

THE IMPACT OF GLOBAL CHANGE ON MOSQUITO-BORNE DISEASE

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SUMMARY

Over 80% of the global population is at risk of a vector-borne disease, with mosquito-borne diseases being the largest contributor to human disease burden. Although many global processes such as land-use and socioeconomic change are thought to influence mosquito-borne disease dynamics, research to-date has strongly focused on the role of climate change. We show, through a review of contemporary modelling studies, that there is no consensus on how future changes in climatic conditions will impact mosquito-borne diseases, 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, enabling a better understanding and mitigation of mosquito-borne diseases in a changing world.

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 human population being infected with a vector-borne pathogen at any moment.² In particular, mosquito-borne diseases (MBDs) are a key group of concern, as they include both very high burden and important emerging diseases such as: Human malaria (~212 million cases per year), Dengue (~96 million cases per year), Chikungunya (~693 000 cases per year) and Zika virus disease (~500,000 cases per year) (Table 1).³

Globally, many MBDs are thought to be increasing in incidence and geographic distribution; both emerging in new areas,^{4,5} and re-emerging in previously eradicated regions.^{6,7} For example, there has been a 30-fold increase in the global incidence of dengue over the past 50 years, following its expansion 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 levels of morbidity and mortality, have the potential to exert significant 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 been targeted at understanding the current and future geographic distributions of disease risk, in the context of on-going global change, to help guide interventions and safeguard public health.¹⁰⁻¹²

In this context, there has previously been a strong research focus 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 (e.g. poverty, trade and travel).^{3,16,17} Indeed, these additional global processes, and the interactions between them, may reasonably be

shown to have a stronger immediate impact on future MBD burden than climate change effects.¹⁸ This would mean a more complete understanding of the role of global change in modulating the spatial and temporal distributions of MBDs will be essential for the successful prediction and management of disease risk in the future.¹⁹ In this review, we synthesise current knowledge on the relative impact of global change processes on MBD risk and critically examine how these have been incorporated into existing analyses. We argue that the current focus on the effects of climate change is insufficient, considering growing evidence for the key role of other global change processes in modulating MBD risk. We suggest an alternative approach to modelling MBD risk and recommend future directions for research.

CLIMATE CHANGE AS A DRIVER OF MOSQUITO-BORNE DISEASE

Systematic review of current literature

We conducted a systematic literature search to better understand the scope and outcome of climate-based MBD modelling studies (search strategy and selection criteria), structuring the search to explore two main axes: First, we considered different mechanisms examined by each study as climate and climate change may affect MBD epidemiology via different pathways, such as influencing pathogen development within the mosquito, and vector population dynamics.^{20,21} Second, we examined how different modelling approaches, such as mechanistic and correlation-based methods, have been used to predict the effect of climate on the risk of multiple MBDs over different geographic 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 MBD risk being inferred from variations in disease incidence or vector populations.

Of 234 papers identified, 46 met the inclusion criteria (Supplementary materials; Table S1). Overall 54% of studies demonstrated a positive relationship between climate change and MBD risk, with increased variations in meteorological values associated with increased vector abundance or disease incidence. However, the proportion of studies showing this positive relationship varied depending on the geographic scale of the study (Figure 1a). 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 (Figure 1b). Global change processes examined in the 46 studies included land use in 17%, human population density in 11%, of which less than half considered future human density projections, and socioeconomics in 7%.

Temperature, precipitation and humidity were the main parameters used to model climate change (Supplementary materials; Table S1). Over 97% of studies included the effect of temperature change in their analyses, whereas 78% included precipitation and 22% considered humidity. Temperature has been a predominant research focus since mosquitoes are ectothermic and so ambient temperature strongly influences important epidemiological processes including vector development, biting rates and pathogen development rate within the vector (Reiter 2001; Mordecai et al. 2017). Precipitation is regularly included as parameters in models of MBD risk as water pools are required for mosquito development and associated humidity levels influence mosquito survival and flight.^{23,24}

Changes in these meteorological variables were determined from recorded climatic data or from projected climatic values using different scenarios of climate change (e.g. IPCC emissions).²⁵ Regarding modelling approaches, over 50% of the studies used correlative models to investigate statistical associations between MBD risk and explanatory variables²². Other studies used mechanistic models which incorporated biological or environmental mechanisms assumed to drive disease dynamics (e.g., 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 for small geographic area analyses such as zonal and national, compared with correlative methods which tended to be used for large-scale regional or global analyses. Most studies were prospective (i.e., predicting to into future) but a few were retrospective or theoretical.

The overall results indicate that there is no consensus on how changes in climatic conditions will impact MBD risk. This equivocal conclusion may reflect choice of modelling parameters (i.e., selected climatic variables), spatial or temporal scales of the analyses, modelling approach and/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 MBD research^{11,26-28} appears to have led to a body of international scientific reports concluding that MBD expansion will likely 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 relationships 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 mosquito body size has been associated with reductions in fecundity, bloodmeal size and immunocompetence.³⁴ Therefore, paradoxically, climate change may actually reduce the risk of transmission in certain regions via the negative effects of

increasing temperatures on vector competence (i.e., the ability of vectors to become infectious).

Temperature also influences the time taken for pathogen development within the mosquito (i.e., extrinsic incubation period [EIP]).^{15,30} The EIP 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 MBD models do not include this parameter and when it is included, it is often based on out-dated, temperature-dependent models developed from a single mosquito species that do not consider the influence of other abiotic (e.g., larval habitat quality) or biotic (e.g., parasite competition within the mosquito) factors.³⁵ Studies have typically demonstrated EIP to be shortened with increasing temperatures, and suggested related high infection and transmission rates.^{36–38} However, this effect may vary considerably depending on the specific vector and pathogen.³⁵ For example, in *Aedes* vectors, low temperatures have been shown to shorten EIPs and cause high viral infection rates by suppressing mosquito antiviral immunity.³³ Other studies have found large temperature fluctuations at low mean temperatures cause shorter EIPs and higher infection in vectors of dengue virus^{39,40} and malaria⁴¹, when compared with more consistent conditions. The lack of clarity about the relationship between EIP and temperature is a critical knowledge gap that requires further empirical research to inform accurate forecasting of MBD risk.

There is considerable debate about how future climate change will impact precipitation trends,^{42,43} but the consensus is that an increasing frequency of extreme precipitation levels is likely.⁴⁴ With regard to MBDs, increased variation in precipitation may either augment vector breeding habitat formation or reduce it via detrimental periods of drought and extreme flooding. Similar to the effects of temperature, the relationship between precipitation and MBD risk is non-linear^{27,45}. Several lagged effects (i.e., time-lags 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; this will also depend on species-specific preferences (i.e., water depth) and hydrological factors (e.g., as soil type, vegetation) that control temporary water body development.^{45,47} A few studies have incorporated hydrological processes into their regional disease risk models,⁴⁷⁻⁴⁹ but the practice has not been widely adopted possibly because of the increased complexity needed to model these processes or lack of collaboration between disease researchers and hydrological experts.

Although climate-based models have proved useful in understanding MBD risk at local scales⁵⁰ and short timescales,⁵¹ models based solely on approximating the impacts of climatic factors are unlikely to be as effective over large spatial and temporal scales. We already know of other important mechanisms that influence the geographic distributions of vector populations, such as dispersal (e.g., via host movement, wind and trade routes), and biotic interactions (e.g., competition and predation).^{20,52,53} For instance, although West Nile Virus was theoretically able to exist in the Americas due to climatic suitability, it was not until 1999 that it spread from its original range in Africa, southern Europe, and Southwest Asia, to the whole of North America, likely due to dispersal by migratory birds.⁵³ Likewise, *Aedes aegypti* was expected to occupy rural habitats of southern USA due to climatic suitability, but these predictions proved inaccurate when competitor, *Aedes albopictus* was present.²⁰

The burden of disease from MBDs felt by human populations, therefore, is likely an emergent property of a set of interacting processes which 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 impact 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 may be additive as demonstrated by the synergistic effects

of climate change, urbanisation, international trade and travel that have promoted the global expansion in dengue transmission risk.⁵⁵ Alternatively, they may be subtractive as seen with the global malaria recession which has occurred in parallel with increasing urbanisation⁵⁶ and economic development.⁵⁷ The usefulness of climate-based models of MBD risk should not be underestimated however, to predict distributions of MBD risk in the context of on-going global change, there is a need for more complex models that consider multiple global change processes.²⁸

THE IMPACT OF LAND-USE CHANGE ON MOSQUITO-BORNE DISEASE

Land-use change, from natural to human-dominated landscapes, is a key signature of the Anthropocene⁵⁸ and can alter disease risk by influencing the interactions between people, pathogens, vectors and vertebrate hosts.^{3,17,59–62} The immediacy and strength of land-use change impacts on local ecology⁶³ supports the argument that it may 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 MBD risk will depend on several factors such as its geographic region and mode of the change, i.e., whether it was due to deforestation, agriculture, irrigation, and/or urbanisation. Each of these types of change are discussed below.

Deforestation

Deforestation has been associated with increased human exposure to MBDs^{65,66} via its effect on the ecology of vertebrate hosts of zoonotic pathogens, vectors, and vector-host interactions. For example, biodiversity declines are associated with primary forest clearance⁶⁷ and may result in shifts in the community composition of wildlife hosts^{3,60,68} and emergence of infectious diseases.⁶⁴ It is postulated that in biodiverse regions, multi-host community structures may be able to buffer against disease outbreaks since pathogen transmission may

be diluted.⁶⁹⁻⁷¹ Despite the theoretical and empirical evidence for this ‘dilution effect’ being strongest for vector-borne pathogen transmission,^{70,72} the generality of this theory remains disputed.⁷²⁻⁷⁴

Since mosquito ecology is dependent on abiotic and biotic environmental conditions, land-use changes will have a significant effect on populations²¹ via altering microclimates, biotic interactions (e.g., predation and competition), and nutrient availability.⁷⁵ Deforestation promotes the growth of certain mosquito populations due to changes in sunlight and pH of water pools in cleared areas.⁷⁶ For instance, increased sunlight has been shown to assist mosquito survival by providing nutrients for larvae,⁷⁷ and limiting entomophagic fungi growth.⁷⁸ Nevertheless, the effect of these changes on mosquito populations will vary depending on the specific microclimate created 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 may reflect 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 cover.⁸⁰ Although agricultural land conversion has led to enhanced global food production and economic development, there has been an associated increase in MBD risk.^{2,81-87} Agricultural land has specific localised impacts on important MBD correlates such as livestock numbers and water management practices.⁸⁰ In particular, livestock production, may modify MBD dynamics by increasing blood meal availability for

the vectors⁸⁸ and provide competent reservoir hosts to maintain^{76,89} and even amplify⁷⁶ zoonotic pathogens. For instance, domestic pigs are ‘amplification’ hosts for Japanese encephalitis virus (JEV) since they mount high levels 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 JEV in Asia.⁹¹ Furthermore, livestock production may influence MBD risk via its interaction with climate change since it significantly contributes to global greenhouse gas emissions; conversely, climate change may influence disease transmission in domestic animal populations.⁴⁴

Irrigation and dam creation have led to marked changes in the risk of global MBDs such as Japanese encephalitis, lymphatic filariasis (LF) and malaria.^{83,84,86,92,93} These practices lead to a dramatic expansion in vector breeding habitat⁹⁴ and may extend disease transmission seasons,⁸³ alter seasonal transmission dynamics in endemic areas⁸⁶ and enable pathogen spread into non-endemic areas.^{91,95,96} However, the effects of these schemes on vector populations are complex and will also depend on vector species-specific life-history traits.²¹ For example, *Culex quinquefasciatus*, a major vector of LF in Asia, prefers to breed in clean water whereas conspecific, *Culex tritaeniorhynchus*, principal vector of JEV, favours stagnant water.⁹⁷

Importantly, irrigation practices may also affect the socioeconomic status of a region which can influence MBD dynamics. The ‘paddies paradox’, whereby land conversion for irrigation leads to an initial increase and then decrease in MBD risk, has been reported for malaria in Africa⁸³ and Asia.⁸⁶ This phenomenon is postulated to reflect increasing socioeconomic status in the region associated with improved crop production. Other possible mechanisms include changes in ecology which limit vector abundance⁹⁸ and reduce pathogen spread over time.⁹⁹ With future expansion of irrigation practices and dam construction expected,^{93,100,101} their influence on disease risk requires consideration.

Urbanisation

The majority of recent urbanisation has occurred in developing countries, where rapid and unregulated urban settlements have caused a huge strain on public health programmes. In 2016, 54% of the global population was reported to reside in urban areas; a significant increase from 34% in 1960. This trend looks set to continue¹⁰² with 2.5 billion people predicted to augment the world's urban population by 2050, predominantly in Asia and Africa.¹⁰³ Increasing numbers of people living in high densities may lead to higher overall pathogen transmission risk for some MBDs,¹⁰⁴ while high levels of travel and trade in urban hubs can enable the spread of vectors and pathogens between population centres.^{9,104-106} Nevertheless, the impact of urbanisation on MBD risk is complex since evidence suggests both an expansion of some diseases and contraction of others.

For instance, urban expansion has promoted the emergence of arboviruses transmitted by *Ae. aegypti*, such as dengue, chikungunya and zika (Table 1),^{9,106-108} by influencing resource availability and climatic factors that alter mosquito community ecology.²¹ The phenomenon known as the urban heat island (UHI), whereby urban areas experience warmer temperatures than surrounding rural areas,¹⁰⁹ may 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 Vectors such as *Ae. aegypti* and *Ae. albopictus*, are well-adapted to urban areas,¹¹⁰ and breed in water containers, drains and gutters, with limited competition or predation.²¹ However, the relative impact of urbanisation on vector populations is unlikely to be geographically uniform since urban environments represent a diverse spectrum of habitat mosaics which vary in microclimatic features¹¹¹ and socioeconomic status.²¹

In contrast, increased urban development has also been associated with the global decrease in malaria over the past century.^{56,112} However, the underlying mechanisms remains unclear.

Urbanisation has been shown to reduce infectious disease burdens, likely via improved health care, education and employment when compared with rural areas.¹¹³ Nevertheless, reductions in disease risk may mask strong inequalities that exist within urban populations, especially in low 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 further important drivers of MBD risk.^{114–116} For malaria, there is a strong negative association between reported disease risk and national gross domestic product per capita (GDPpc).¹¹⁵ This association may reflect either high rates of malaria transmission in impoverished settings or 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 MBDs includes direct costs of health provision and control programmes (i.e., vaccination and vector control), and indirect costs (i.e., impacts on education, demographics and human movement).^{57,115} Furthermore, macroeconomic costs may occur due to the influence of disease on foreign investment, trade and tourism.⁵⁷

Sometimes these factors combine to impede economic development and strengthen the relationship between poverty and disease^{57,118,119} leading to ‘poverty traps’; a self-reinforcing mechanism enabling poverty and diseases to persist.¹²⁰ This may be accelerated by the

development of synergistic diseases referred to as syndemics, as seen with LF and HIV in East Africa.¹²¹ Escaping from these traps is particularly difficult for underprivileged rural populations who generally rely on subsistence agriculture, have poor access to healthcare and suffer high rates of infectious diseases. A further complexity arises when disease risk is a function of underlying production systems, e.g., livestock are a major feeding resource for Rift Valley Fever vectors and rice paddies are a major habitat component for JEV vectors. Since the currency of the rural poor is often biological (i.e., crops and livestock, human health and nutrition) and the dynamics of this currency can exist within ecological systems, economic development may be tied to 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 (e.g., use of federal funds or international aid) can allow areas with high endemic disease burden to escape disease-poverty feedbacks.¹²² This economic development may then act to reduce contact between people and mosquitoes via vector protection, improved housing and environmental management (e.g., larvicide treatment, vector habitat destruction).^{3,123} Moreover, there is often a reduction in hazardous behaviours such as accessing high risk areas for resource exploitation or settlement.⁶² While the weight of evidence suggests economic growth reduces MBD risk, it also results in increased movement of people, animals and commodities, with 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 MBD research that considers interactions between global change processes,^{55,126} these dynamics and potential resulting trade-offs that either positively or negatively impact 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 last 30 years and malaria which has contracted in the same period (Figure 2). This comparison helps to illustrate the fact that climate is just one part of an overall mechanism that is changing the epidemiology of MBDs.

Dengue

Although climate change is known to directly influence dengue transmission, Messina et al.¹²⁷ suggested that other global change processes and their interactions with climate are likely to have a greater effect in the more immediate future.¹²⁷ The rapid global emergence of dengue within the past 50 years¹²⁸ is related to interacting drivers including urbanisation, socioeconomics, climate change, travel and trade.^{129,130} For instance, the significant expansion of urban areas after World War II, especially in Asia, meant 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 vectors then increased in urban landscapes due to the higher numbers of human hosts and the abundance of suitable breeding habitats.^{12,21} Furthermore, complex interplay between UHI, pesticide use and vector competition have been reported to impact vector competence and influence dengue transmission.²¹

Malaria

Much research has pointed to interactions between malaria transmission, land conversion, socioeconomics and human movement.^{86,131,132} For instance, a recent study coupled MBD dynamics with socioeconomic outcomes that occurred during land transitions¹³² and found it was common for an initial increase in malaria transmission to occur after land-use change, followed by either a further rise or a decline in transmission. This is postulated to arise due to ecological changes that promote transmission (e.g., altered breeding sites and human-vector contact rates) occurring at a much faster rate than economic changes which can reduce transmission risk (e.g., improved housing and public health infrastructure). This analysis provided a theoretical explanation for empirical observations 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 on which each driver acts on a system.

The interacting effects of climate change and socioeconomic factors are also predicted to dramatically influence malaria risk over longer timescales. A study found that the projected population at risk in 2050 was estimated to be 5.2 billion when only climatic effects were considered, 1.74 billion when only GDP effects were considered and 1.95 billion when both factors were considered.¹³³ This indicates that climate change may 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 MBD risk are significant, the influence of other global change processes and their interactions occur over shorter timescales and therefore are likely to have greater impact in the immediate future.¹³⁴ Considering the effect of climate change in isolation may result in inaccurate predictions of MBD risk which may influence the formulation of robust policy recommendations for these emerging diseases. This 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 (e.g., health, environmental and socioeconomic), future global change scenarios (e.g., climate emission scenarios), and the structure of models and their outputs.

We advocate future research to adopt a holistic system dynamics approach (Figure 3) whereby the relationships and the feedbacks between socioeconomic and environmental systems are considered.¹³⁵ However, to achieve this, several research gaps need to be addressed: Firstly, enhanced surveillance and evaluation of public health measures is needed to improve health data and define the factors that promote disease risk. Secondly, empirical research is required to describe the relationships between vectors, pathogens and global change processes to improve parameterisation of MBD risk models. Thirdly, more high resolution, large-scale datasets for other global change processes are needed to match the quantity of climatic data available. Furthermore, research is required to understand the scale at which different global change processes influence MBD risk, and how to incorporate multiple scales into MBD transmission models.^{16,28,44}

Addressing these gaps requires improved funding for empirical research and long-term surveillance at varying geographic scales, and enhanced collaboration between researchers working within different disciplines of MBD 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 from real-time perspectives.^{136–138} High-resolution satellite remote sensing (RS) data is available for variables including land-use, climate and human populations at a global scale over large time periods. For example, current Sentinel satellite RS data products are available weekly at 10 metre resolution¹³⁹ and can be produced into environmental datasets via machine learning approaches. Mobile phone data has also been used to map patterns and processes in human populations,¹⁴⁰ and to examine the effect of human movement on disease transmission data.¹⁴¹ For example, human mobility estimates generated from mobile phone data can accurately predict the distribution and timing of dengue epidemics in Pakistan.¹⁴¹ In addition, citizen science projects are engaging members of the public to record data such as mosquito occurrence via applications on their mobile phones.^{142,143}

CONCLUSION

Previous MBD research has tended to focus 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, whereby relationships between socioeconomic and environmental drivers are considered, may improve future MBD projections and facilitate stakeholder engagement by demonstrating 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.¹³⁵

CONTRIBUTORS

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

DECLARATION OF INTERESTS

We declare no competing interests.

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SEARCH STRATEGY AND SELECTION CRITERIA

We searched PubMed and Web of Science, for all papers from 1st January 2014 to 28th March 2018 inclusive to reflect the field since the publication of the WHO published ‘A global brief on vector-borne diseases’ in 2014 which called for further research (WHO 2014). 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 studies were included in the analysis if they considered the effects of climate change over several decades rather than within-decade timescales.

GLOSSARY

Mosquito-borne disease risk: the probability that the simultaneous presence of an infected host and competent vector may impact a susceptible population.¹⁴⁴

Correlative models of MBD: use statistical approaches to identify correlative associations of disease risk to a suite of explanatory variables such as environmental or socioeconomic conditions.

Mechanistic models of MBD: make explicit assumptions about the biological or environmental processes that drive disease risk.

TABLES

Disease	Mosquito vectors	Estimated or reported number of cases per annum
Malaria	<i>Anopheles</i>	212 million (148–304 million)
Dengue	<i>Aedes</i>	96 million (67–136 million)
Lymphatic filariasis	<i>Aedes, Anopheles, Culex</i>	38.5 million (31.3–46.7 million)
Chikungunya	<i>Aedes, Anopheles, Culex, Mansonia</i>	693 000 (Americas)
Zika virus disease	<i>Aedes</i>	500 000 (Americas)
Yellow fever	<i>Aedes, Haemagogus</i>	130 000 (84 000–170 000) (Africa)
Japanese encephalitis	<i>Culex</i>	42 500 (35 000–50 000)
West Nile fever	<i>Culex</i>	2 588

Table 1. Number of cases per annum for the major mosquito-borne diseases of global health significance and the genera of associated mosquito vectors. Adapted from WHO ‘A global brief on vector-borne diseases’,² and ‘Global vector control response 2017–2030’.¹

FIGURES

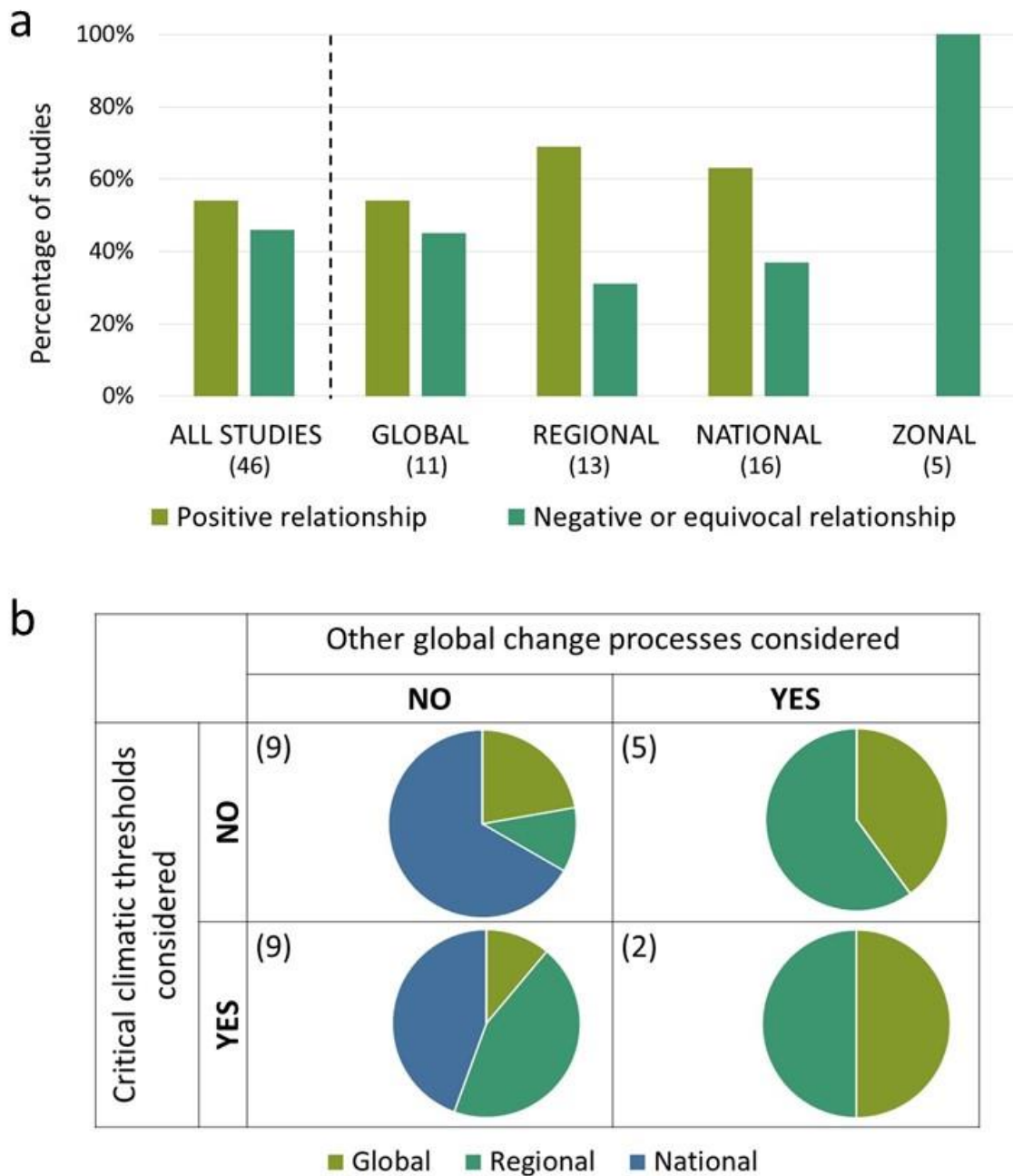


Figure 1. Systematic review of the impact of climate change on MBD risk. (a) Percentage of studies predicting a positive (light green), negative or equivocal (dark green) relationship between climate change and MBD risk per geographic region; number of studies reviewed per region are indicated in parenthesis. (b) Number of positive studies that consider the influence of other global change drivers in their models and/or critical climatic thresholds affecting the vector competence of mosquitoes, per by geographic region.

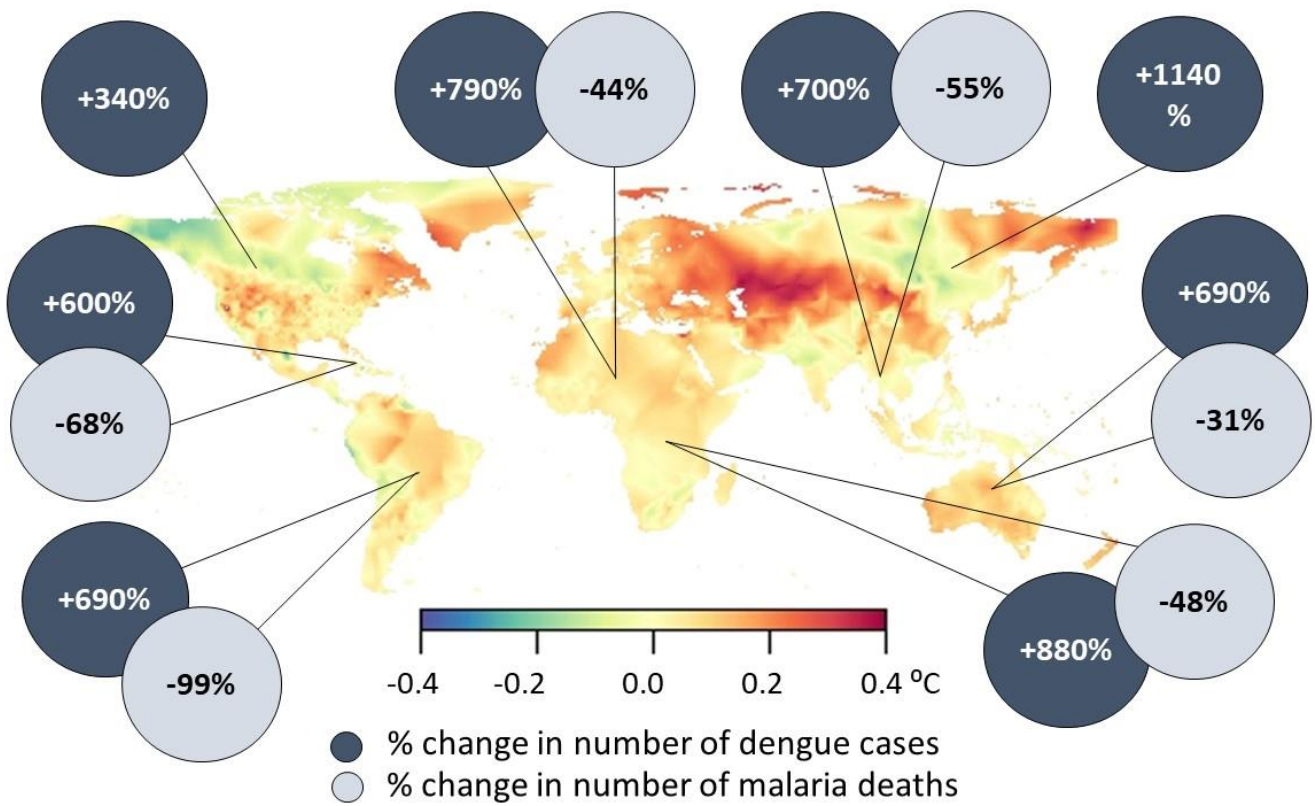


Figure 2. Percentage change in dengue cases and malaria deaths between 1993 and 2013 per WHO region overlaying annual mean land temperature (°C) change within the same period. WHO regions include; Latin America, Caribbean, North America, North Africa and Middle East, South and Southeast Asia, Central and East Asia, Oceania, Sub-Saharam Africa. Climatic data was accessed via the Climatic Research Unit and case data retrieved from the Global Burden of Disease Survey 2013.^{5,144}

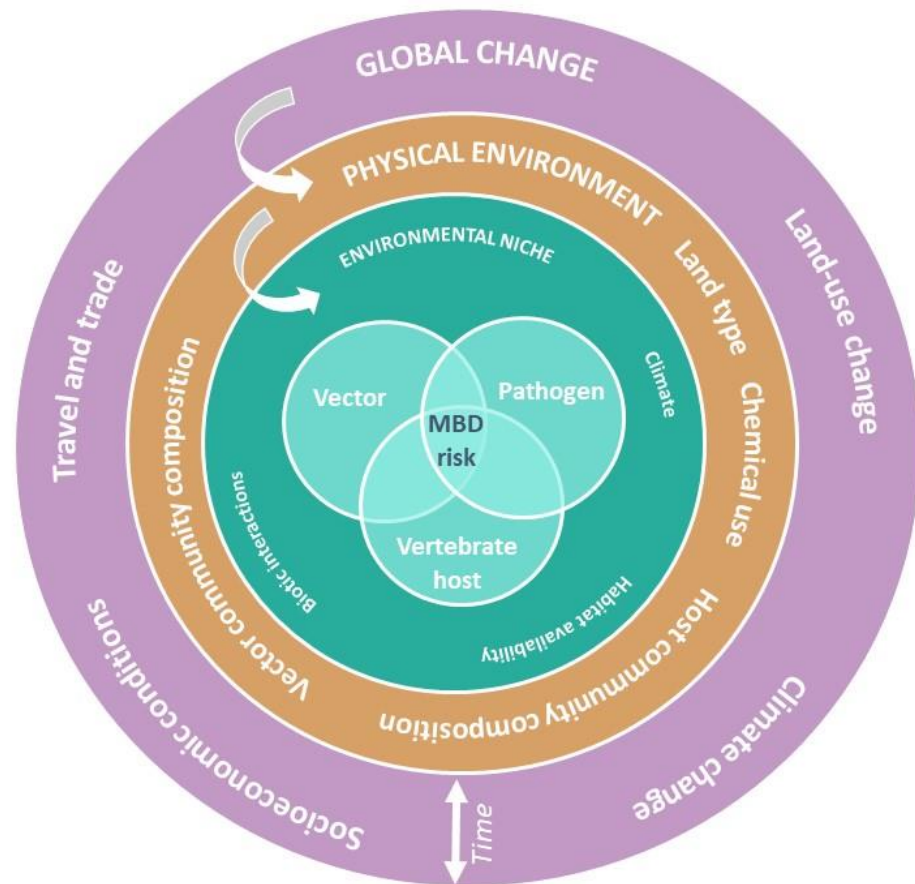


Figure 3. A system dynamics approach to understanding MBD risk. A conceptual model to show a system approach to understanding MBD risk whereby public health outcomes are influenced by complex interactions between environmental and socioeconomic systems. For disease transmission to occur requires the environmental niche of the pathogen, vector and vertebrate host to overlap. The environmental niches of these groups are influenced by the wider physical environment which varies in habitat quality and composition of vector and host (animal and human) communities. Acting on these environmental systems are major global change drivers such as land-use type, climate change, socioeconomic conditions, travel and trade that interact to influence MBD risk.

SUPPLEMENTARY MATERIALS

Table S1. Results of systematic review of modelling studies published from 2014- March 2018, that investigated the impact of climate change on mosquito-borne disease. The table shows the spatial scale of the study, the disease and mosquito vectors, the type of model and projection and, the climatic parameters analysed. The table illustrates the direction of the relationship between the climatic parameters and the change in distribution of disease transmission risk. Details are provided regarding whether mosquito biological thresholds and other global change drivers were considered within the study.

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Table S1. Results of systematic review of modelling studies published from 2014- March 2018, that investigated the impact of climate change on mosquito-borne disease. The table shows the spatial scale of the study, the disease and mosquito vectors, the type of model and projection and, the climatic parameters analysed. The table illustrates the direction of the relationship between the climatic parameters and the burden of disease or vectors. Details are provided regarding whether mosquito biological thresholds and other global change drivers were considered within the study.

SPATIAL SCALE and AUTHORS	DISEASE	MOSQUITO VECTORS	MODEL TYPE	STUDY PROJECTION	CLIMATE PARAMETERS INCLUDED	DIRECTION OF RELATIONSHIP (+ or -)	CONSIDERED CRITICAL CLIMATE THRESHOLDS*	CONSIDERED OTHER GLOBAL CHANGE DRIVERS
ZONAL								
Australia								
(1)	Dengue	<i>Aedes aegypti</i>	Mechanistic	Prospective	T, P, H	(equivocal)	Y	N
(2)	MVEV	<i>Culex annulirostris</i>	Mechanistic	Prospective	T, P, H	-	Y	Y [#]
China								
(3)	(NA)	<i>Aedes albopictus</i>	Mechanistic	Retrospective	T	+/-	Y	N
Kenya								
(4)	Malaria	(NA)	Mechanistic	Prospective	T	+/-	Y	N
(5)	RVF	<i>Culex quinquefasciatus</i> , <i>Culex univittatus</i> , <i>Mansonia africana</i> , <i>Mansonia uniformis</i>	Correlative	Prospective	T, P	+/-	N	Y ^δ
Spain								
(6)	(NA)	<i>Anopheles atroparvus</i> , <i>Culex pipiens</i> , <i>Culex theileri</i> , <i>Culex modestus</i> , <i>Culex perexiguus</i> , <i>Ochlerotatus caspius</i> , <i>Ochlerotatus detritus</i>	Correlative	Prospective	T, P, H, W, S, E, Ph	(equivocal)	N	N
NATIONAL								
Australia								
(7)	(NA)	<i>Ae. albopictus</i>	Hybrid correlative	Prospective	T, P, S, Sm	+	Y	N
(8)	Dengue	(NA)	Mechanistic	Prospective	T, P, H	-	Y	N

Brazil								
(9)	Dengue	<i>Ae. aegypti</i>	Correlative	Prospective	T, P	-	N	N
Germany								
(10)	(NA)	<i>Ae. albopictus</i>	Correlative	Prospective	T, P	+	N	N
Iran								
(11)	Malaria	<i>Anopheles</i> spp.	Correlative	Retrospective	T, P, H	+/-	N	N
Mexico								
(12)	(NA)	<i>Ae. albopictus</i>	Correlative	Prospective	T, P	+	N	N
(13)	Dengue	<i>Ae. aegypti</i>	Correlative	Prospective	T, P	+	N	N
Republic of Korea								
(14)	Malaria	(NA)	Mechanistic	Retrospective	T	+	N	N
Serbia								
(15)	(NA)	<i>Ae. albopictus</i>	Mechanistic	Prospective	T, P, Ph	+/-	Y	N
Taiwan								
(16)	JEV	(NA)	Correlative	Retrospective	T, P, H, Ph	+	N	N
Tanzania								
(17)	Dengue	<i>Ae. aegypti</i>	Correlative	Prospective	T, P	+	N	N
(18)	RVF	<i>Culex pipiens</i> complex	Correlative	Prospective	T, P	+/-	N	N
United Kingdom								
(19)	(NA)	<i>Cx. pipiens</i>	Mechanistic	Prospective	T	+	Y	N
USA								
(20)	WNV	<i>Cx. pipiens, Culex tarsalis</i>	Mechanistic	Prospective	T, P	+	Y	N
(21)	Dengue	<i>Ae. aegypti</i>	Mechanistic	Prospective	T, P	+	Y	N
(22)	(NA)	<i>Ae. albopictus</i>	Mechanistic	Prospective	T, Ph	-	Y	N
REGIONAL								
Africa								
(23)	Malaria	<i>Anopheles arabiensis</i>	Correlative	Prospective	T, P	-	N	N

(24)	Malaria	<i>An. gambiae</i>	Mechanistic	Prospective	T	+	Y	Y ^v
Europe								
(25)	(NA)	<i>Ae. albopictus</i>	Correlative	Prospective	T, P	+	N	Y ^e
(26)	Dengue	(NA)	Correlative	Prospective	T, P, H	+	N	Y ^β
(27)	WNV	<i>Ae. albopictus</i>	Correlative	Prospective	T, P	+	N	N
(28)	(NA)	<i>Ae. albopictus</i>	Mechanistic	Prospective	T, P, H	+	Y	N
(29)	(NA)	<i>Aedes albopictus</i> , <i>Aedes japonicus</i>	Correlative	Prospective	T, P	+/-	N	N
(30)	(NA)	<i>Ae. albopictus</i>	Correlative	Prospective	T, P, Ph	+	Y	N
(31)	Dengue	<i>Ae. aegypti</i> , <i>Ae. albopictus</i>	Mechanistic	Retrospective and prospective	T	+	Y	N
(32)	WNV	(NA)	Correlative	Prospective	T	+	N	Y ^γ
North America								
(33)	(NA)	<i>Ae. albopictus</i>	Mechanistic	Prospective	T, P	+	Y	N
South America								
(34)	Malaria	<i>Anopheles</i> spp.	Correlative	Prospective	T, P	+/-	N	Y ^δ
South and Southeast Asia								
(35)	Malaria	<i>Anopheles</i> spp.	Hybrid correlative	Prospective	T, P, H	+/-	Y	N
GLOBAL								
(36)	(NA)	<i>Ae. aegypti</i>	Mechanistic	Prospective	T	+/-	Y	N
(37)	Dengue	<i>Ae. aegypti</i>	Correlative	Prospective	T, P, H	+/-	Y	N
(38)	(NA)	<i>Ae. aegypti</i>	Correlative	Prospective	T, P	+	N	N
(39)	(NA)	<i>Ae. aegypti</i> , <i>Ae. albopictus</i>	Correlative	Prospective	T, P	+	N	N
(40)	Zika, Dengue	<i>Ae. aegypti</i> , <i>Aedes africanus</i> , <i>Ae. albopictus</i>	Correlative	Prospective	T, P	+	N	Y ^δ
(41)	Malaria	<i>An. gambiae</i> , <i>Anopheles stephensi</i>	Correlative	Prospective	T	-	Y	N
(42)	WNV, LF, SLEV	<i>Cx. quinquefasciatus</i>	Correlative	Prospective	T, P	+/-	N	N
(43)	Zika	<i>c.</i> , <i>Ae. albopictus</i>	Mechanistic	Retrospective	T, P, El Nino event	+	Y	N
(44)	(NA)	<i>Cx. quinquefasciatus</i>	Mechanistic	Theoretical	P	+/-	Y	N

(45)	Chikungunya	(NA)	Correlative	Prospective	T, P	+	N	Y ^λ
(46)	(NA)	<i>Ae. aegypti</i>	Correlative	Prospective	T, P	+	Y	Y ^β

Abbreviations: (NA), data not available; MVEV, Murray Valley encephalitis virus; RVF, Rift valley fever; JEV, Japanese encephalitis virus; SLEV, St Louis encephalitis virus; LF, lymphatic filariasis; WNV, West Nile virus; T, temperature; P, precipitation; H, humidity; W, wind; S, solar radiation; E, evapotranspiration; Ph, photoperiod; Sm, soil moisture;

*Inclusion of critical climate thresholds that may impact specific vector life history traits (e.g. temperature thresholds for mosquito survival).

Land cover, human population density; animal host migration

δ Land cover

¥ Land cover, human population density

€ Trade

β Human population density, urbanisation, GDP per capita

γ Land cover, animal host migration

λ Human population density

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