zika temperature-dependent transmission profiles must, however, be tempered with the caveat that these findings are based on infection experiments of mosquitoes in lab conditions with lab strains of the viruses, and both local adaptation of mosquitoes and evolution of viral strains will certainly occur in the 'real world'(52). Future investigations will start to reveal how much deviation this can induce from our broad scale projections.

Climate Change and Demographic Shifts

One important aspect to keep in mind when thinking about global change is that we are prone to model single axes of change, assuming others remain constant. This is often for

practical reasons, because to measure the impact of something we need a baseline to hold as a comparison. If we adjust both numerator and denominator together, it is harder to assess the impact and make that comparison. However, in order to understand demographic impact of future scenarios, we need to consider that the population is both changing (increasing overall), but also altering both compositionally (age structure, economics), and geographically (moving in response to climate change itself). The Shared Socioeconomic Pathways (SSP) projections (53) of demographic change are products of a series of modeled future population responses to climate change. The projections align with some of the SRES scenarios described by the RCP (Representative Concentration Pathway) framework in the IPCC (54), but are also informed by the Millennium Ecosystem Assessment (MEA) (55), UNEP's Global Environment Outlook (GEO) scenarios (56), and others.

The SSPs present a range of five responses to climate change along a pair of axes representing the challenges of mitigation and adaptation, where responses are functions of how socioeconomic development will occur in terms of economic growth, environmental awareness, education, spatial patterns of urbanization, health equity, technological development, and economic inequalities (57,58). SSP1, on the lower end of both axes, is named "Sustainability" and emphasizes human well-being, achieving development goals, increasing sustainable consumption, reducing inequality, and concentrating urbanization. SSP3, placed high on both axes, is named "Regional Rivalry" and describes a world in which there is slowing global economic growth, increased inequality, regional conflict, continued fossil-fuel dependency, environmental degradation in some regions, and low technological advances to address mitigation or adaptation. SSPs 4 and 5, "Inequality", and "Fossil-Fueled Development", respectively, sit at opposing comers, with SSP 4 high on mitigation challenge (but adaptation in the form of a divided world between labor-intensive, low-tech economies, and a small but powerful high tech elite); and SSP 5 high on adaptation challenge, seeing continued global economic growth with high energy consumption, accelerated global development, local technological solutions to environmental issues, but overall de-prioritizing environmental concerns. The remaining SSP, SSP2, presents a 'middle road' scenario, to balance the four others. Although a given RCP might fit within the framing of several SSPs, not all combinations of RCP and SSP are plausible, given the role of mitigation (59,60).

Incorporating SSP scenarios into current modeling workflows can enhance our efforts to anticipate the future risk of vector-borne disease exposure, where we can plan for a wider breadth of possible scenarios that account for non-climatic changes. In a recent study, Rohat et al. (61) explored the combinations of projected demographic future risk of *Aedes spp.* transmitted diseases in the USA, first by overlaying the combinations of Ryan et al.'s projected future transmission models by RCP and year onto SSP1, SSP3 and SSP5. They then explored projected vulnerable population groups by age-sex-race/ethnicity (ASRE) cohorts (62) at the county level across the continental USA – those that are either more likely to get bitten, such as outdoor workers (projected from Bureau of Labor Statistics), children playing outside, or those more likely to suffer more adverse health effects if infected, such as the elderly. Additional considerations for vulnerability included being part of urban populations, as *Aedes spp.* mosquitoes are more likely to impact populations occupying urban and built environments. Under most combinations of scenarios in the study,

exposure to transmission suitability in the USA is projected to increase, and the changes in exposure are driven largely by projected population change in vulnerable groups. In terms of climate change mitigation potential, Rohat et al. (61) found that changing emissions scenarios from RCP 8.5, under SSP3 (worst case climate scenario, 'regional rivalry' demographic trend – see above) to RCP 2.6, under SSP1 (best case climate scenario, 'sustainability' demographic trend – see above) would result in a difference of around 1.97 billion (3.16 vs. 1.19 billion) fewer people facing exposure risk to *Aedes aegypti* transmitted in the continental USA. This study underscores the importance of understanding the range of potential changes in future demography when assessing the impact of shifting geography of transmission risk under climate change.

The capacity for undertaking geospatial analyses of combined vulnerabilities is growing, as is our ability to explore more nuanced ways to describe potential climate impacts. This is due in no small part to the open data sharing data products for a range of spatial extents (e.g. regional to global) and projections of future scenarios. As recent work has suggested, we must now think not only of intersecting vulnerability, but also of overlapping risk. Carlson and Mendenhall (63) called attention to the potential for syndemics – co-occurring or overlapping epidemics – in the context of Zika emergence and spread, bringing the term into the spotlight for vector-borne diseases. This overview of temperature dependent, model derived projections of vector-borne diseases highlights the way in which vector-pathogen coupling proves to be an essential component of the geospatial suitability for *Aedes spp.* transmitted diseases. Within this framework we have illustrated overlapping areas of suitability for Zika and dengue, two diseases of major public health concern. However, it is important to note that there have been multiple waves of arboviral outbreaks in the Americas over the past decade (64–66). Whether these diseases will have multiplicative effects of risk and impact as syndemics in the future, or not, is complicated to assess at this point. In addition to considering overlaps, considering co-occurring shifts in suitability resulting in 'swaps' of risk is important. Mordecai et al. (67) (explored the changing suitability of the African landscape under climate change, in which many parts are becoming too hot for malaria transmission suitability while also becoming more suitable for *Ae. aegypti* transmission of dengue fever. In this study, both projected geospatial comparisons and empirical evidence support a changing febrile risk environment. This phenomenon is something which will also likely occur in other regions, or with other vector-pathogen systems. It was recently recognized that *Anopheles stephensi*, an urban, container-breeding malaria vector common in India, has become established in several African urban centers (68). With a 'hotter' transmission profile than the *Anopheles gambiae* complex (18), the expansion of *An. stephensi* is likely facilitated by longer periods of warmer climate, which in the context of ongoing global mobility, leads to increasing introductions of multiple potential vectors to new regions (69)

Using temperature-dependent models of transmission to describe future suitability, with available large-scale monthly mean temperature projections, captures a very broad outline of what we may expect to occur with regards to risk of vector-borne diseases. The role of variation in temperature at multiple scales – diurnal variation, seasonal anomalies, extreme events – remains to be explored, as do additional axes of bioclimatic limits on vector borne disease transmission (e.g. humidity, aridity, soil moisture capacity), and more nuanced

descriptions of biologically meaningful features on the landscape (e.g. capturing larval habitat availability at large scales for mosquitoes). Given the range of variation in projected climate futures at such broad time horizons as those illustrated here, unpacking which uncertainty components or assumptions influence model outcomes is important for future work.

Reflections and Application

Synthesizing the important findings of this type of work for a journal article is a different endeavor than summarizing all the findings for a report to an organization, government agency, or surveillance unit. As has been asked of me by reporters: why do you (scientists) put the best stuff in supplementary information? In the 2019 *Aedes spp.* paper, we summarized our findings for policy (and journalists) further, to describe which regions, from the Global Burden of Disease regions (70) would see increases in novel exposures to risk, decreases, and by how many people. This allowed us to pinpoint parts of the globe that would move into greater exposure, and those that would move out of suitability – and for which vector. Just as there is a need for nuanced discussions on the impacts of biological limits, climate change, and human demographics on future risk of vector-borne disease transmission, so is there a need for clear communication and interpretation of these complex topics for agency partners and other stakeholders. Mapping remains a powerful tool when communicating the findings of complex models, providing the community of researchers an accessible means of presenting results and highlighting where, and when, populations are at risk.

Acknowledgements

SJR was funded by NSF EED DEB 1518681

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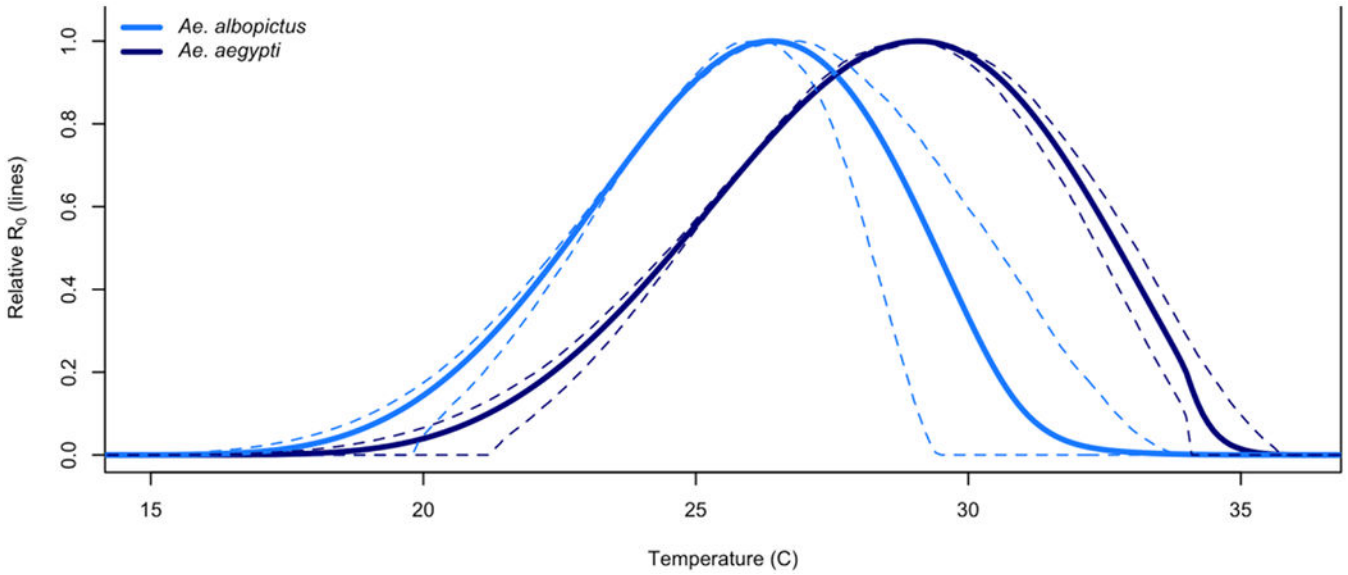

Figure 1:

Temperature dependent transmissibility curves for Ae. aegypti (dark blue) and Ae. albopictus (light blue), with the 95% credible intervals shown as dashed lines, demonstrating the 'hotter' transmission suitability of Ae aegypti, and 'cooler' suitability for Ae albopictus. Adapted from Figure 2 in Mordecai et al. 2017 (4).

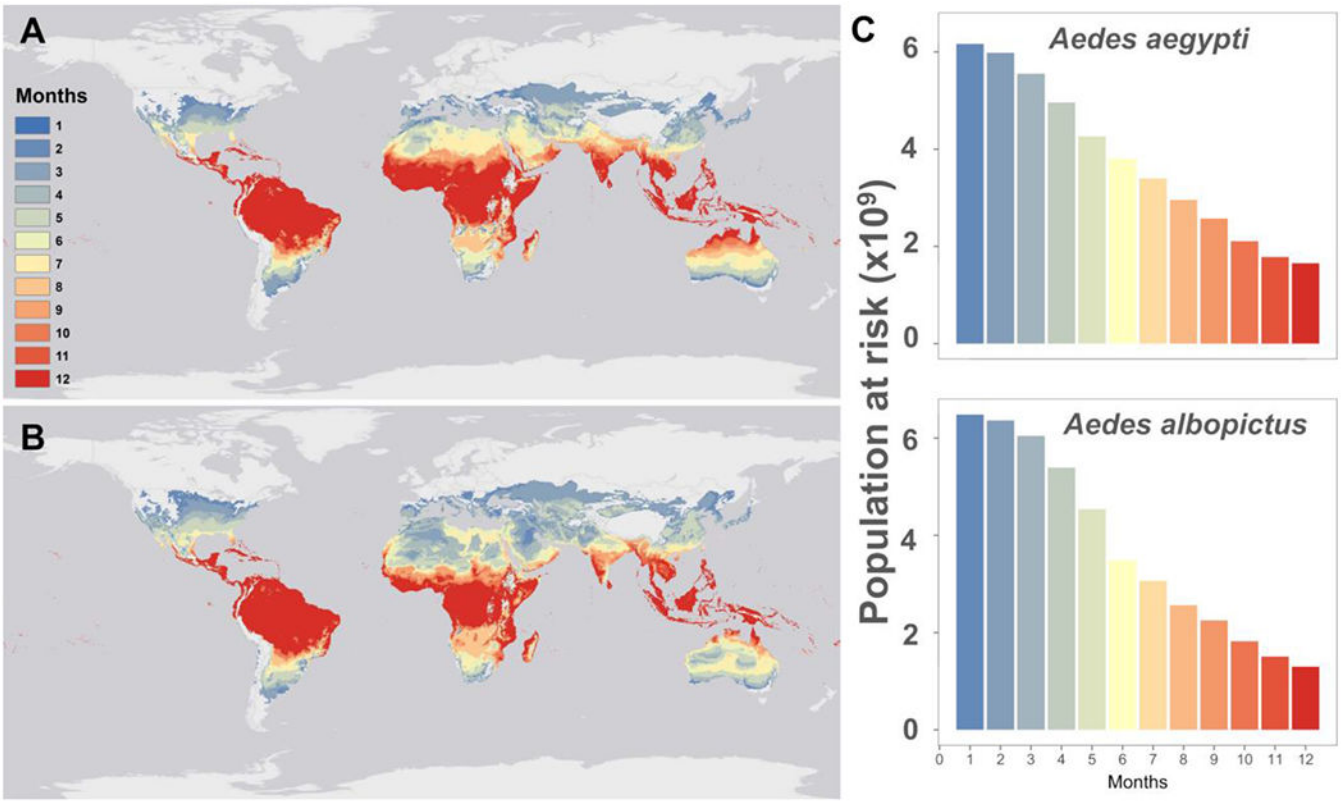

Figure 2.

The differences in the thermal responses of two mosquito vectors results in different geographies of suitability for transmission – the cooler tolerant Ae. albopictus (b) has a much more temperate potential, while at baseline, current climate, Ae. aegypti (a) is constrained to warmer, more tropical areas, for much of the year (reproduced from Ryan et al. 2019 (17)).

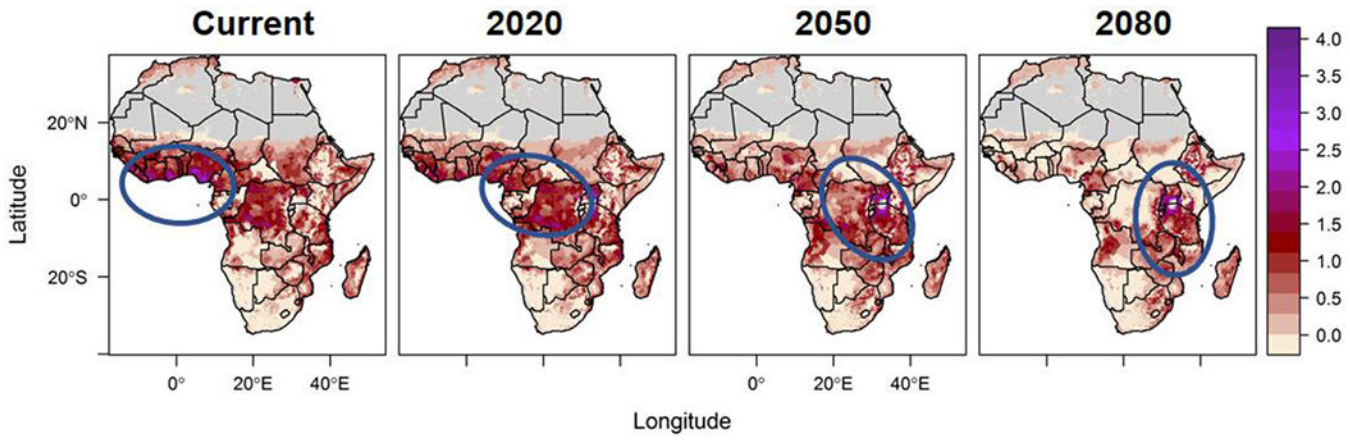

Figure 3:

A hotspot of combined longer thermally suitable malaria transmission season and population density moves across the African continent under climate change scenarios (From Ryan et al. 2015 (15))

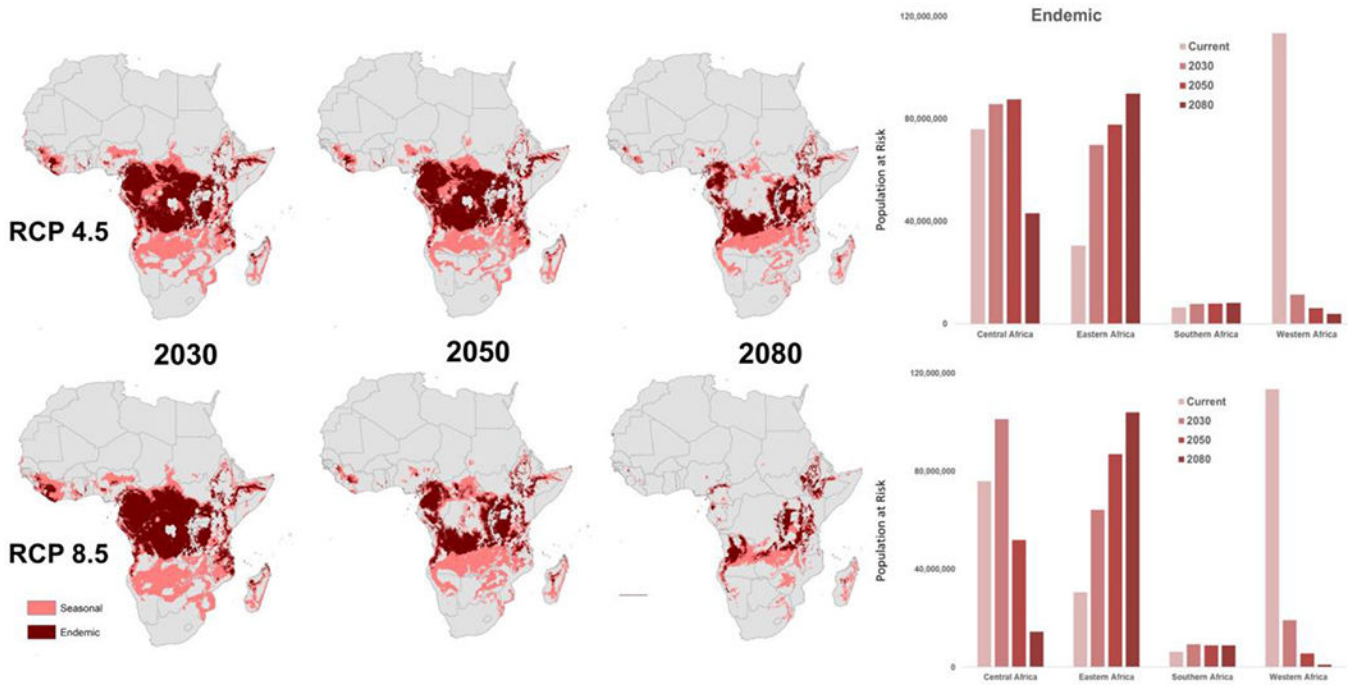

Figure 4:

Shifting geographic zones of predicted seasonal (7-9 months) and endemic (10-12 months) suitability for transmission across three time horizons, under two Representative Concentration Pathways (RCP), and the corresponding PAR for endemic risk, for four African regions: Central, Eastern, Southern, and Western Africa (Adapted from Ryan et al. 2020 (16)).