# Global expansion and redistribution of Aedes-borne virus transmission risk

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with climate change 2 3 Sadie J. Ryan<sup>1,2,3\*†</sup>, Colin J. Carlson<sup>4,5\*</sup>, Erin A. Mordecai<sup>6</sup>, Leah R. Johnson<sup>7</sup> 4 5 **Affiliations:** 6 <sup>1</sup>Department of Geography, University of Florida, Gainesville, Florida, United States of America 7 <sup>2</sup> Emerging Pathogens Institute, University of Florida, Gainesville, Florida, United States of 8 9 America 10 <sup>3</sup> School of Life Sciences, University of KwaZulu-Natal, Durban, South Africa 11 <sup>4</sup>Department of Biology, Georgetown University, Washington, DC 2007, U.S.A. <sup>5</sup> National Socio-Environmental Synthesis Center, University of Maryland, Annapolis, Maryland 12 21401, U.S.A. 13 <sup>6</sup> Department of Biology, Stanford University, 371 Serra Mall, Stanford, California, United 14 States of America 15 <sup>7</sup> Department of Statistics, Virginia Polytechnic and State University, 250 Drillfield Drive, 16 Blacksburg, Virginia, United States of America 17 18 \*These authors share lead author status. 19 † Corresponding author: sjryan@ufl.edu 20

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**Abstract:** Forecasting the impacts of climate change on *Aedes*-borne viruses—especially dengue, chikungunya, and Zika—is a key component of public health preparedness. We apply an empirically parameterized Bayesian transmission model of Aedes-borne viruses for the two vectors Aedes aegypti and Aedes albopictus as a function of temperature to predict cumulative monthly global transmission risk in current climates, and compare with projected risk in 2050 and 2080 based on general circulation models (GCMs). Our results show that if mosquito range shifts track optimal temperatures for transmission (26-29 °C), we can expect poleward shifts in Aedes-borne virus distributions. However, the differing thermal niches of the two vectors produce different patterns of shifts under climate change. More severe climate change scenarios produce proportionally worse population exposures from Aedes aegypti, suggesting a strong coupling of climate change and continued emergence of dengue virus; but not from Aedes albopictus in the most extreme cases, suggesting a less straightforward climate link for chikungunya. Expanding risk of transmission from both mosquitoes will likely be a serious problem, even in the short term, for most of Europe; but significant reductions are also expected for Aedes albopictus, most noticeably in southeast Asia and west Africa. Within the next century, nearly a billion people are threatened with new exposure to both Aedes spp. in the worst-case scenario; but massive net losses in risk are noticeable for Aedes albopictus, especially in terms of year-round transmission, marking a global shift towards more seasonal risk across regions. Many other complicating factors (like mosquito range limits and viral evolution) exist, but overall our results indicate that while climate change will lead to both increased and new exposures to vector-borne disease, partial mitigation may accrue major unanticipated health costs from diseases that are mainly spread by Aedes albopictus.

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**Author Summary:** The established scientific consensus indicates that climate change will severely exacerbate the risk and burden of Aedes-transmitted viruses, including dengue, chikungunya, Zika, West Nile virus, and other significant threats to global health security. Here, we show that the story is more complicated, first and foremost due to differences between the more heat-tolerant Aedes aegypti and the more heat-limited Aedes albopictus. Almost a billion people could face their first exposure to viral transmission from either mosquito in the worst-case scenario, especially in Europe and high-elevation tropical and subtropical regions. On the other hand, while year-round transmission from Ae. aegypti is likely to expand (especially in south Asia and sub-Saharan Africa), Ae. albopictus loses significant ground in the tropics, marking a global shift towards seasonal risk as the tropics eventually become too hot for transmission. Complete mitigation of climate change to a pre-industrial baseline could protect almost a billion people from arbovirus range expansions; but middle-of-the-road mitigation may actually increase exposure, especially for viruses mainly transmitted by *Aedes albopictus* (such as chikungunya). Mitigating climate change also shifts the burden of both dengue and chikungunya (and potentially other Aedes viruses) from higher-income regions back onto the tropics where transmission might otherwise be curbed by rising temperatures.

#### Introduction

Climate change will almost certainly have a profound effect on the global distribution and burden of infectious diseases [1–3]. Current knowledge suggests that the range of mosquitoborne diseases could expand dramatically in response to climate change [4,5]. However, the physiological and epidemiological relationships between mosquito vectors and the environment are complex and often non-linear, and experimental work has showed an idiosyncratic relationship between warming temperatures and disease transmission [6,7]. In addition, pathogens can be vectored by related species, which may be sympatric, or several pathogens may be transmitted by the same vector. Accurately forecasting the potential impacts of climate change on *Aedes*-borne viruses—which include widespread threats like dengue and yellow fever, as well as several emerging threats like chikungunya and Zika—thus becomes a key problem for public health preparedness [4,8,9]. In this paper, we compare the roles and impact of two vectors, *Aedes aegypti* (the primary vector of dengue virus around the world) and *Aedes albopictus* (the primary vector of chikungunya virus in its recent emergence), in their contribution to potential transmission landscapes in a changing climate.

The intensification and expansion of vector-borne disease is likely to be one of the most significant threats posed by climate change to human health [2,10]. Mosquito vectors are of special concern, due to the global morbidity and mortality from diseases like malaria and dengue fever, as well as the prominent public health crises caused by (or feared from) several recently-emergent viral diseases like West Nile, chikungunya, and Zika. The relationship between climate change and mosquito-borne disease is perhaps best studied, in both experimental and modeling work, for malaria and its associated *Anopheles* vectors. While climate change could exacerbate the burden of malaria at local scales, more recent evidence challenges the "warmer-sicker world" expectation [11,12]. The optimal temperature for malaria transmission has recently been demonstrated to be much lower than previously expected [13], likely leading to net decreases in optimal habitat at continental scales in the coming decades [12].

Relative to malaria, less is known about the net impact of climate change on *Aedes*-borne diseases. At a minimum, the distribution of *Aedes* mosquitoes is projected to shift in the face of climate change, with a mix of expansions in some regions and contractions in others, and no overwhelming net global pattern of gains or losses [3,8]. Ecophysiological differences between *Aedes* vector species are likely to drive differences in thermal niches, and therefore different

distributions of transmission risk [6,14], now and in the future. The consequences of those range shifts for disease burden are therefore likely to be important, but are challenging to summarize across landscapes and pathogens. Of all *Aedes*-borne diseases, dengue fever has been most frequently modeled in the context of climate change, and several models of the potential future of dengue have been published over the last two decades, with some limited work building consensus among them [4]. Models relating temperature to vectorial capacity (the number of new infectious mosquito bites generated from a human case), and applying general circulation models (GCMs) to predict the impacts of climate change, date back to the late 1990s [5]. A study from 2002 estimated that the population at risk (PAR) from dengue would rise from 1.5 billion in 1990, to 5-6 billion by 2085, as a result of climate change [15]. A more recent study suggested that climate change alone should increase the global dengue PAR by 0.28 billion by 2050, but accounting for projected changes in global economic development (using GDP as a predictor for dengue risk) surprisingly reduces the projected PAR by 0.12 billion over the same interval [16]. Mechanistic models have shown that increases or decreases in dengue risk can be predicted for the same region based on climate models, scenario selection, and regional variability [17].

Chikungunya and Zika viruses, which have emerged more recently as a public health crisis, are less well-studied in the context of climate change. A monthly model for chikungunya in Europe, constrained by the presence of *Ae. albopictus*, found that the A1B and B1 scenarios both correspond to substantial increases in chikunguya risk surrounding the Mediterranean [18]. A similar modeling study found that dengue is likely to expand far more significantly due to climate change than Zika [9] (though epidemiological differences among these three viruses remain unresolved [19–21]). However, the combined role of climate change and El Niño has already been suggested as a possible driver of the 2016 Zika pandemic's severity [9]. Global mechanistic forecasts accounting for climate change are all but nonexistent for both chikungunya and Zika, given how recently both emerged as public health crises, and how much critical information is still lacking in the basic biology and epidemiology of both pathogens.

In this study, we apply a new mechanistic model of the spatiotemporal distribution of *Aedes*-borne viral outbreaks to resolve the role climate change could play in the emergence of diseases like dengue, chikungunya, and Zika. Whereas other mechanistic approaches often rely on methods like dynamic energy budgets to build complex biophysical models for *Aedes* mosquitoes [22,23], and subsequently (sometimes) extrapolate potential epidemiological

dynamics [5], our approach uses a single basic cutoff for the thermal interval where viral transmission is possible. The simplicity and transparency of the method masks a sophisticated underlying model that links the basic rate of reproduction  $R_0$  for Aedes-borne viruses to temperature, via experimentally-determined physiological response curves for traits like biting rate, fecundity, mosquito lifespan, extrinsic incubation rate, and transmission probability [6]. The model is easily projected into geographic space by defining model-based measures of suitability and classifying each location in space as suitable or not; we take a Bayesian approach in order to take into account uncertainty in the experimental data. This threshold condition defines the temperatures at which transmission is not prevented, rather than the more familiar threshold at which disease invasion is expected ( $R_0 > 1$ , which cannot be predicted in the absence of assumptions about vector and human population sizes and other factors). We then classify each location by suitability in each month based on already published projections for current climates in the Americas [6].

Here, we expand the framework for both *Ae. aegypti* and *Ae. albopictus* to project cumulative months of suitability in current and future (2050 and 2080) climates, and further examine how global populations at risk might change in different climate change scenarios. We explore variation among both climate model selection (general circulation models; GCMs), and potential emissions pathways described in the IPCC 5 (representative concentration pathways; RCPs). In doing so, we provide the first mechanistic forecast for the potential future transmission risk of chikungunya and Zika, which have been forecasted primarily via phenomenological methods (like ecological niche modeling [9]). Our study is also the first to address the seasonal aspects of population at risk for *Aedes*-borne diseases in a changing climate.

### Methods

#### The Bayesian Model

Our study presents geographic projections of published experimentally-derived mechanistic models of viral transmission by *Aedes aegypti* and *Aedes albopictus*. The approach to fit the thermal responses in a Bayesian framework and combine them to obtain the posterior distribution of  $R_0$  as a function of these traits is described in detail in Johnson *et al.* [7] and the particular traits and fits for *Aedes aegypti* and *Ae. albopictus* are presented in Mordecai *et al.* [24]. In the original modeling study, the underlying data was compiled on transmission of

dengue virus by both mosquito species, and the models for each mosquito were subsequently validated on data compiled for three viruses (dengue, chikungunya, and Zika). Once we obtain our posterior samples for  $R_0$  as a function of temperature we can evaluate the probability that  $R_0$ > 0 (Prob $(R_0 > 0)$ ) at each temperature, giving a distinct curve for each mosquito species. We then define cutoff of  $Prob(R_0 > 0) = \alpha$  to determine our estimates of the thermal niche; here, we use  $\alpha = 0.975$ . This very high probability allows us to isolate a temperature window for which transmission is almost certainly not excluded; this provides a conservative approach. For Aedes aegypti, these bounds are 21.3—34.0 °C, and for Aedes albopictus, 19.9—29.4 °C. **Current & Future Climates** Current mean monthly temperature data was derived from the WorldClim dataset (www.worldclim.org) [25] For future climates, we selected four general circulation models (GCMs) that are most commonly used by studies forecasting species distributional shifts, at a set of four representative concentration pathways (RCPs) that account for different global responses to mitigate climate change. These are the Beijing Climate Center Climate System Model (BCC-CSM1.1); the Hadley GCM (HadGEM2-AO and HadGEM2-ES); and the National Center for Atmospheric Research's Community Climate System Model (CCSM4). Each of these can respectively be forecasted for RCP 2.6, RCP 4.5, RCP 6.0 and RCP 8.5. RCP numbers correspond to increased radiation in  $\ensuremath{W/m^2}$  by the year 2100, therefore expressing scenarios of increasing severity. (However, even these scenarios are nonlinear over time; for example, in 2050, RCP 4.5 is a more severe change than 6.0.) Climate model output data for future scenarios were acquired from the research program on Climate Change, Agriculture, and Food Security (CCAFS) web portal (http://ccafs-climate.org/data\_spatial\_downscaling/), part of the Consultative Group for International Agricultural Research (CGIAR). We used the model outputs created using the delta downscaling method, from the IPCC AR5. For visualizations presented in the main paper (Figure 2), we used the HadGEM2-ES model, the most commonly used GCM. The mechanistic transmission model was projected onto the climate data using the 'raster' package in R 3.1.1. Subsequent visualizations were generated in ArcMap.

## Population at Risk

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To quantify a measure of risk, comparable between current and future climate scenarios, we used population count data from the Gridded Population of the World, version 4 (GPW4) [26], predicted for the year 2015. We selected this particular population product as it is minimally modeled *a priori*, ensuring that the distribution of population on the earth's surface has not been predicted by modeled covariates that would also influence our mechanistic vector-borne disease model predictions. These data are derived from most recent census data, globally, at the smallest administrative unit available, then extrapolated to produce continuous surface models for the globe for 5-year intervals from 2000-2020. These are then rendered as globally gridded data at 30 arc-seconds; we aggregated these in R ('raster'<sup>30</sup>) to match the climate scenario grids at 5 minute resolution (approximately 10 km<sup>2</sup> at the equator). We used 2015 population count as our proxy for current, and explored future risk relative to the current population counts. This prevents arbitrary demographic model-imposed patterns emerging, possibly obscuring climategenerated change. We note that these count data reflect the disparities in urban and rural patterns appropriately for this type of analysis, highlighting population dense parts of the globe. Increasing urbanization would likely amplify the patterns we see, as populations increase overall, and the lack of appropriate population projections at this scale for 30-50 years in the future obviously limits the precision of the forecasts we provide. We thus opted for a most conservative approach. We finally subdivide global populations into geographic and socioeconomic regions as used by the Global Burden of Disease studies (Figure S1) [28].

## **Results**

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The current pattern of suitability suggested by our model based on mean monthly temperatures (**Figure 1**) reproduces the known or projected distributions of dengue [29], chikungunya [30], and Zika [9,31,32] well. For both *Ae. aegypti* and *Ae. albopictus*, most of the tropics is currently optimal for viral transmission year-round, with suitability declining along latitudinal gradients. Many temperate regions are suitable for up to 6 months of the year currently, but outside the areas mapped as "suitable" by previous disease-specific distribution models, or where *Aedes* mosquitoes are established; in some cases, limited outbreaks may only happen when cases are imported from travelers (e.g. in northern Australia, where dengue is not presently endemic but outbreaks happen in suitable regions [17]; or in mid-latitude regions of the United States, where it has been suggested that traveler cases could result in limited autochthonous transmission

[31,33]). In total, our model predicts that 6.01 billion people currently live in areas suitable for *Ae. aegypti* transmission at least part of the year (i.e., 1 month or more) and 6.33 billion in areas suitable for *Ae. albopictus* transmission (using mean temperatures).

Even by 2050, warming temperatures are expected to produce dramatic expansions of *Aedes* transmission risk (**Figure 2**). For *Aedes aegypti*, the pattern is (visually, even) fairly straightforward: major expansions of one- or two-month transmission risk in temperate regions are paired with expansion of year-round transmission in the tropics, even into the high-elevation regions that were previously protected. *Aedes albopictus* transmission risk similarly expands majorly (more so, even) into temperate regions, especially high latitude parts of Eurasia and North America. But the upper thermal limits to *Aedes albopictus* transmission are passed in many places, producing major reductions in regions of seasonal risk (like North Africa) and year-round suitability (northern Australia, the Amazon basin, central Africa and southern Asia). Whereas the conventional tropical-temperate gradient of mosquito-borne transmission is preserved for *Aedes aegypti*, warming becomes so severe in the tropics that year-round *Aedes albopictus* starts to look more unfamiliar, especially in the more extreme climate pathways. By 2080, year-round transmission by *Ae. albopictus* is mostly confined to high elevation regions, southern Africa, and the Atlantic coast of Brazil; and even *Aedes aegypti* has begun to lose some core area of year-round transmission in the Amazon basin especially.

Globally, our models suggest a net increase in population at risk from *Aedes*-borne virus exposure, closely tracking the global rise in mean temperatures (**Figure 3**). For both mosquitoes, populations at risk of any exposure will experience a major net increase by 2050, on the order of roughly half a billion people; but even then, increases are more severe for *Ae. aegypti* than for *Ae. albopictus*. But by 2080, the differences between the mosquitoes produce a different result: while more severe warming continues to increase exposure for *Ae. aegypti*, up to nearly a billion net new exposures, the most extreme expansions for *Ae. albopictus* are in middle of the road scenarios (RCP 4.5 and 6.0). For year-round exposure, net changes tell an even more different story between the two mosquitoes. For *Ae. aegypti*, warming temperatures lead to a net increase of roughly 100-300 million people in areas of year-round transmission; though in fact, in RCP 8.5 by 2080, some parts of the tropics become so warm that even *Ae. aegypti* is no longer able to transmit. But even by 2050 in the mildest scenarios, there are drastic net losses of year-round

transmission for *Aedes albopictus*, and these only become more severe – approaching roughly 700 million – in the warmest timelines.

Breaking these results down by region (**Table 1 & 2**) highlights just how much regional velocity of climate change is likely to determine future disparities in global health. For *Aedes aegypti*, the most notable net increases in all transmission risk are in all regions of Europe, with additional notable gains in east Asia, high-elevation parts of central America and east Africa, and the United States and Canada. But increases are expected across the board except in the Caribbean, where minor net losses are expected across scenarios and years. In contrast, for *Aedes albopictus*, there are much more regionally-variable changes anticipated. Major gains in Europe are again expected across the board, as well as less significant increases in central America, east Africa and east Asia, and the U.S. and Canada. But major net losses are also expected in several regions, including tropical Latin America, western Africa, south Asia and most of all southeast Asia, with a net loss of nearly 125 million people at risk by 2080 in RCP 8.5. In some cases, as for western Africa and southeast Asia, the difference between RCP 6.0 and 8.5 is on the order of 50 and 100 million people respectively, highlighting just how large a (negative) difference minor levels of climate mitigation might make in those regions.

For year-round transmission, the patterns are again less straightforward (**Table S1 & S2**), but overall, they highlight a global shift towards more seasonal risk for both mosquitoes, especially in the warmest scenarios. For *Aedes aegypti*, some of the largest net gains in people at risk are expected in southern Africa, with additional notable increases expected in Latin America. But even for *Ae. aegypti*, warming temperatures exceed levels suitable for year-round transmission in some cases; for example, of all pathways, RCP 4.5 leads to the most severe increases in southern Asia. Overall, almost 600 million people will move into areas with year-round suitability for transmission, though the net increase will be much less (**Table S3**). For *Aedes albopictus*, major net losses are expected in south and southeast Asia (totaling more than 400 million with the most extreme warming), and additional losses are expected in east Africa and Latin America. Only the southern part of sub-Saharan Africa consistently experiences net gains in year-round transmission risk; but gross increases are also expected in several regions, most of all east Africa, moving roughly 250 million people into areas of year-round transmission despite nearly triple that number in net losses.

We finally consider the idea of "first exposures" separately (gross gains, not accounting for losses), which may be the most epidemiologically significant form of exposure. As the 2005 epidemic of chikungunya in India and the 2015 pandemic of Zika virus in the Americas highlight, arboviral introductions into naïve populations can produce atypically severe outbreaks on the order of millions of infections. We rank regions by these first exposures (**Table 3**), and we find that consistently the most significant new exposures are expected in Europe and east Africa for both mosquitoes, confirming fears that both regions may—as a consequence of climate change, if not currently—be at risk from these types of black swan outbreaks. With an outbreak of chikungunya virus in Kenya concurrent to the development of this study, these results seem especially prescient.

#### **Discussion**

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The dynamics of mosquito-borne illnesses are climate driven, and current work mostly suggests that climate change will create massive opportunities for the expansion and intensification of Aedes-borne illnesses within the next century. Especially since the emergence of Zika in the Americas, many modeling studies have anticipated climate-driven emergence of dengue and chikungunya at higher latitudes [34,35] and higher elevations [36,37]. Within this literature, there have been several global studies of potential expansion [9,17,38], as well as significant focused interest in North America and Europe (perhaps reflecting geographic biases in research priorities and research institutions) [39]. The vast majority of this work has suggested that climate change will probably increase the global burden of morbidity and mortality from dengue and chikungunya, and therefore, that mitigation will likely improve global health outcomes [40,41]. Perhaps most concerning are fears that Aedes-borne viruses will be introduced into regions that have previously been unsuitable for transmission, given the potential for explosive outbreaks (like Zika in the Americas, or chikungunya in India) when viruses are first introduced into naïve populations [42]. The emergence of a Zika pandemic in the Old World [43], the establishment of chikungunya in Europe beyond small outbreaks [18], or introduction of dengue anywhere the virus (or any given serotype) has not recently been found, is still a critical concern.

Overall, our findings support the general view that climate change will produce major

expansions of Aedes-borne viral transmission risk. However, we also find more nuanced patterns

emerging between the two species, and among different climate pathways. The largest increases in population at risk are consistently in Europe, with additional increases in high altitude regions in the tropics (eastern Africa and the northern Andes) and in the United States and Canada. These increases are expected not only for occasional exposure, but also for longer seasons of transmission, especially for *Ae. aegypti*. But mosquitoes are adapted to their existing climatic range, and while viral transmission will surely track warming temperatures into new places over some intervals, there is no reason to think warming temperatures would produce a unilateral and indefinite increase in disease transmission. Here we show that in the tropics, for *Aedes albopictus* in particular, more extreme climate pathways produce warming temperatures that exceed the suitable range for transmission in many parts of the world; and in the long term, even though total exposure may increase from both mosquitoes in our study, we predict a global shift towards seasonal regimes of exposure from *Aedes albopictus* and therefore, probably, chikungunya.

As warming temperatures may begin to exceed the upper thermal bounds of transmission, this produces an unexpected problem in terms of climate change mitigation. Total mitigation (down to pre-industrial baselines) would presumably prevent this redistribution of global risk. But partial mitigation of climate change, i.e. less severe RCPs, could keep *Ae. albopictus* mosquitoes especially within optimal thermal ranges for more of the year, and thereby produce worse clinical outcomes. If our model continues to appropriately predict thermal bounds of viral transmission into the future, this suggests a potential tradeoff in global health priorities, where the scenarios that mitigate global dengue exposure, for example, might come with expanded risk of chikungunya. But it is also unlikely that decisions about climate change mitigation will strictly be decided based on global health priorities, given the already insufficient response to curb carbon emissions and keep temperatures below the 2° C target [44]. In light of this, models such as the ones we present here are probably most useful as a means to anticipate possible futures, depending on the degree of mitigation achieved.

These global disease futures are inherently and incredibly stochastic, and the degree to which our models correspond to reality depend not only on uncertainty about climate change, but uncertainty about the biotic homogenization process for disease. For example, reductions in transmission may be less prevalent than we expect here, as—even accounting for the velocity of climate change—viruses will probably have sufficient time to adapt to warming temperatures (within whatever evolvability they possess). Increases in transmission risk are also complicated

by many factors, such as the presence or absence of *Aedes* mosquitoes, which are also undergoing their own semi-independent range shifts facilitated by both climate change and human movement; our model already describes areas where *Aedes albopictus* and *Ae. aegypti* are absent but could be present in the future (and even now the ranges of these mosquitoes are not static, by any standard). Whether expanding transmission risk leads to future establishment and viral outbreaks depends not only on disease introduction, but also on land use patterns and urbanization at regional scales, a fact that may ultimately buffer some high-elevation regions like the Andes from increased disease risk [45,46].

In practice, these models are a first step towards an adequate understanding of potential global health futures, and the forecast horizon of these models will ultimately be determined by a number of confounding factors [47,48]. In particular, the link from transmission risk to clinical outcomes is confounded by other health impacts of climate change, including changing precipitation patterns, socioeconomic development, changing patterns of land use and urbanization, potential vector (and virus) evolution and adaptation to warming temperatures, and changing healthcare and vector management landscapes, all of which covary strongly (potentially leading to nonlinearities). Moreover, human adaptation to climate change will matter just as much as mitigation in determining how risk patterns shift; for example, increased drought stress will likely encourage water storage practices that increase proximity to *Aedes* breeding habitat [49]. Together these will determine the burden of *Aedes*-borne outbreaks, in ways that determine the eventual relevance of the forecasts we present here.

These models are certainly not the only ones to address this pressing topic, and different approaches control for data limitations, confounding processes, climate model uncertainty and disease model uncertainty, different concepts of population at risk, and preferences towards experimental, mechanistic, or phenomenological approaches differently. While climate change poses perhaps the most serious growing threat to global health security, the relationship between climate change and worsening clinical outcomes for *Aedes*-borne diseases is unlikely to be straightforward, and no single model will accurately predict the complex process of a global regime shift in *Aedes*-borne viral transmission. Our models only set an outer spatiotemporal bound to where transmission is thermally plausible; climate change is likely to change the risk-burden relationship at fine scales within those zones of transmission in nonlinear ways, such that areas with shorter seasons of transmission could still experience worse overall disease burdens,

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or vice versa. Combining broad spatial models with finer-scale models of attack rates or outbreak size is a critical step towards bridging scales [43,50], but more broadly, research building consensus between all available models is of paramount importance [51]. This task is not limited to research on dengue and chikungunya; with several emerging flaviviruses on the horizon [52,53], and countless other emerging arboviruses likely to test the limits of public health infrastructure in coming years [54], approaches like ours that bridge the gap between experimental biology and global forecasting can be one of the foundational methods of anticipating and preparing for the "Next Big One." Acknowledgements This work was funded by the National Science Foundation (DEB-1518681 to SJR, LRJ, EAM, NSF DEB-1641145 to SJR, and DEB-1640780 to EAM), and CDC grant 1U01CK000510-01: Southeastern Regional Center of Excellence in Vector-Borne Diseases: the Gateway Program, to SJR. This publication was supported by the Cooperative Agreement Number above from the Centers for Disease Control and Prevention. Its contents are solely the responsibility of the authors and do not necessarily represent the official views of the Centers for Disease Control and Prevention. Support was also provided by the Stanford Woods Institute for the Environment (https://woods.stanford.edu/research/environmental-venture-projects), and the Stanford Center for Innovation in Global Health (http://globalhealth. stanford.edu/research/seed-grants.html). Van Savage, Naveed Heydari, Jason Rohr, Matthew Thomas, and Marta Shocket provided helpful discussions on modeling approaches. **Author Information** The authors declare no competing interests. Correspondence and requests for materials should be addressed to S.J.R. (sjryan@ufl.edu). **Author Contributions** SJR and LJ ran the models, and CJC and SJR ran the analyses. CJC, SJR, EAM, and LJ wrote the manuscript. CJC and SJR made the figures.

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## **Figures and Tables**

**Figure 1** | **Mapping current transmission risk.** Maps of current monthly suitability based on mean temperatures for a temperature suitability threshold corresponding to the posterior probability that scaled  $R_0 > 0$  is 97.5% for (a) *Aedes aegypti* and (b) *Aedes albopictus*, and (c) the number of people at risk (in billions) as a function of their months of exposure for *Aedes aegypti* and *Aedes albopictus*.

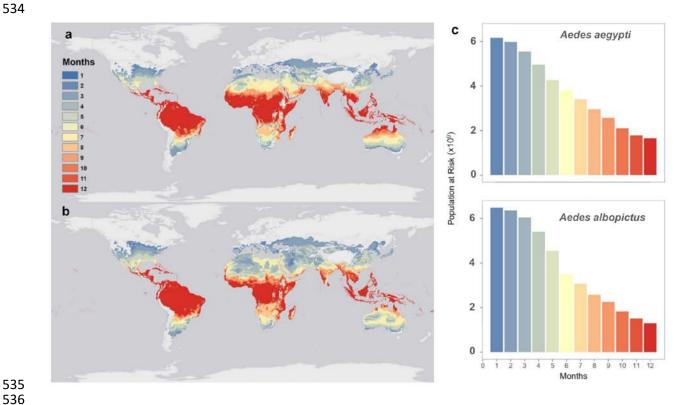
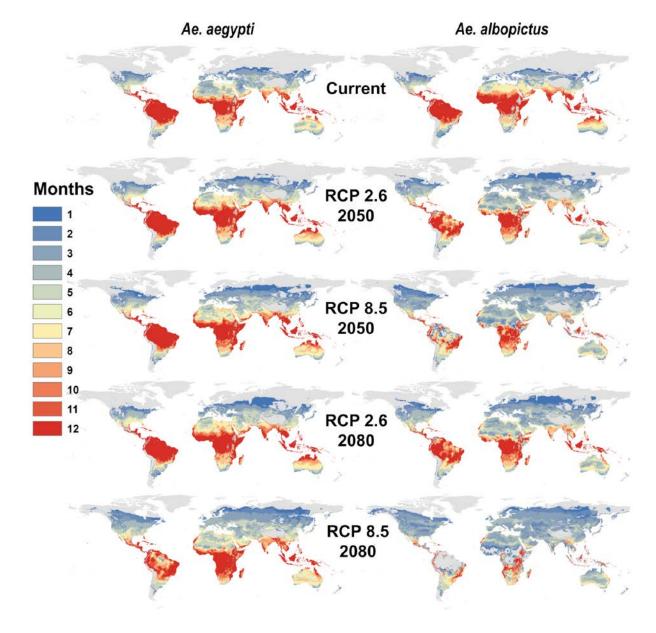
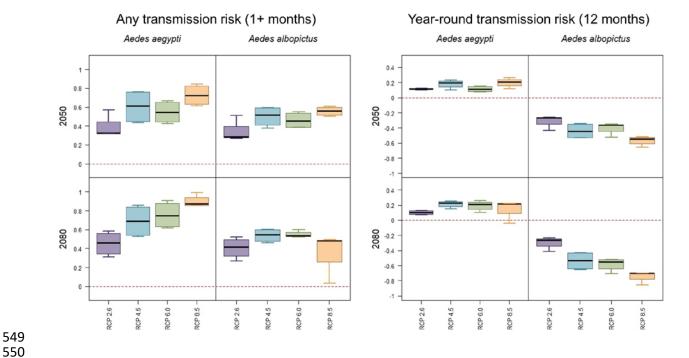


Figure 2 | Mapping future transmission risk scenarios for *Aedes aegypti and Aedes albopictus*. Maps of monthly suitability based on a temperature threshold corresponding to the posterior probability that scaled  $R_0 > 0$  is greater or equal to 97.5%, for transmission by *Aedes aegypti* and *Aedes albopictus* for predicted mean monthly temperatures under current climate and future scenarios for 2050: RCP 2.6 and RCP 8.5 in HadGEM2-ES.



**Figure 3** | **Projected net changes in population at risk**. Projections are given as the net difference in billions at risk, for *Aedes aegypti* and *Aedes albopictus* transmission, between current maps and 2050 (top row) or 2080 (bottom row). Results are further broken down by representative climate pathways (RCPs), each averaged across 4 general circulation models.



**Table 1. Changing population at risk patterns for** *Aedes aegypti.* All values are given in millions; future projections are averaged across GCMs, broken down by year (2050, 2080) and RCP (2.6, 4.5, 6.0, 8.5), and are given as net change from current population at risk. 0+/0- denote the sign of smaller non-zero values that rounded to 0.0, whereas "0" denotes true zeros.

Dogion	C		20	50		2080			
Region	Current	2.6	4.5	6.0	8.5	2.6	4.5	6.0	8.5
Asia (Central)	69.9	8.4	10.5	9.9	12.2	8.1	11.8	12.5	15.6
Asia (East)	1,321.9	42.5	49.2	46.4	58.9	38.8	56.7	61.9	72.7
Asia (High Income Pacific)	164.0	-0.5	0+	-0.5	0.7	-0.6	0.6	1.0	1.7
Asia (South)	1,666.4	-0.1	1.6	0.7	3.7	-0.5	3.4	4.3	8.2
Asia (Southeast)	593.9	-2.1	0+	-0.6	2.3	-2.4	1.6	2.6	5.5
Australasia	12.9	3.6	5.7	5.3	6.7	4.3	6.2	6.9	8.0
Caribbean	40.4	-1.8	-1.7	-1.7	-1.6	-1.8	-1.6	-1.6	-1.5
Europe (Central)	22.7	44.2	71.8	69.0	83.3	59.0	79.3	85.5	90.6
Europe (Eastern)	41.3	57.9	110.4	93.5	133.9	80.0	124.7	130.7	156.2
Europe (Western)	114.6	47.2	132	112.0	166.8	90.3	156.4	180.8	220.9
Latin America (Andean)	31.3	2.8	3.4	3.3	4.0	2.6	3.9	4.1	5.5
Latin America (Central)	160.3	20.4	24.6	23.4	36	18.4	34.6	39.0	61.1
Latin America (Southern)	42.8	8.1	8.9	8.8	9.9	7.6	9.6	10.2	12.8
Latin America (Tropical)	181.8	19.2	19.5	19.5	19.6	18.9	19.6	19.7	19.8
North Africa & Middle East	439.5	19.7	24.1	23.8	27.2	19.3	25.9	27.3	30.3
North America (High Income)	281.9	36.2	48.3	42.6	55.0	37.8	53.6	57.1	62.8
Oceania	6.2	0.3	0.6	0.5	0.8	0.2	0.8	0.9	1.5
Sub-Saharan Africa (Central)	115.6	5.7	6.8	6.5	7.8	5.3	7.7	8.3	9.5
Sub-Saharan Africa (East)	274.8	48.8	63.7	59.1	72.2	44.7	70.8	76.6	90.9
Sub-Saharan Africa (Southern)	46.1	23.6	25.8	25.6	26.7	23.4	26.7	27.1	28.0
Sub-Saharan Africa (West)	384.0	-0.9	-0.7	-0.8	-0.7	-0.9	-0.6	-0.6	-0.4

**Table 2. Changing population at risk patterns for** *Aedes albopictus*. All values are given in millions; future projections are averaged across GCMs, broken down by year (2050, 2080) and RCP (2.6, 4.5, 6.0, 8.5), and are given as net change from current population at risk. 0+/0- denote the sign of smaller non-zero values that rounded to 0.0, whereas "0" denotes true zeros.

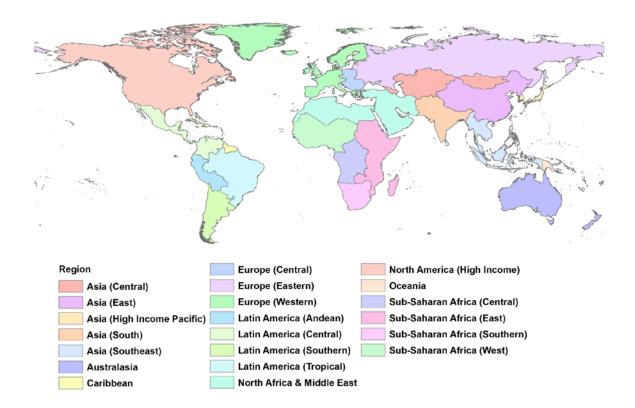
Dogion	C		20	50		2080			
Region	Current	2.6	4.5	6.0	8.5	2.6	4.5	6.0	8.5
Asia (Central)	75.7	5.0	6.9	6.4	8.8	4.7	8.1	9.1	11.2
Asia (East)	1,367.0	16.1	20.8	18.9	25.2	15.0	24.0	26.5	32.4
Asia (High Income Pacific)	167.7	-2.6	-2.3	-2.6	-2.0	-2.7	-2.1	-1.9	-2.8
Asia (South)	1,673.8	-3.2	-1.7	-2.3	0+	-3.5	-0.5	-0.3	-19.1
Asia (Southeast)	602.5	-5.3	-3.8	-4.0	-6.7	-5.4	-8.5	-20.1	-124.8
Australasia	16.6	3.2	3.9	3.8	4.5	3.3	4.2	4.7	5.3
Caribbean	40.8	-1.8	-1.8	-1.8	-1.8	-1.9	-1.8	-1.8	-2.3
Europe (Central)	44.8	51.3	65.0	65.1	68.3	60.6	67.8	68.9	70.7
Europe (Eastern)	70.4	84.0	116.6	104.2	123.1	101.4	122.0	123.3	129.9
Europe (Western)	135.3	98.5	179.8	161.4	208.9	149.2	199.4	215.3	243.0
Latin America (Andean)	33.9	1.6	2.2	2.0	2.6	1.6	2.6	2.7	2.5
Latin America (Central)	179.1	21.9	27.0	27.9	31.1	17.6	29.7	30.3	23.6
Latin America (Southern)	50.4	3.2	3.6	3.6	4.8	2.8	4.2	4.9	7.6
Latin America (Tropical)	203.0	-1.5	-2.0	-1.6	-6.0	-1.5	-5.6	-8.0	-26.3
North Africa & Middle East	455.0	10.6	13.0	12.9	14.2	10.4	13.5	14.1	11.8
North America (High Income)	311.6	20.6	28.4	26.0	32.1	22.6	31.6	32.3	34.7
Oceania	6.8	0.5	0.8	0.6	1.0	0.4	0.9	1.0	0.8
Sub-Saharan Africa (Central)	120.8	2.8	3.5	3.3	4.2	2.5	4.1	4.4	-3.8
Sub-Saharan Africa (East)	320.2	30.3	39.1	36.3	42.4	27.9	41.8	42.8	34.2
Sub-Saharan Africa (Southern)	70.1	3.4	3.8	3.8	3.9	3.4	4.0	4.0	4.3
Sub-Saharan Africa (West)	384.9	-1.4	-1.5	-1.5	-2.0	-1.4	-1.9	-3.5	-59.0

**Table 3. Top 10 regional increases in overall transmission risk (one or more months).** Regions are ranked based on millions of people exposed for the first time to any transmission risk; parentheticals give the net change (first exposures minus populations escaping transmission risk). All values are given for the worst-case scenario (RCP 8.5) in the longest term (2080).

Aedes aegypti		Aedes albopictus				
1. Europe (Western)	224 (220.9)	1. Europe (Western)	246.2 (243)			
2. Europe (Eastern)	156.4 (156.2)	2. Europe (Eastern)	130.1 (129.9)			
3. Sub-Saharan Africa (East)	92.8 (90.9)	3. Europe (Central)	71 (70.7)			
4. Europe (Central)	90.9 (90.6)	4. Sub-Saharan Africa (East)	58.1 (34.2)			
5. Asia (East)	81.7 (72.7)	5. Latin America (Central)	51.9 (23.6)			
6. North America (High Income)	65.7 (62.8)	6. Asia (East)	41.4 (32.4)			
7. Latin America (Central)	62 (61.1)	7. North America (High Income)	37.7 (34.7)			
8. North Africa & Middle East	34.3 (30.3)	8. North Africa & Middle East	19.4 (11.8)			
9. Sub-Saharan Africa (Southern)	28 (28)	9. Asia (South)	12.1 (-19.1)			
10. Latin America (Tropical)	21.7 (19.8)	10. Asia (Central)	11.2 (11.2)			
Total (across all 21 regions)	951.3 (899.7)	Total (across all 21 regions)	721.1 (373.9)			

## **Supplementary Figures & Tables**

**Figure S1. Global health regions.** We adopt the same system as the Global Burden of Disease Study in our regional breakdown.



**Table S1.** Changing year-round (12 month) population at risk patterns for *Aedes aegypti*. All values are given in millions; future projections are averaged across GCMs, broken down by year (2050, 2080) and RCP (2.6, 4.5, 6.0, 8.5), and are given as net change from current population at risk. 0+/0- denote the sign of smaller non-zero values that rounded to 0.0, whereas "0" denotes true zeros. (Losses do not indicate loss of any transmission, only to reduction 11 or fewer months.).

Dogion	C		2050				2080			
Region	Current	2.6	4.5	6.0	8.5	2.6	.6 4.5	6.0	8.5	
Asia (Central)	0	0	0	0	0	0	0	0	0	
Asia (East)	0+	1.4	1.8	1.1	3.7	1.6	4.5	4	8.3	
Asia (High Income Pacific)	3.6	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	-0.2	
Asia (South)	286.4	21.8	71.8	13.7	73.6	12.1	89.7	72.6	29.6	
Asia (Southeast)	499.4	19.2	22.4	19.9	25.1	18.9	26.3	15.4	-10.3	
Australasia	0.2	0+	0+	0+	0.1	0+	0.2	0.2	0.3	
Caribbean	34.8	1.8	2.2	2.1	2.8	1.7	2.6	2.9	3.3	
Europe (Central)	0	0	0	0	0	0	0	0	0	
Europe (Eastern)	0	0	0	0	0	0	0	0	0	
Europe (Western)	0	0	0	0	0	0	0	0	0+	
Latin America (Andean)	14.0	3.9	4.8	4.6	5.7	3.5	5.4	5.8	7.5	
Latin America (Central)	88.1	13.0	18.8	17.0	25.8	12.0	24.4	27.4	34.1	
Latin America (Southern)	0	0	0	0	0	0	0	0	0.2	
Latin America (Tropical)	67.5	27.2	34.5	30.8	41.5	27.3	39	42.9	54.9	
North Africa & Middle East	12.5	-5.2	-5.5	-6.0	-5.6	-4.7	-5.4	-5.4	-3.9	
North America (High Income)	0.5	0.3	0.9	0.6	1.5	0.3	1.9	1.6	5.5	
Oceania	0	0	0	0	0	0	0	0	0	
Sub-Saharan Africa (Central)	5.3	0.3	0.6	0.4	0.9	0.3	0.7	0.9	1.7	
Sub-Saharan Africa (East)	79.0	19.1	23.1	22.4	26.8	16.6	25.4	28.0	36.1	
Sub-Saharan Africa (Southern)	126.9	43.8	60.7	56.7	78.3	37.9	74.3	85.5	110.3	
Sub-Saharan Africa (West)	0	0+	0.1	0.1	0.3	0+	0.2	0.6	4.4	

**Table S2.** Changing year-round (12 month) population at risk patterns for *Aedes albopictus*. All values are given in millions; future projections are averaged across GCMs, broken down by year (2050, 2080) and RCP (2.6, 4.5, 6.0, 8.5), and are given as net change from current population at risk. 0+/0- denote the sign of smaller non-zero values that rounded to 0.0, whereas "0" denotes true zeros. (Losses do not indicate loss of any transmission, only to reduction 11 or fewer months).

Doctor	C4		2050				2080			
Region	Current	2.6	4.5	6.0	8.5	2.6	4.5	6.0	8.5	
Asia (Central)	0	0	0	0	0	0	0	0	0	
Asia (East)	1.3	1.4	-0.4	-0.5	-1	1	-0.9	-1	-1.2	
Asia (High Income Pacific)	3.6	-0.3	-0.5	-0.4	-2.9	-0.2	-2.2	-3.1	-3.6	
Asia (South)	98.3	-73	-80.3	-78.9	-87.3	-67.7	-86.1	-88.5	-92.6	
Asia (Southeast)	435.3	-133.9	-213.3	-190.9	-277.4	-131.9	-254.8	-282.7	-343.6	
Australasia	0.2	0+	0+	0+	0-	0+	0-	0-	0-	
Caribbean	39.3	-5.9	-11.7	-9.4	-17.5	-4.5	-16.1	-18.1	-28.0	
Europe (Central)	0	0	0	0	0	0	0	0	0	
Europe (Eastern)	0	0	0	0	0	0	0	0	0	
Europe (Western)	0	0	0	0	0+	0	0+	0+	0.1	
Latin America (Andean)	17.9	2	0.1	0.5	-3	1.8	-2	-3.1	-5	
Latin America (Central)	97.2	-23.2	-26.8	-25.3	-31.0	-20.8	-29.3	-31.4	-33.6	
Latin America (Southern)	0	0	0	0	0+	0	0	0+	0+	
Latin America (Tropical)	93.6	-0.8	-5.2	-6.1	-9.7	-2.9	-10.1	-12.9	-37.1	
North Africa & Middle East	2.6	0+	0+	-0.2	-0.2	0.1	0-	-0.2	-0.1	
North America (High Income)	1	2.8	1.4	1	0+	1.6	0.1	-0.2	-0.2	
Oceania	0	0	0	0	0	0	0	0	0	
Sub-Saharan Africa (Central)	5.9	0.4	0.4	0.5	0.1	0.4	0.1	0-	-1.4	
Sub-Saharan Africa (East)	96.6	8.0	5.1	6.8	-4.5	7.5	-9.1	-9.9	-45.8	
Sub-Saharan Africa (Southern)	133.5	31.9	38.8	38.8	43.4	29.7	39.5	43.9	39.2	
Sub-Saharan Africa (West)	0+	0+	0.5	0.4	1.8	0+	0.9	2	6.2	

# **Table S3. Top 10 regional increases in year-round transmission risk (12 months).** All calculations are otherwise the same as in Table 3.

Aedes aegypti		Aedes albopictus				
1. Asia (South)	209.9 (29.6)	1. Sub-Saharan Africa (East)	114.3 (39.2)			
2. Sub-Saharan Africa (East)	152.6 (110.3)	2. Latin America (Tropical)	39.7 (-37.1)			
3. Latin America (Tropical)	63.2 (54.9)	3. Latin America (Central)	38.1 (-33.6)			
4. Asia (Southeast)	44 (-10.3)	4. Sub-Saharan Africa (Central)	23.1 (-45.8)			
5. Latin America (Central)	40.7 (34.1)	5. Asia (Southeast)	16.3 (-343.6)			
6. Sub-Saharan Africa (Central)	36.6 (36.1)	6. Latin America (Andean)	8.6 (-5)			
7. Sub-Saharan Africa (West)	8.7 (-130.2)	7. Sub-Saharan Africa (Southern)	6.2 (6.2)			
8. Asia (East)	8.3 (8.3)	8. Sub-Saharan Africa (West)	2.5 (-194)			
9. Latin America (Andean)	8 (7.5)	9. North Africa & Middle East	2.4 (-0.1)			
10. North Africa & Middle East	7.4 (-3.9)	10. Oceania	2 (-1.4)			
Total (across all 21 regions)	597.2 (151.6)	Total (across all 21 regions)	256.5 (-740.8)			

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