The effect of global change on mosquito-borne disease

Lydia H V Franklinos, Kate E Jones, David W Redding, Ibrahim Abubakar

More than 80% of the global population is at risk of a vector-borne disease, with mosquito-borne diseases being the largest contributor to human vector-borne disease burden. Although many global processes, such as land-use and socioeconomic change, are thought to affect mosquito-borne disease dynamics, research to date has strongly focused on the role of climate change. Here, we show, through a review of contemporary modelling studies, that no consensus on how future changes in climatic conditions will impact mosquito-borne diseases exists, possibly due to interacting effects of other global change processes, which are often excluded from analyses. We conclude that research should not focus solely on the role of climate change but instead consider growing evidence for additional factors that modulate disease risk. Furthermore, future research should adopt new technologies, including developments in remote sensing and system dynamics modelling techniques, to enable a better understanding and mitigation of mosquito-borne diseases in a changing world.

Lancet Infect Dis 2019; 19: e302–12

Published Online June 18, 2019 http://dx.doi.org/10.1016/S1473-3099(19)30161-6

Centre for Biodiversity and Environment Research, Division of Biosciences (L H V Franklinos MSc, Prof K E Jones PhD, D W Redding PhD)**, and Institute for Global Health** (L H V Franklinos, Prof I Abubakar PhD)**, University College London, London, UK; and Institute of Zoology, Zoological Society of London, London, UK** (Prof K E Jones)

Correspondence to: Dr Lydia H V Franklinos, Centre for Biodiversity and Environment Research, Division of Biosciences, University College London, London WC1E 6BT, UK **lydia.franklinos.16@ucl.ac.uk**

The global threat of mosquito-borne disease

Diseases transmitted by arthropod vectors, such as mosquitoes and ticks, are major contributors to the global burden of infectious disease,[1] with nearly half the world's population at risk of infection with a vector-borne pathogen at any moment.[2] Mosquito-borne diseases are a key group of concern as they include both very high burden and important emerging diseases, including human malaria (around 212 million cases per year), dengue (around 96 million cases per year), chikungunya (around 693 000 cases per year), and Zika virus disease (around 500 000 cases per year; table 1).[3]

Globally, many mosquito-borne diseases are thought to be increasing in incidence and geographical distribution, with diseases both emerging in new areas[4,5] and re-emerging in regions from which they had previously been eradicated.[6,7] For example, the global incidence of dengue over the past 50 years has increased 30-times, following its spread into many new countries;[5,8,9] while, yellow fever cases are reported to be increasing again in many endemic countries, after previous dramatic declines.[7] These diseases, with their corresponding high morbidity and mortality, have the potential to exert substantial negative financial and societal effects and can dramatically inhibit the development and structure of economies, societies, and politics.[6] As a consequence, much research has focused on understanding the current and future geographical distributions of disease risk, in the context of ongoing global change, to help guide interventions and safeguard public health.[10–12]

In this context, previous research has strongly focused on modelling the direct effects of climate change on spatial and temporal disease risk,[13–15] paying less attention to other factors that are already known to interact with both climate change and vector-borne diseases, such as land-use and socioeconomics (eg, poverty, trade, and travel).[3,16,17] These additional global processes, and the interactions between them, might reasonably be shown to have a stronger immediate impact on future mosquito-borne disease burden than climate change effects.[18] This effect would mean a more complete understanding of the role of global change in modulating the spatial and temporal distributions of mosquito-borne diseases will be essential for the successful prediction and management of disease risk in the future.[19] In this Review, we assess current knowledge on the relative effect of global change processes on mosquito-borne diseases risk and examine how these have been incorporated into existing analyses. We argue that the focus on the effects of climate change is insufficient to predict future risk, considering growing evidence for the key role of other global change processes in modulating mosquito-borne diseases. We suggest an alternative approach to modelling mosquito-borne disease risk and recommend future directions for research.

Climate change as a driver of mosquito-borne disease

Narrative review

We did a narrative literature review to improve the understanding of the scope and outcome of climate-based mosquito-borne disease modelling studies, structuring the search to explore two main areas. First, because climate and climate change might affect mosquito-borne disease epidemiology via different pathways, we considered the different mechanisms examined by each study, including influencing pathogen development within the mosquito, and vector population dynamics.[20,21] For the second area, we examined how different modelling approaches, such as mechanistic and correlation-based methods, have been

	Predominant vectors by genus	Estimated or reported number of cases per annum
Malaria	*Anopheles*	212 million (range 148–304 million)
Dengue	*Aedes*	96 million (range 67–136 million)
Lymphatic filariasis	*Aedes*, *Anopheles*, and *Culex*	38·5 million (range 31·3–46·7 million)
Chikungunya	*Aedes*, *Anopheles*, *Culex*, and *Mansonia*	693 000 (Americas)
Zika virus	*Aedes*	500 000 (Americas)
Yellow fever	*Aedes* and *Haemagogus*	130 000 (range 84 000–170 000) (Africa)
Japanese encephalitis	*Culex*	42 500 (range 35 000–50 000
West Nile fever	*Culex*	2588

Data are from WHO.[1,2]

Table 1: **Number of cases of the major mosquito-borne diseases of global health significance per year**

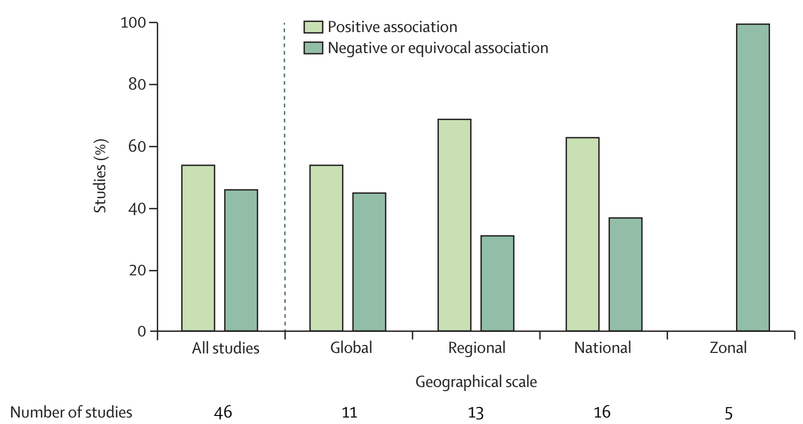

Figure 1: **The percentage of studies predicting a positive or a negative or equivocal association between climate change and mosquito-borne disease risk per geographical region following review of the effect of climate change on disease risk**

	National (%)	Regional (%)	Global (%)	Total (%)
Critical climatic thresholds and other global change drivers both excluded	24	4	8	36
Critical climatic thresholds included	16	16	4	36
Other global change drivers included	0	12	8	20
Critical climatic thresholds and other global change drivers both included	0	4	4	8

In total, 25 positive studies were included.

Table 2: **Percentage of studies that consider the influence of other global change drivers in their models and critical climatic thresholds affecting the vector competence of mosquitoes, per geographical region**

used to predict the effect of climate change on the risk of multiple mosquito-borne diseases over different geographical and temporal scales.[22] Within this search we defined climate change as an alteration (either observed or projected) in climatic parameters over several decades, with changes in mosquito-borne disease risk inferred from variations in disease incidence or vector populations.

See **Online** for appendix

Of the 234 papers identified, 46 studies met the inclusion criteria (appendix p 1–4). Overall 54% of studies showed a positive association between climate change and mosquito-borne disease risk, with increased variations in meteorological values associated with increased vector abundance or disease incidence. However, the proportion of studies showing this positive association varied depending on the geographical scale of the study (figure 1). Of those studies that predicted increased disease risk with climate change, less than half included key biological information, such as vector critical climatic thresholds, and 28% considered other global processes (table 2). Of the global change processes examined in the 46 studies, 17% included land use; 11% included human population density, of which less than half considered future human density projections; and 7% included socioeconomics (appendix p 1–4).

Temperature, precipitation, and humidity were the main parameters used to model climate change (appendix p 1–4). More than 97% of studies included the effect of temperature change in their analyses, 78% included precipitation, and 22% considered humidity. Temperature has been a predominant research focus because mosquitoes are ectothermic and ambient temperature strongly influences important epidemiological processes, including vector development, biting rates, and pathogen development within the vector.[15] Precipitation is regularly included as a parameter in models of mosquito-borne disease risk because water pools are required for mosquito development and associated humidity affects mosquito survival and flight.[23,24]

Changes in temperature, precipitation, and humidity were determined from recorded climatic data or from projected climatic values by use of different scenarios of climate change (eg, the 2014 Intergovernmental Panel on Climate Change report).[25] Regarding modelling approaches, more than 50% of the studies used correlative models to investigate statistical associations between mosquito-borne disease risk and explanatory variables.[22] Other studies used mechanistic models that incorporated biological or environmental mechanisms assumed to drive disease dynamics (eg, increased rainfall providing water pools for vector development). In addition, a few studies combined correlative and mechanistic approaches in hybrid correlative models. Mechanistic models were used more commonly in small geographical area (ie, zonal [states or districts] or national) analyses compared with correlative methods, which tended to be used for large-scale regional (ie, international) or global analyses. Most studies were prospective (ie, predicting the future), but a few were retrospective or theoretical.

The overall results indicate that no consensus exists on how changes in climatic conditions will impact mosquito-borne disease risk. This equivocal conclusion might reflect choice of modelling parameters (ie, selected climatic variables), spatial or temporal scales of the analyses, modelling approach or exclusion of important factors or biological processes from the analyses.

Climate change and mosquito-borne disease risk

The strong focus on the effects of temperature change in the field of mosquito-borne disease research[11,26–28] appears to have led to a body of international scientific reports concluding that mosquito-borne disease expansion will probably occur in parallel with climate change.[25,29] However, the conclusions are based on the assumption that temperature is a robust predictor of mosquito population dynamics, despite many temperature-dependent associations and their interactions remaining poorly defined.[14,30,31] For example, the effect of increasing temperature on physiological traits in ectotherms has been shown to be generally non-linear,[15,32] and can result in negative outcomes, such as reduced survivorship[14] and fast larval development, resulting in small adult mosquitoes.[33] Small adult mosquito body size has been associated with reductions in fecundity, blood meal size, and immunocompetence.[34] Therefore, paradoxically, increasing temperatures associated with some aspects of climate change can actually reduce the risk of transmission in certain regions via the negative effects of the increasing temperatures on vector competence (ie, the ability of vectors to become infectious).

Temperature changes also affects the time taken for pathogen development within the mosquito (ie, the extrinsic incubation period).[15,30] The extrinsic incubation period has a major impact on disease transmission because small changes in this parameter can greatly affect the number of mosquitoes that live long enough to become infectious. However, most climate-based mosquito-borne disease models do not include this parameter; furthermore, when it is included in a study it is often based on out-dated temperature-dependent models developed from a single mosquito species that do not consider the effect of other abiotic (eg, larval habitat quality) or biotic (eg, parasite competition within the mosquito) factors.[35] Studies have typically shown the extrinsic incubation period to be shortened with increasing temperature, and suggested related high infection and transmission.[36–38] However, this effect can vary considerably depending on the specific vector and pathogen.[35] For example, in vectors of the genus *Aedes*, low temperatures have been shown to shorten extrinsic incubation periods and cause high numbers of viral infections by suppressing mosquito antiviral immunity.[33] Other studies have shown that large temperature fluctuations at low mean temperatures cause shorter extrinsic incubation periods and higher infection in vectors of dengue virus[39,40] and malaria,[41] when compared with more consistent conditions. The lack of clarity about the association between the extrinsic incubation period and temperature is an essential knowledge gap that requires further empirical research to inform accurate forecasting of mosquito-borne disease risk.

There is considerable debate about how future climate change will affect precipitation trends,[42,43] but the consensus is that the frequency of extreme precipitation is likely to increase.[44] With regard to mosquito-borne diseases, increased variation in precipitation might either increase vector breeding habitat formation or reduce it via detrimental periods of drought and extreme flooding. Similar to the effects of temperature, the association between precipitation and mosquito-borne disease risk is non-linear.[27,45] Several time-lagged effects (eg, the time between water pooling and adult mosquito emergence) need to be considered in any analysis.[46] Furthermore, precipitation alone does not account for the presence of vector breeding habitat. It will also depend on species-specific preferences (eg, water depth) and hydrological factors (eg, soil type and vegetation) that control temporary water body development.[45,47] Some studies have incorporated hydrological processes into their regional disease risk models;[47–49] however, the practice has not been widely adopted, possibly because of the increased complexity needed to model these processes or infrequent collaboration between disease researchers and hydro-logical experts.

Although climate-based models have proved useful in improving the understanding of mosquito-borne disease risk at the local level[50] and over short timescales,[51] models based solely on approximating the impact of climatic factors are unlikely to be as effective over large spatial and temporal scales. We already know of other important mechanisms that affect the geographical distributions of vector populations, such as dispersal (eg, via host movement, wind, and trade routes), and biotic interactions (eg, competition and predation).[20,52,53] For instance, although the West Nile virus was theoretically able to exist in the Americas because of climatic suitability, it only spread from its original range in Africa, southern Europe, and southwest Asia, to the whole of North America in 1999, probably because of dispersal by migratory birds.[53] Likewise, *Aedes aegypti* was expected to occupy rural habitats of southern USA because of climatic suitability, but these predictions proved inaccurate when the *Aedes albopictus* vector was present.[20]

As a result, the burden of disease from mosquito-borne diseases felt by human populations is likely to be an emergent property of a set of interacting processes that will vary at different spatiotemporal scales. For instance, although climate change is likely to cause some predictable range shifts in vector species,[54] the precise effect of these changes can only be understood in the wider context of a set of non-biological factors, such as land-use change and socioeconomic development.[52] Such interactions can be additive as shown by the synergistic effects of climate change, urbanisation, international trade, and travel that have promoted the global expansion in dengue virus transmission risk.[55] Alternatively, the factors affecting mosquito-borne diseases can be subtractive as seen with the global malaria recession that has occurred in parallel with increasing urbanisation[56] and economic development.[57] The usefulness of climate-based models of mosquito-borne disease risk should not be underestimated; however, to predict distributions of mosquito-borne disease risk in the context of ongoing global change, more complex models that consider multiple global change processes are needed.[28]

The impact of land-use changes on mosquito-borne disease

Land-use change, from natural to human-dominated landscapes, is a key feature of the Anthropocene[58] and can alter disease risk by affecting the interactions between people, pathogens, vectors, and vertebrate hosts.[3,17,59–62] The immediacy and strength of land-use change impacts on local ecology[63] support the argument that land-use change could prove to be the most important driver of recent disease emergence and global spread.[3,62,64] However, the impact of land-use change on mosquito-borne disease risk will depend on several factors, including geographical region of the land and mode of the change (ie, whether it was due to deforestation, agriculture, irrigation, or urbanisation, or a combination of factors).

Deforestation

Deforestation has been associated with increased human exposure to mosquito-borne diseases by its effect on the ecology of vertebrate hosts of zoonotic pathogens, vectors, and vector-host interactions.[65,66] For example, reductions in biodiversity are associated with primary forest clearance[67] and can result in changes to the community composition of wildlife hosts[3,60,68] and emergence of infectious diseases.[64] The ability of multihost-community structures to buffer against disease outbreaks as a result of pathogen transmission dilution has been suggested in biodiverse regions.[69–71] Despite the theoretical and empirical evidence for this dilution effect being strongest for vector-borne pathogen transmission,[70,72] the generalisability of this theory remains disputed.[72–74]

Mosquito ecology is dependent on abiotic and biotic environmental conditions; as a result, land-use changes will have a significant effect on mosquito populations[21] via altering microclimates, biotic interactions (eg, predation and competition), and nutrient availability.[75] Deforestation promotes the growth of certain mosquito populations because of changes in sunlight and the pH of water pools in cleared areas.[76] For example increased sunlight following deforestation has been shown to assist mosquito survival by providing nutrients for larvae[77] and limiting entomopathogenic fungi growth.[78] Nevertheless, the effect of these changes on mosquito populations will vary depending on the specific microclimate created by the change in land use and the species' ecology.[21] Frequently, deforestation has been associated with an increased abundance of mosquitoes that act as vectors of disease, with non-vector species favouring undisturbed forest.[75,79] The mechanisms behind this remain unclear but might reflect the evolutionary processes that, due to a history of human–mosquito co-occurrence, have enabled pathogens carried by disturbance-specialist mosquito species to adapt to infect humans and proliferate in anthropogenic landscapes.[79]

Agriculture

Agricultural land, including cropland, livestock production, and irrigated land, accounts for more than 30% of the world's land use.[80] Although agricultural land conversion has led to enhanced global food production and economic development, associated mosquito-borne disease risk has increased.[2,81–87] Agricultural land has specific localised effects on important mosquito-borne disease correlates, such as livestock number and water management practices.[80] Livestock production, in particular, can modify mosquito-borne disease dynamics by increasing blood meal availability for the vectors[88] and provide competent reservoir hosts to maintain,[76,89] and even amplify,[76] zoonotic pathogens. For instance, domestic pigs are amplification hosts for Japanese encephalitis virus because the animals can mount high concentrations of the virus in their blood, which augments the proportion of infected vectors.[89,90] Indeed, pig farming is reported to be a key correlate in the prevalence of Japanese encephalitis virus in Asia.[91] Furthermore, livestock production might influence mosquito-borne diseases risk via its interaction with climate change because it contributes substantially to global greenhouse gas emissions; conversely, climate change might influence disease transmission in domestic animal populations.[44]

Irrigation and dam creation have led to marked changes in the risk of global mosquito-borne diseases, such as Japanese encephalitis, lymphatic filariasis, and malaria.[83,84,86,92,93] These practices lead to a dramatic expansion in vector breeding habitat[94] and can extend disease transmission seasons,[83] alter seasonal transmission dynamics in endemic areas,[86] and enable pathogen spread into non-endemic areas.[91,95,96] However, the effects of these schemes on vector populations are complex and depend on vector species-specific life-history traits.[21] For example, *Culex quinquefasciatus*, a major vector of lymphatic filariasis in Asia, prefers to breed in clean water whereas conspecific *Culex tritaeniorhynchus*, a principal vector of Japanese encephalitis virus, favours stagnant water.[97]

Importantly, irrigation practices can also affect the socioeconomic status of a region, which can also influence mosquito-borne disease dynamics. The so-called paddies paradox, where land conversion for irrigation leads to an initial increase and then decrease in mosquito-borne disease risk, has been reported for malaria in Africa[83] and Asia.[86] This occurrence is postulated to reflect increasing socioeconomic status in the region associated with improved crop production. Other possible mechanisms include changes in ecology that limit vector abundance[98] and reduce pathogen spread over time.[99] With future expansion of irrigation practices and dam construction expected,[93,100,101] the influence of agricultural land-use changes on disease risk requires consideration.

Urbanisation

The majority of urbanisation over the past 30 years has occurred in developing countries, where rapid and unregulated urban settlements have caused a strain on public health programmes. In 2016, 54% of the global population was reported to reside in urban areas, a substantial increase from 34% in 1960. This trend looks set to continue,[102] with 2·5 billion people predicted to increase the world's urban population by 2050, predominantly in Asia and Africa.[103] Increasing numbers of people living in high densities could lead to higher overall pathogen transmission risk for some mosquito-borne diseases;[104] additionally, high volumes of travel and trade in urban hubs can enable the spread of vectors and pathogens between population centres.[9,104–106] Nevertheless, the effect of urbanisation on mosquito-borne disease risk is complex and evidence suggests both an expansion of some disease risks and a contraction of others. For instance, urban expansion has promoted the emergence of arboviruses transmitted by *Ae aegypti*, such as dengue, chikungunya, and Zika virus (table 1),[9,106–108] by influencing resource availability and climatic factors that alter mosquito community ecology.[21] The occurrence known as the urban heat island, where urban areas experience warmer temperatures than surrounding rural areas,[109] can increase the speed of vector development.[21] In addition, the interplay between the structural complexity of urban landscapes and precipitation has been associated with greater vector numbers and several dengue outbreaks in Asia.[44] Some vectors, including *Ae aegypti* and *Ae albopictus,* are well adapted to urban areas;[110] these vectors can breed in water containers, drains, and gutters with little competition or predation.[21] However, the relative effect of urbanisation on vector populations is unlikely to be geographically uniform because urban environments represent a diverse spectrum of habitat mosaics, which vary in microclimatic features[111] and socioeconomic status.[21]

By contrast, increased urban development has also been associated with the global decrease in malaria over the past century.[56,112] However, the underlying mechanisms behind this decrease remain unclear. Urbanisation has been shown to reduce infectious disease burdens, probably via improved health care, education, and employment levels when compared with rural areas.[113] Nevertheless, reductions in disease risk can mask strong inequalities that exist within urban populations, especially in low-income and middle-income countries where urban communities with high levels of poverty show higher disease transmission than nearby rural communities.[105]

Socioeconomics and mosquito-borne disease risk

Socioeconomic factors are increasingly recognised as important drivers of mosquito-borne disease risk.[114–116] For malaria, a strong negative association exists between reported disease risk and national gross domestic product per person.[115] This association reflects either high prevalence of malaria transmission in impoverished settings, the development of poverty due to the burden of malaria on economic growth, or a combination of the two processes.[57,115] Although poverty has been cited as an important factor in the spread of several arboviruses,[116,117] there is a paucity of literature on this topic to support this hypothesis.[114] The economic burden associated with mosquito-borne diseases includes the direct costs of health provision and control programmes (eg, vaccination and vector control schemes), and indirect costs (eg, impacts on education, demographics, and human movement).[57,115] Furthermore, macroeconomic costs might occur because of the effect of disease on foreign investment, trade, and tourism.[57]

Sometimes these factors combine to impede economic development and strengthen the association between poverty and disease[57,118,119] leading to poverty traps, a self-reinforcing mechanism enabling poverty and diseases to persist.[120] Poverty traps can be accelerated by the development of synergistic diseases, referred to as syndemics, as seen with lymphatic filariasis and HIV in east Africa.[121] Escaping from poverty traps is particularly difficult for underprivileged rural populations who generally rely on subsistence agriculture, have poor access to health care, and have a high prevalence of infectious diseases. A further complexity arises when disease risk is a function of underlying production systems (eg, livestock are a major feeding resource for Rift Valley fever vectors and rice paddies are a major habitat component for Japanese encephalitis vectors). The currency of people in poverty is often biological (eg, crops and livestock, human health, and nutrition), the dynamics of which are dependent on ecological systems; as a result, economic development could be tied to the ecological processes.[119] Models representing this relationship show that poverty traps are features of coupled ecological–economic systems and within these systems, infectious diseases can limit economic growth.[119]

External intervention (eg, use of federal funds or international aid) can allow areas with high endemic disease burden to escape disease–poverty feedbacks.[122] This economic development could then act to reduce contact between people and mosquitoes via vector protection, improved housing, and environmental management (eg, larvicide treatment and vector habitat destruction).[3,123] Moreover, hazardous behaviours are often reduced, such as accessing high-risk areas for resource exploitation or settlement.[62] The weight of evidence to date suggests economic growth reduces mosquito-borne diseases risk; however, it also results in increased movement of people, animals, commodities, and accompanying pathogens and vectors via travel and trade.[9,76,124,125]

The interplay between global change processes: case studies of dengue and malaria

Despite growing convergence in the field of mosquito-borne disease research that considers interactions between global change processes,[55] these dynamics and potential resulting trade-offs that either positively or negatively affect global health,[19] are often not represented in models. Below, we outline the impact of these interactions on the global distribution of dengue, which has dramatically expanded over the past 30 years, and malaria, the incidence of which has contracted during the same period (figure 2). This comparison helps to illustrate that climate change is just one part of an overall mechanism that is changing the epidemiology of mosquito-borne diseases.

Dengue

Although climate change is known to directly influence dengue virus transmission, Messina and colleagues[128] suggested that other global change processes and their

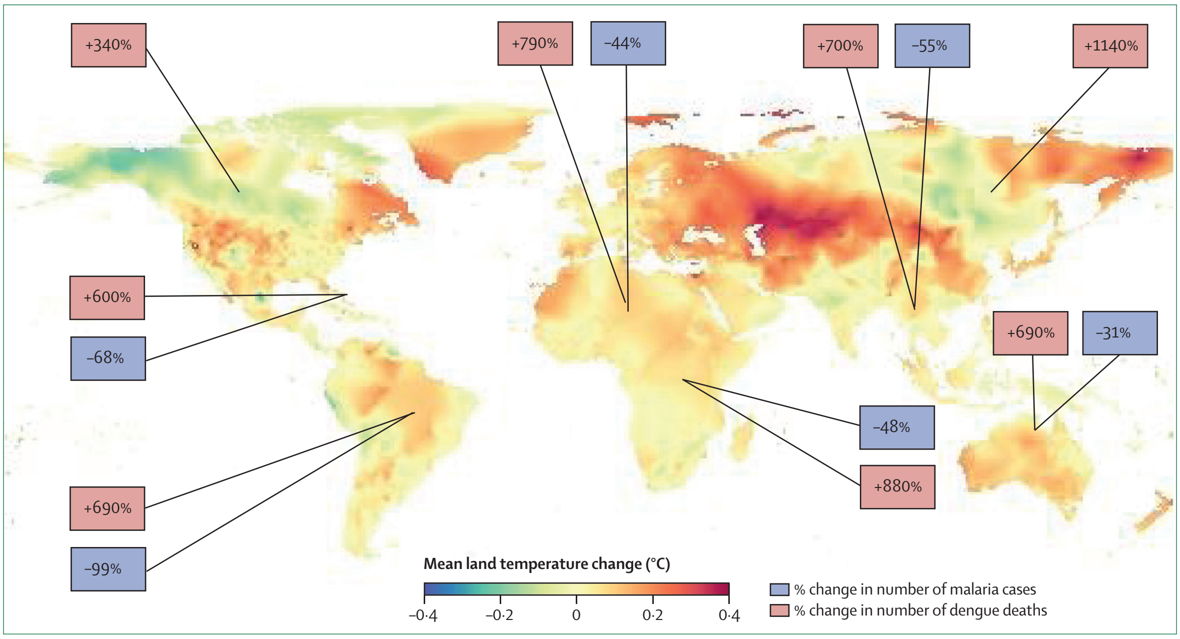

Figure 2: **Percentage change in dengue cases and malaria deaths and annual mean land temperature change between 1993 and 2013**
WHO regions include Latin America, the Caribbean, North America, north Africa and the Middle East, south and southeast Asia, central and east Asia, Oceania, sub-Saharan Africa. Climatic data were accessed via the Climatic Research Unit[126] and case data retrieved from the Global Burden of Disease Survey 2013.[5,127]

interactions with the climate are likely to have a greater effect on dengue incidence in the more immediate future. The rapid global re-emergence of dengue virus within the past 50 years[129] is related to a number of interacting factors, including urbanisation, socio-economics, climate change, travel, and trade.[130,131] For instance, the substantial expansion of urban areas after World War 2, especially in Asia, meant that large numbers of people migrated into cities, often residing in housing with no sanitation or running water.[9] These factors, combined with poor health-care infrastructure, meant that by the 1980s dengue virus had escalated from causing sporadic epidemics to being a leading cause of morbidity and mortality in southeast Asia.[9] However, the expansion of dengue was preceded by the spread of its principal vectors, *Ae aegypti* and *Ae albopictus*. Originally zoophilic and sylvatic, these mosquitoes became domesticated and were introduced to global urban hubs via travel and trade.[12,110] Local populations of dengue viral vectors then increased in urban landscapes because of the higher numbers of human hosts and the abundance of suitable breeding habitats.[12,21] Furthermore, complex interplay between urban heat island, pesticide use, and vector competition have been reported to affect vector competence and influence dengue virus transmission.[21]

Malaria

Much research has pointed to interactions between malaria transmission, land conversion, socioeconomics, and human movement.[86,132,133] For instance, one study coupled mosquito-borne disease dynamics with socioeconomic outcomes that occurred during land transitions[133] and found that an initial increase in malaria transmission to occur after land-use change was common, followed by either a further rise or a decline in transmission. This pattern of malaria transmission is postulated to arise because of ecological changes that promote transmission (eg, altered breeding sites and human-vector contact rates) occurring at a much faster rate than economic changes that can reduce trans-mission risk, such as improved housing and public health infrastructure among other factors. This analysis provided a theoretical explanation for empirical observ-ations of higher malaria risk during the early stages of irrigation schemes compared with well established irrigated land[82,86] and highlighted the need to consider both wide-ranging sets of underlying drivers and appropriate timescales over which each driver acts on a system.

The interacting effects of climate change and socio-economic factors are also predicted to dramatically influence malaria risk over longer timescales. A study found that the projected population at risk of mosquito-borne diseases in 2050 was estimated to be 5·2 billion people when only climatic effects were considered, 1·74 billion when only gross domestic product effects were considered, and 1·95 billion when both sets of factors were considered.[134] This outcome indicates that climate change might act to negate the continued contraction in malaria expected with economic development. However, feedback loops between climate change and economic development need to be better understood to improve predictions.

Recommendations for future research

Although the effects of climate change on mosquito-borne disease risk are substantial, the influence of other global change processes and their interactions occur over shorter timescales and are likely to have a greater impact in the immediate future.[135] Considering the effect of climate change in isolation might result in inaccurate predictions of mosquito-borne diseases risk, which might influence the formulation of robust policy recommendations for these emerging diseases. This issue is compounded by the fact that many studies do not account for the multiple sources of uncertainty in their predictions,[28,43] including the data (eg, health, environmental, and socioeconomic), future global change scenarios (eg, climate emission scenarios), and the structure of models and their outputs.

We advocate future research to adopt a holistic system dynamics approach (figure 3) where the associations and the feedbacks between socioeconomic and environmental systems are considered.[136] However, to achieve this approach several research gaps need to be addressed. First, enhanced surveillance and evaluation of public health measures are needed to improve health data and define the factors that promote disease risk. Second, empirical research is required to describe the associations between vectors, pathogens, and global change processes to improve parameterisation of mosquito-borne diseases risk models. Third, more high-resolution, large-scale datasets for other global change processes are needed to match the quantity of climatic data available. Finally, further research is required to understand the scale at which different global change processes influence mosquito-borne diseases risk, and how to incorporate multiple scales into mosquito-borne diseases transmission models.[16,28,44]

Addressing these gaps requires improved funding for empirical research and long-term surveillance at varying geographical scales, and enhanced collaboration between researchers working within different disciplines of mosquito-borne diseases research. In addition, greater funding for transdisciplinary studies is required to overcome unilateral modelling approaches and improve our understanding of disease risk. The ever-increasing availability of big data, sensor technology, and innovative software means researchers have the ability to understand environmental heterogeneity and global change over multiple spatial and temporal scales, including real-time perspectives.[137–139] High-resolution satellite remote sensing data are available for some disease risk modifying variables, including land-use, climate, and human populations at a global scale over long periods. For example, remote sensing data from the European Space Agency satellite Sentinel are available weekly at a 10 m resolution[140] and can be processed into environmental datasets via machine learning approaches. Mobile phone data have also been used to map patterns and processes in human populations,[141] and to examine the effect of human movement on disease transmission data.[142] For example, human mobility estimates generated from mobile phone data can accurately predict the distribution and timing of dengue epidemics in Pakistan.[142] In addition, citizen science projects are engaging members of the public to record data, such as mosquito occurrence, via applications on their mobile phones.[143,144]

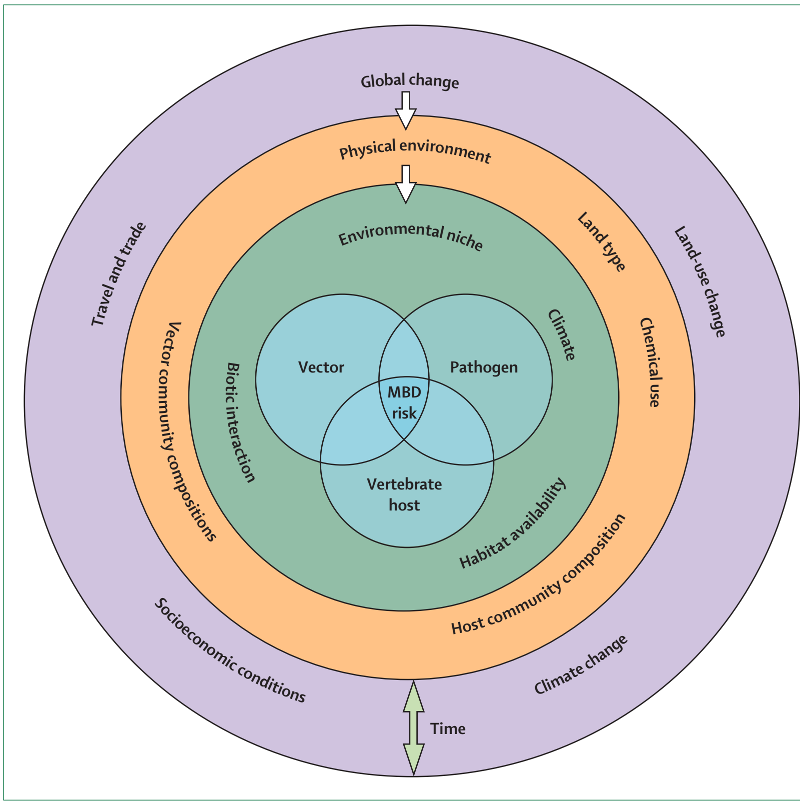

Figure 3: **A system dynamics approach to understanding mosquito-borne disease risk**
A conceptual model to show a system approach to understanding mosquito-borne (MBD) disease risk whereby public health outcomes are influenced by complex interactions between environmental and socioeconomic systems.

Conclusion

Previous mosquito-borne disease research has focused on unilateral climate change analyses despite the growing evidence that other global change processes are important determinants of disease risk. Adopting a system dynamics approach, where the association between socioeconomic and environmental factors are considered, could improve future mosquito-borne disease projections and facilitate stakeholder engagement by showing the effectiveness of common goals in a changing world. Enhanced funding for transdisciplinary research and new opportunities in data availability and analyses will enable a better understanding of the interacting mechanisms that drive disease transmission, which will help to guide interventions and safeguard global health.[134]

Search strategy and selection criteria

We searched PubMed and Web of Science, for all papers published from Jan 1, 2014, to March 28, 2018, inclusive to reflect the field since the publication of the WHO report *A global brief on vector-borne diseases* in 2014, which called for further research into vector-borne diseases. Search terms were related to models of human mosquito-borne diseases and climate change: ("mosquito*" or "mosquito-borne disease*" or "mosquito borne disease*") AND ("climate chang*" or "climat* change*" or "climat* warm*" or "chang* climat*") AND ("model*" or "modelling"). We excluded treatment papers, reviews, case studies, and surveillance reports and focused on modelling studies that evaluated the effect of climate change on mosquito-borne diseases and their vectors. Climate change was defined as an alteration (either observed or projected) to climatic parameters and we included studies in our analysis if they considered the effects of climate change over several decades rather than within-decade timescales.

Contributors

All authors conceived this literature review. LHVF undertook the literature review and created the figures and tables. All authors interpreted and critically revised the draft.

Declaration of interests

We declare no competing interests.

Acknowledgments

The authors thank Rory Gibb, Sue Daly, and Flora Spooner for their discussion and comments on the previous versions of the manuscript. This research was financially supported by the Natural Environment Research Council (NERC; grant number NE-J001570–1) for KEJ and DWR; a PhD NERC studentship (grant number NE/L002485/1) for LHVF; a Medical Research Council UK Research and Innovation Rutherford Fellowship (MR/R02491X/1) and Wellcome Trust Institutional Strategic Support Fund (204841/Z/16/Z; both DWR); IA was funded by National Institute for Health Research (SRF-2011–04–001; Senior Investigator Award NF-SI-0616–10037), Medical Research Council, UK Department of Health and the Wellcome Trust. The funding sources had no involvement in the writing or decision to submit the paper for publication. IA had final responsibility for the decision to submit for publication.

References

1 WHO. Global vector control response 2017–2030. Geneva: World Health Organization, 2017.
2 WHO. A global brief on vector-borne diseases. Geneva: World Health Organization, 2014.
3 Kilpatrick AM, Randolph SE. Drivers, dynamics, and control of emerging vector-borne zoonotic diseases. *Lancet* 2012; **380:** 1946–55.
4 Paixão ES, Teixeira MG, Rodrigues LC. Zika, chikungunya and dengue: the causes and threats of new and re-emerging arboviral diseases. *BMJ Glob Health* 2017; **2:** e000530.
5 Stanaway JD, Shepard DS, Undurraga EA, et al. The global burden of dengue: an analysis from the Global Burden of Disease Study 2013. *Lancet Infect Dis* 2016; **16:** 712–23.
6 WHO. World Malaria Report 2017. Geneva: World Health Organization, 2017.
7 Grobbelaar AA, Weyer J, Moolla N, Van Vuren PJ, Moises F, Paweska JT. Resurgence of yellow fever in Angola, 2015–2016. *Emerg Infect Dis* 2016; **22:** 1854–55.
8 Bhatt S, Gething PW, Brady OJ, et al. The global distribution and burden of dengue. *Nature* 2013; **496:** 504–07.
9 Gubler DJ. Dengue, urbanization and globalization: the unholy trinity of the 21(st) century. *Trop Med Health* 2011; **39:** 3–11.
10 Longbottom J, Browne AJ, Pigott DM, et al. Mapping the spatial distribution of the Japanese encephalitis vector, *Culex tritaeniorhynchus* Giles, 1901 (Diptera: Culicidae) within areas of Japanese encephalitis risk. *Parasit Vectors* 2017; **10:** 148.
11 Campbell LP, Luther C, Moo-Llanes D, Ramsey JM, Danis-Lozano R, Peterson AT. Climate change influences on global distributions of dengue and chikungunya virus vectors. *Philos Trans R Soc B Biol Sci* 2015; **370:** 20140135.
12 Kraemer MUG, Sinka ME, Duda KA, et al. The global distribution of the arbovirus vectors *Aedes aegypti* and *Ae. albopictus. Elife* 2015; **4:** 1–18.
13 Brady OJ, Golding N, Pigott DM, et al. Global temperature constraints on *Aedes aegypti* and *Ae. albopictus* persistence and competence for dengue virus transmission. *Parasit Vector* 2014; **7:** 338.
14 Christiansen-Jucht C, Parham PE, Saddler A, Koella JC, Basáñez MG. Temperature during larval development and adult maintenance influences the survival of *Anopheles gambiae* s.s. *Parasit Vectors* 2014; **7:** 489.
15 Mordecai E, Cohen J, Evans M V, et al. Detecting the impact of temperature on transmission of Zika, dengue, and chikungunya using mechanistic models. *PLoS Neg Trop Dis* 2017; **11:** e0005568.
16 Parham PE, Waldock J, Christophides GK, et al. Climate, environmental and socio-economic change: weighing up the balance in vector-borne disease transmission. *Philos Trans R Soc B Biol Sci* 2015; **370:** 20130551.
17 Gottdenker NL, Streicker DG, Faust CL, Carroll CR. Anthropogenic land use change and infectious diseases: a review of the evidence. *Ecohealth* 2014; **11:** 619–32.
18 Newbold T. Future effects of climate and land-use change on terrestrial vertebrate community diversity under different scenarios. *Proc R Soc London B Biol Sci* 2018; **285:** 20180792.
19 Whitmee S, Haines A, Beyrer C, et al. Safeguarding human health in the Anthropocene epoch: report of The Rockefeller Foundation–Lancet Commission on planetary health. *Lancet* 2015; **386:** 1973–2028.
20 Lounibos LP, Juliano SA. Where vectors collide: the importance of mechanisms shaping the realized niche for modeling ranges of invasive *Aedes* mosquitoes. *Biol Invasions* 2018; **8:** 1913–29.
21 Ladeau SL, Allan BF, Leisnham PT, Levy MZ. The ecological foundations of transmission potential and vector-borne disease in urban landscapes. *Funct Ecol* 2015; **29:** 889–901.
22 Tjaden NB, Caminade C, Beierkuhnlein C, Thomas SM. Mosquito-borne diseases: advances in modelling climate-change impacts. *Trends Parasitol* 2017; **34:** 227–45.
23 Bates M. The natural history of mosquitoes. New York, NY: Harper and Row Publishers, 1949.
24 Lo Iacono G, Cunningham AA, Bett B, Grace D, Redding DW, Wood JLN. The environmental limits of Rift Valley fever revealed using ecoepidemiological mechanistic models. *Proc Natl Acad Sci USA* 2018; **11**: E7448–56.
25 IPCC. Summary for policymakers. Field CB, Barros VR, Dokken DJ, et al. In: Climate change 2014: impacts, adaptation, and vulnerability. part a: global and sectoral aspects. contribution of working group ii to the fifth assessment report of the Intergovernmental Panel on Climate Change. Cambridge and New York, NY: Cambridge University Press, 2014: 1–32.
26 Tjaden NB, Suk JE, Fischer D, Thomas SM, Beierkuhnlein C, Semenza JC. Modelling the effects of global climate change on Chikungunya transmission in the 21st century. *Sci Rep* 2017; **7:** 3813.
27 Paz S. Climate change impacts on West Nile virus transmission in a global context. *Philos Trans R Soc B Biol Sci* 2015; **370:** 20130561.
28 Caminade C, Kovats S, Rocklov J, et al. Impact of climate change on global malaria distribution. *Proc Natl Acad Sci USA* 2014; **111:** 3286–91.
29 Watts N, Amann M, Ayeb-Karlsson S, et al. The *Lancet* Countdown on health and climate change: from 25 years of inaction to a global transformation for public health. *Lancet* 2018; **391:** 581–630.
30 Paaijmans KP, Blanford S, Chan BHK, Thomas MB. Warmer temperatures reduce the vectorial capacity of malaria mosquitoes. *Biol Lett* 2012; **8:** 465–68.

31 Ewing DA, Cobbold CA, Purse BV, Nunn MA, White SM. Modelling the effect of temperature on the seasonal population dynamics of temperate mosquitoes. *J Theor Biol* 2016; **400:** 65–79.

32 Paaijmans KP, Heinig RL, Seliga RA, et al. Temperature variation makes ectotherms more sensitive to climate change. *Glob Chang Biol* 2013; **19:** 2373–80.

33 Westbrook CJ, Reiskind MH, Pesko KN, Greene KE, Lounibos LP. Larval environmental temperature and the susceptibility of *Aedes albopictus* Skuse (Diptera: Culicidae) to chikungunya virus. *Vector Borne Zoonotic Dis* 2010; **10:** 241–47.

34 Murdock CC, Paaijmans KP, Bell AS, et al. Complex effects of temperature on mosquito immune function. *Proc Biol Sci* 2012; **279:** 3357–66.

35 Ohm JR, Baldini F, Barreaux P, et al. Rethinking the extrinsic incubation period of malaria parasites. *Parasit Vectors* 2018; **11:** 1–9.

36 Barbazan P, Guiserix M, Boonyuan W, Tuntaprasart W, Pontier D, Gonzalez J. Modelling the effect of temperature on transmission of dengue. *Med Vet Entomol* 2010; **24:** 66–73.

37 Tjaden NB, Thomas SM, Fischer D, Beierkuhnlein C. Extrinsic incubation period of dengue: knowledge, backlog, and applications of temperature dependence. *PLoS Negl Trop Dis* 2013; **7:** e2207.

38 Reisen WK, Fang Y, Martinez VM. Effects of Temperature on the transmission of West Nile virus by *Culex tarsalis* (Diptera: Culicidae). *J Med Entomol* 2006; **43:** 309–17.

39 Carrington LB, Armijos MV, Lambrechts L, Scott TW. Fluctuations at a low mean temperature accelerate dengue virus transmission by *Aedes aegypti*. *PLoS Negl Trop Dis* 2013; **7:** e2190.

40 Lambrechts L, Paaijmans KP, Fansiri T, et al. Impact of daily temperature fluctuations on dengue virus transmission by *Aedes aegypti*. *Proc Natl Acad Sci USA* 2011; **108:** 7460–65.

41 Paaijmans KP, Blanford S, Bell AS, Blanford JI, Read AF, Thomas MB. Influence of climate on malaria transmission depends on daily temperature variation. *Proc Natl Acad Sci USA* 2010; **107:** 15135–39.

42 IPCC. Summary for policymakers. In: Stocker TF, Qin D, Plattner G, et al, eds. Climate change 2013: the physical science basis. contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change. Cambridge and New York, NY: Cambridge University Press, 2013: 1–33.

43 Harris RMB, Grose MR, Lee G, Bindoff NL, Porfirio LL, Fox-Hughes P. Climate projections for ecologists. *Wiley Interdiscip Rev Clim Chang* 2014; **5:** 621–37.

44 Booth M. Climate change and the neglected tropical diseases. In: Rollinson D, Stothard JR. Advances in parasitology. 1st ed. London: Elsevier, 2018: 39–126.

45 Davis JK, Vincent G, Hildreth MB, Kightlinger L, Carlson C, Wimberly MC. Integrating environmental monitoring and mosquito surveillance to predict vector-borne disease: prospective forecasts of a West Nile virus outbreak. *PLoS Curr* 2017; **23:** currents.outbreaks.90e80717c4e67e1a830f17feeaaf85de.

46 Stewart Ibarra AM, Ryan SJ, Beltrán E, Mejía R, Silva M, Muñoz Á. Dengue vector dynamics (*Aedes aegypti*) influenced by climate and social factors in Ecuador: implications for targeted control. *PLoS One* 2013; **8:** e78263.

47 Day JF, Shaman J. Using hydrologic conditions to forecast the risk of focal and epidemic arboviral transmission in peninsular Florida. *J Med Entomol* 2008; **45:** 458–65.

48 Soti V, Tran A, Degenne P, Chevalier V, Lo Seen D, Thiongane Y. Combining hydrology and mosquito population models to identify the drivers of Rift Valley fever emergence in semi-arid regions of West Africa. *PLoS Negl Trop Dis* 2012; **6:** e1795.

49 Asare EO, Tompkins AM, Bomblies A. A regional model for malaria vector developmental habitats evaluated using explicit, pond-resolving surface hydrology simulations. *PLoS One* 2016; **11:** e0150626.

50 Siraj A, Santos-Vega M, Bouma MJ, Yadeta D, Ruiz Carrascal D, Pascual M. Altitudinal changes in malaria incidence in highlands of Ethiopia and Colombia. *Science* 2014; **343**: 1154–58.

51 Lowe R, Stewart-Ibarra AM, Petrova D, et al. Climate services for health: predicting the evolution of the 2016 dengue season in Machala, Ecuador. *Lancet Planet Health* 2017; **1:** e142–51.

52 Dobson A. Climate variability, global change, immunity, and the dynamics of infectious diseases. *Ecology* 2009; **90:** 920–27.

53 Peterson AT. Biogeography of diseases: a framework for analysis. *Naturwissenschaften* 2008; **95:** 483–91.

54 Warren R, Price J, Graham E, Forstenhaeusler N, VanDerWal J. The projected effect on insects, vertebrates, and plants of limiting global warming to 1·5°C rather than 2°C. *Science* 2018; **360:** 791–95.

55 Campbell-Lendrum D, Manga L, Bagayoko M, Sommerfeld J. Climate change and vector-borne diseases: what are the implications for public health research and policy? *Philos Trans R Soc London* 2015; **370:** 20130552.

56 Tatem AJ, Gething PW, Smith DL, Hay SI. Urbanization and the global malaria recession. *Malaria J* 2013; **12:** 133.

57 Sachs J, Malaney P. The economic and social burden of malaria. *Nature* 2002; **415:** 680.

58 Steffen W, Grinevald J, Crutzen P, Mcneill J. The Anthropocene: conceptual and historical perspectives. *Philos Trans A Math Phys Eng Sci* 2011; **369:** 842–67.

59 Gibb R, Moses LM, Redding DW, Jones KE. Understanding the cryptic nature of Lassa Fever in west Africa. *Pathog Glob Health* 2017; **111:** 276–88

60 Hassell JM, Begon M, Ward MJ, Fèvre EM. Urbanization and disease emergence: dynamics at the wildlife–livestock–human interface. *Trends Ecol Evol* 2016; **32:** 1–13.

61 Johnson PTJ, de Roode JC, Fenton A. Why infectious disease research needs community ecology. *Science* 2015; **349:** 1259504.

62 Lambin EF, Tran A, Vanwambeke SO, Linard C, Soti V. Pathogenic landscapes: interactions between land, people, disease vectors, and their animal hosts. *Int J Health Geogr* 2010; **9:** 54.

63 Hudson LN, Newbold T, Contu S, et al. The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts. *Ecol Evol* 2014; **4:** 1–35.

64 Jones KE, Patel NG, Levy MA, et al. Global trends in emerging infectious diseases. *Nat Lett* 2008; **451:** 990–4.

65 Fornace KM, Abidin TR, Alexander N, et al. Association between landscape factors and spatial patterns of *Plasmodium knowlesi* infections in Sabah, Malaysia. *Emerg Infect Dis J* 2016; **22:** 201.

66 Chaves LSM, Conn JE, López RVM, Sallum MAM. Abundance of impacted forest patches less than 5 km² is a key driver of the incidence of malaria in Amazonian Brazil. *Sci Rep* 2018; **8:** 1–11.

67 Newbold T, Hudson LN, Hill SLL, et al. Global effects of land use on local terrestrial biodiversity. *Nature* 2015; **520:** 45–50.

68 Roche B, Rohani P, Dobson AP, Guégan JF. The impact of community organization on vector-borne pathogens. *Am Nat* 2013; **181:** 1–11.

69 Wilcox BA, Gubler DJ. Disease ecology and the global emergence of zoonotic pathogens. *Environ Health Prev Med* 2005; **10:** 263–72.

70 Ostfeld RS, Keesing F. Biodiversity and disease risk: the case of Lyme disease. *Conserv Biol* 2000; **14:** 722–28.

71 Civitello DJ, Cohen J, Fatima H, et al. Biodiversity inhibits parasites: broad evidence for the dilution effect. *Proc Natl Acad Sci USA* 2015; **112:** 8667–71.

72 Faust CL, Dobson AP, Gottdenker N, et al. Null expectations for disease dynamics in shrinking habitat: dilution or amplification? *Philos Trans R Soc Lond B Biol Sci* 2017; **372:** 20160173.

73 Randolph SE, Dobson ADM. Pangloss revisited: a critique of the dilution effect and the biodiversity-buffers-disease paradigm. *Parasitology* 2012; **139:** 847–63.

74 Luis AD, Kuenzi AJ, Mills JN. Species diversity concurrently dilutes and amplifies transmission in a zoonotic host–pathogen system through competing mechanisms. *Proc Natl Acad Sci USA* 2018; **115:** 7979–84.

75 Burkett-Cadena ND, Vittor AY. Deforestation and vector-borne disease: forest conversion favors important mosquito vectors of human pathogens. *Basic Appl Ecol* 2017; **26:** 101–10.

76 Patz JA, Graczyk TK, Geller N, Vittor AY. Effects of environmental change on emerging parasitic diseases. *Int J Parasitol* 2000; **30:** 1395–405.

77 Brouard O, Le Jeune AH, Leroy C, et al. Are algae relevant to the detritus-based food web in tank-bromeliads? *PLoS One* 2011; **6:** e20129.

78 Rueda Páramo ME, López Lastra CC, García JJ. Persistence and pathogenicity of a native isolate of *Leptolegnia chapmanii* against *Aedes aegypti* larvae in different anthropic environments. *Biocontrol Sci Technol* 2015; **25:** 238–43.

79 Loaiza JR, Dutari LC, Rovira JR, et al. Disturbance and mosquito diversity in the lowland tropical rainforest of central Panama. *Sci Rep* 2017; **7:** 1–13.

80 Hurtt GC, Chini LP, Frolking S, et al. Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. *Clim Change* 2011; **109:** 117–61.

81 WHO. Agricultural development and vector-borne diseases training and information materials on vector biology and control. Geneva: World Health Organization, 1996.

82 Lindblade KA, Walker ED, Onapa AW, Katungu J, Wilson ML. Land use change alters malaria transmission parameters by modifying temperature in a highland area of Uganda. *Trop Med Int Health* 2000; **5:** 263–74.

83 Ijumba JN, Lindsay SW. Impact of irrigation on malaria in Africa: paddies paradox. *Med Vet Entomol* 2001; **15:** 1–11.

84 Erlanger TE, Keiser J, Caldas De Castro M, et al. Effect of water resource development and management on lymphatic filariasis, and estimates of populations at risk. *Am J Trop Med Hyg* 2005; **73:** 523–33.

85 Keiser J, De Castro MC, Maltese MF, et al. Effect of irrigation and large dams on the burden of malaria on a global and regional scale. *Am J Trop Med Hyg* 2005; **72:** 392–406.

86 Baeza A, Bouma MJ, Dobson AP, Dhiman R, Srivastava HC, Pascual M. Climate forcing and desert malaria: the effect of irrigation. *Malar J* 2011; **10:** 190.

87 Jaleta KT, Hill SR, Seyoum E, et al. Agro-ecosystems impact malaria prevalence: large-scale irrigation drives vector population in western Ethiopia. *Malar J* 2013; **12:** 350.

88 Service MW. Agricultural development and arthropod-borne diseases: a review. *Rev Saude Publica* 1991; **25:** 165–78.

89 Le Flohic G, Porphyre V, Barbazan P, Gonzalez JP. Review of climate, landscape, and viral genetics as drivers of the Japanese encephalitis virus ecology. *PLoS Negl Trop Dis* 2013; **7:** 5–11.

90 Buescher EL, Scherer WF, Rosenberg MZ, McClure HE. Immunologic studies of Japanese encephalitis virus in Japan. III. Infection and antibody response of birds. *J Immunol* 1959; **83:** 605–13.

91 Erlanger TE, Weiss S, Keiser J, Utzinger J, Wiedenmayer K. Past, present, and future of Japanese encephalitis. *Emerg Infect Dis* 2009; **15:** 1–7.

92 Keiser J, Maltese MF, Erlanger TE, et al. Effect of irrigated rice agriculture on Japanese encephalitis, including challenges and opportunities for integrated vector management. *Acta Trop* 2005; **95:** 40–57.

93 Kibret S, Lautze J, McCartney M, Nhamo L, Wilson GG. Malaria and large dams in sub-Saharan Africa: future impacts in a changing climate. *Malar J* 2016; **15:** 448.

94 Patz JA, Daszak P, Tabor GM, et al. Unhealthy landscapes: policy recommendations on land use change and infectious disease emergence. *Environ Health Perspect* 2004; **112:** 1092–98.

95 Fuller DO, Parenti MS, Hassan AN, Beier JC. Linking land cover and species distribution models to project potential ranges of malaria vectors: an example using *Anopheles arabiensis* in Sudan and Upper Egypt. *Malar J* 2012; **11:** 264.

96 van den Hurk AF, Ritchie SA, Mackenzie JS. Ecology and geographical expansion of Japanese encephalitis virus. *Annu Rev Entomol* 2009; **54:** 17–35.

97 Bashar K, Rahman MS, Nodi IJ, Howlader AJ. Species composition and habitat characterization of mosquito (Diptera: Culicidae) larvae in semi-urban areas of Dhaka, Bangladesh. *Pathog Glob Health* 2016; **110:** 48–61.

98 Chase JM, Knight TM. Drought-induced mosquito outbreaks in wetlands. *Ecol Lett* 2003; **6:** 1017–24.

99 Moore SM, Borer ET, Hosseini PR. Predators indirectly control vector-borne disease: linking predator-prey and host-pathogen models. *J R Soc Interface* 2010; **7:** 161–76.

100 Alexandratos N, Bruinsma J. World agriculture towards 2030/2050: the 2012 revision. 2012. http://www.fao.org/fileadmin/templates/esa/Global_persepctives/world_ag_2030_50_2012_rev.pdf (accessed June 7, 2018).

101 Anderson EP, Jenkins CN, Heilpern S, et al. Fragmentation of Andes-to-Amazon connectivity by hydropower dams. *Sci Adv* 2018; **4:** 1–8.

102 The World Bank. The United Nations population divisions world urbanization prospects: urban population (% of total). 2016. https://data.worldbank.org/indicator/SP.URB.TOTL.IN.ZS?view=chart (accessed Feb 21, 2018).

103 UN. World urbanization prospects: the 2014 revision, highlights. New York, NY: United Nations, 2014.

104 Weaver SC, Reisen WK. Present and future arboviral threats. *Antiviral Res* 2010; **85:** 328–45.

105 Saker L, Lee K, Cannito B, Gilmore A, Campbell-Lendrum D. Globalization and infectious diseases: a review of the linkages. Geneva: World Health organization, 2004.

106 Weaver SC. Urbanization and geographic expansion of zoonotic arboviral diseases: mechanisms and potential strategies for prevention. *Trends Microbiol* 2013; **21:** 360–63.

107 Hotez PJ. Global urbanization and the neglected tropical diseases. *PLoS Negl Trop Dis* 2017; **11:** 1–5.

108 Kwa BH. Environmental change, development and vectorborne disease: Malaysia's experience with filariasis, scrub typhus and dengue. *Environ Dev Sustain* 2008; **10:** 209–17.

109 Imhoff ML, Zhang P, Wolfe RE, Bounoua L. Remote sensing of the urban heat island effect across biomes in the continental USA. *Remote Sens Environ* 2010; **114:** 504–13.

110 Brown JE, McBride CS, Johnson P, et al. Worldwide patterns of genetic differentiation imply multiple "domestications" of *Aedes aegypti*, a major vector of human diseases. *Proc Biol Sci* 2011; **278:** 2446–54.

111 Murdock CC, Evans M V, McClanahan TD, Miazgowicz KL, Tesla B. Fine-scale variation in microclimate across an urban landscape shapes variation in mosquito population dynamics and the potential of *Aedes albopictus* to transmit arboviral disease. *PLoS Negl Trop Dis* 2017; **11:** e0005640.

112 Qi Q, Guerra CA, Moyes CL, et al. The effects of urbanization on global *Plasmodium vivax* malaria transmission. *Malar J* 2012; **11:** 403.

113 Wood CL, McInturff A, Young HS, Kim D, Lafferty KD. Human infectious disease burdens decrease with urbanization but not with biodiversity. *Philos Trans R Soc Lond B Biol Sci* 2017; **372:** 20160122.

114 Mulligan K, Dixon J, Sinn C-LJ, Elliott SJ. Is dengue a disease of poverty? A systematic review. *Pathog Glob Health* 2015; **109:** 10–18.

115 Gallup JL, Sachs JD. The economic burden of malaria. *Am J Trop Med Hyg* 2001; **64:** 85–96.

116 Oviedo-Pastrana M, Méndez N, Mattar S, Arrieta G, Gomezcaceres L. Epidemic outbreak of chikungunya in two neighboring towns in the Colombian Caribbean: a survival analysis. *Arch Public Heal* 2017; **75:** 1.

117 WHO. First WHO report on neglected tropical diseases: working to overcome the global impact of neglected tropical diseases. Geneva: World Health Organization, 2010: 1–184. https://www.who.int/neglected_diseases/2010report/en/ (accessed February 12, 2018).

118 Alsan MM, Westerhaus M, Herce M, Nakashima K, Farmer PE. Poverty, global health and infectious disease: lessons from Haiti and Rwanda. *Infect Dis Clin North Am* 2012; **25:** 611–22.

119 Ngonghala CN, De Leo GA, Pascual MM, Keenan DC, Dobson AP, Bonds MH. General ecological models for human subsistence, health and poverty. *Nat Ecol Evol* 2017; **1:** 1153–59.

120 Bowles S, Durlauf S, Hoff K. Poverty traps. Princeton, NJ: Princeton University Press, 2006.

121 Singer M, Bulled N. Interlocked infections: the health burdens of syndemics of neglected tropical diseases. *Ann Anthropol Pract* 2013; **36:** 328–45.

122 Bloom DE, Canning D, Sevilla J. The effect of health on economic growth: a production function approach. *World Dev* 2004; **32:** 1–13.

123 Tolle MA. Mosquito-borne diseases. *Curr Probl Pediatr Adolesc Health Care* 2009; **39:** 97–140.

124 Nunes MRT, Palacios G, Faria NR, et al. Air travel is associated with intracontinental spread of dengue virus serotypes 1–3 in Brazil. *PLoS Negl Trop Dis* 2014; **8:** e2769.

125 Kampen H, Jansen S, Schmidt-Chanasit J, Walther D. Indoor development of *Aedes aegypti* in Germany, 2016. *Euro Surveill* 2016; **21:** 2–4.

126 Harris I, Jones PD, Osborn TJ, Lister DH. Updated high-resolution grids of monthly climatic observations - the CRU TS3.10 Dataset. *Int J Climatol* 2014; **34:** 623–42.
127 GBD 2016 Causes of Death Collaborators. Global, regional, and national age-sex specific mortality for 264 causes of death, 1980-2016: a systematic analysis for the Global Burden of Disease Study 2016. *Lancet* 2017; **390:** 1151–1210.
128 Messina JP, Brady OJ, Pigott DM, et al. The many projected futures of dengue. *Nat Rev Microbiol* 2015; **13:** 230–39.
129 WHO. Global strategy for dengue prevention and control 2012–2020. Geneva: World Health Organization, 2012.
130 Guzman MG, Harris E. Dengue. *Lancet* 2015; **385:** 453–65.
131 Ebi KL, Nealon J. Dengue in a changing climate. *Environ Res* 2016; **151:** 115–23.
132 Stratton L, O'Neill MS, Kruk ME, Bell ML. The persistent problem of malaria: addressing the fundamental causes of a global killer. *Soc Sci Med* 2008; **67:** 854–62.
133 Baeza A, Santos-Vega M, Dobson AP, Pascual M. The rise and fall of malaria under land-use change in frontier regions. *Nat Ecol Evol* 2017; **1:** 108.
134 Béguin A, Hales S, Rocklöv J, Åström C, Louis VR, Sauerborn R. The opposing effects of climate change and socio-economic development on the global distribution of malaria. *Glob Environ Chang* 2011; **21:** 1209–14.
135 Millennium Ecosystem Assessment. Ecosystems and human well-being: synthesis. Washington, DC: Island Press, 2005.
136 Pongsiri MJ, Gatzweiler FW, Bassi AM, Haines A, Demassieux F. The need for a systems approach to planetary health. *Lancet Planet Health* 2017; **1:** e257–59.
137 Fleming L, Tempini N, Gordon-Brown H, et al. Big data in environment and human health. 2017. https://oxfordindex.oup.com/view/10.1093/acrefore/9780199389414.013.541 (accessed February 2, 2018).
138 Hay SI, George DB, Moyes CL, Brownstein JS. Big data opportunities for global infectious disease surveillance. *PLoS Med* 2013; **10:** 2–5.
139 Kraemer MUG, Hay SI, Pigott DM, Smith DL, Wint GRW, Golding N. Progress and challenges in infectious disease cartography. *Trends Parasitol* 2016; **32:** 19–29.
140 European Space Agency. Sentinel-1. 2018. https://sentinel.esa.int/web/sentinel/missions/sentinel-1 (accessed Feb 25, 2018).
141 Deville P, Linard C, Martin S, Gilbert M, Stevens FR, Gaughan AE. Dynamic population mapping using mobile phone data. *Proc Natl Acad Sci USA* 2014; **111:** 15888–93.
142 Wesolowski A, Qureshi T, Boni MF, Roe P, Johansson MA, Basit S. Impact of human mobility on the emergence of dengue epidemics in Pakistan. *Proc Natl Acad Sci USA* 2015; **112:** 11887–92.
143 Palmer JRB, Oltra A, Collantes F, et al. Citizen science provides a reliable and scalable tool to track disease-carrying mosquitoes. *Nat Commun* 2017; **8:** 916.
144 Mukundarajan H, Hol FJH, Castillo EA, Newby C, Prakash M. Using mobile phones as acoustic sensors for high-throughput mosquito surveillance. *Elife* 2017; **6:** e27854.