CHAPTER THREE

Climate Change and the Neglected Tropical Diseases

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Abstract

Climate change is expected to impact across every domain of society, including health. The majority of the world's population is susceptible to pathological, infectious disease whose life cycles are sensitive to environmental factors across different physical phases including air, water and soil. Nearly all so-called neglected tropical diseases (NTDs) fall into this category, meaning that future geographic patterns of transmission of dozens of infections are likely to be affected by climate change over the short (seasonal), medium (annual) and long (decadal) term. This review offers an introduction into the terms and processes deployed in modelling climate change and reviews the state of the art in terms of research into how climate change may affect future transmission of NTDs. The 34 infections included in this chapter are drawn from the WHO NTD list and the WHO blueprint list of priority diseases. For the majority of infections, some evidence is available of which environmental factors contribute to the population biology of parasites, vectors and zoonotic hosts. There is a general paucity of published research on the potential effects of decadal climate change, with some exceptions, mainly in vector-borne diseases.

1. INTRODUCTION

Much has been written about climate change and its potential impact on civilisations in the coming decades. The news is rarely positive—from predicting an increasing frequency of el Nino events (Cai et al., 2014) to reduction in biodiversity (Mantyka-Pringle et al., 2015) and reduced wheat production (Asseng et al., 2015). There are likely to be substantial effects on illness and mortality statistics, disproportionately affecting poorer regions (Patz et al., 2005). The consensus now rests with those who consider the anticipated change to be anthropogenic in nature. Despite this consensus, however, there is still much uncertainty about what the future holds for wider aspects of human health (Wardekker et al., 2012).

Within the wider domain of climate and health, the neglected tropical diseases (Hotez et al., 2006), often abbreviated to NTDs, are a collection of infectious diseases affecting hundreds of millions of individuals living

in tropical countries. In recent years, there has been considerable increase in investment towards reducing the burden of several NTDs (Molyneux et al., 2017), but they still collectively contribute to productivity loss (reviewed by Conteh et al., 2010), illness and suffering in many countries, including several within the G20 (Hotez, 2014). Recent estimates of their overall burden suggest NTD kill over 350,000 people per annum and cause the loss of between 27 and 56 million disability-adjusted life years (Hotez et al., 2014).

Climate change projections are typically associated looking forward several decades, often reaching out as far as 100 years or more (Collins et al., 2013). NTDs are a contemporary issue and are subject to attempts to eliminate them as a public health problem, or even eradicate them from the planet. The timescale for these activities is typically around a decade. At the time of writing, the dates 2020 and 2030 feature prominently in documents including the WHO roadmaps (World Health Organisation, 2012, 2013a, 2016a).

The latest WHO documents regarding the roadmap for NTD control also mentions climate change in a number of places (World Health Organisation, 2017). There exists a 'Climate and Health atlas', published in 2012 (World Health Organisation, 2013b) that is referred to by the WHO literature, and 'which explores the numerous and variable effects of climate change on infectious diseases, including NTDs'. On closer inspection, however, the Climate and Health Atlas contains only material on meningitis, dengue, malaria and diarrhoea.

Simultaneous to the technical and targeted approaches being recommended by WHO are much wider attempts at sustainable development, most visible through the lens of the sustainable development goals (Griggs et al., 2013). Aspects of the NTD impact on health and productivity permeate many SDG themes (Bangert et al., 2017), including Goal 3 (Health), which even contains a target for NTDs, namely Target 3.3: 'By 2030, end the epidemics of AIDS, tuberculosis, malaria and neglected tropical diseases and combat hepatitis, water-borne diseases and other communicable diseases' (Fitzpatrick and Engels, 2016).

Success in implementing the WHO plans and the SDGs could spell the end for some or all the NTDs. But considerable literature exists, primarily derived from studies of parasites affecting wildlife that global environmental change may lead to responses by hosts, vectors and parasites themselves that could affect the outcome of interventions (Cable et al., 2017). Thus, it will be important to consider not just meeting targets set within the SDG and WHO documents, but how those targets are met.

In reviewing how decadal climate change may impact on the future transmission of the NTDs, it is necessary to be somewhat pessimistic and assume that most NTDs are not going to be eliminated or eradicated by 2030. This includes assuming that policy change associated with SDG Goal 13 'Action on Climate' does not result in returning the climate to preindustrial levels—a target that at the time of writing looked increasingly unreachable (UNEP, 2017).

The tension between contemporary knowledge and future projections can be resolved partially by deploying a universal caveat—namely by stating that future projections may be valid, 'all other things being equal'. Given future uncertainties in terms of climate change scenarios (described below), it is highly unlikely that anything will remain equal over the coming decades. Anthropogenic activities connected to, or independent of, climate change will also have an impact, e.g., through early case detection combined with equal access to medicines. The point of existing research into climate change and health is therefore not to give definitive conclusions but to reach interim conclusions that feed into the next round of projections which can consider a range of natural and anthropogenic interventions.

The 'precautionary principle' as applied widely to environmental science (Kriebel et al., 2001), and specifically to climate change (Hallegatte, 2009) is also relevant in terms of understanding why climate change research is important. Under this principle, it is not necessary to fully understand the factors that underpin and contribute to a particular situation in order to take action. However, it is also important to recognise that (1) any particular action can have unintended consequences and (2) linearly scaled up solutions do not always work as intended across all scales of intervention (Mangham and Hanson, 2010). Thus, applying the precautionary principle in terms of action against climate change, or any other domain contained within the SDGs, may not sufficient to guarantee a future free of NTDs.

2. AIMS

The main aims of this chapter are (1) to review crosscutting issues that are likely to affect future transmission of NTDs, (2) to provide information about the current state of the art with respect to investigations into climate change and NTD transmission and (3) to identify gaps in knowledge with a view to identifying potential areas of research activity. The review considers 34 different species of established or emerging public health importance, drawn from the WHO list of NTDs and the WHO blueprint list of priority diseases. Infections are listed in Table 1 along with brief descriptions of their climate-sensitive life stages.

Table 1 List of Infections Considered Within This Chapter Drawn From the WHO R&D Blueprint Diseases (A) and the WHO NTD List (B), Together With Their Poikilothermic (Climate Sensitive) Stages and/or Vectors and/or Zoonotic Hosts

A. WHO Priority Diseases	Vectors	Zoonotic or Intermediate Hosts	Poikilothermic Stages
Arenaviral haemorrhagic fevers (including Lassa fever)	—	*Mastomys* spp.	*Mastomys* urine, faeces
Crimean Congo Haemorrhagic Fever (CCHF)	Ioxid ticks	—	—
Filoviral diseases (including Ebola and Marburg)	—	Diverse taxa including bats and apes	—
Corona viruses (MERS-CoV and SARS)	—	Bats and palm civets	Bat excreta and aerosolised virus
Nipah and related henipaviral diseases	—	Fruit bats	Bat excreta
Rift Valley fever (RVF)	Various mosquitoes including *Anopheles* and *Culex*	—	—
Severe fever with thrombocytopenia syndrome (SFTS)	Ioxid ticks	—	—
Zika	*Aedes*	—	—

B. WHO NTD List	Vectors	Zoonotic or Intermediate Hosts	Poikilothermic Stages
Buruli ulcer	*Naucoridae*	Fish and shellfish	Unknown
Chagas disease	*Triatominae*	Dogs and other mammals	—
Dengue	*Aedes*		
Echinococcosis	—	*Canidae*, farmed mammals	Eggs in soil
African trypanosomiasis	*Glossina*	—	—

Continued

Table 1 List of Infections Considered Within This Chapter Drawn From the WHO R&D Blueprint Diseases (A) and the WHO NTD List (B), Together With Their Poikilothermic (Climate Sensitive) Stages and/or Vectors and/or Zoonotic Hosts—cont'd

B. WHO NTD List	Vectors	Zoonotic or Intermediate Hosts	Poikilothermic Stages
Leishmaniasis	*Phlebotominae*	Dogs	
Leprosy	—	—	Bacterium in water
Lymphatic filariasis	*Anopheles* and *Culex*	—	—
Onchocerciasis	*Simulium*	—	—
Rabies	—	Dogs and bats	—
Schistosomiasis	—	Water snails	Miracidia and cercaria
Soil-transmitted helminthiasis	—	—	Eggs in soil
Guinea worm		Copepods	Larvae
Cysticercosis	—	Swine	Eggs in soil
Trachoma	*Musca*	—	—
Fascioliasis		Freshwater snails	Eggs, miracidia and cercariae
Paragonimus		Crustaceans	Eggs, miracidia and (meta) cercariae
Clonorchiasis and Opisthorchiasis		Freshwater snails, fish and crustaceans	Eggs, miracidia and (meta) cercariae

3. A PARASITOLOGIST'S GUIDE TO CLIMATE CHANGE

Detailed insights into the causes and drivers of climate change are available elsewhere (IPCC, 2013). To understand how climate change may change the landscape of transmission for NTDs, I begin with some macroscale considerations of the underpinning physics of climate change and a description of how we interpret the climate change vernacular.

Historic observations support the basic tenet of climate change which is that increasing levels of so-called greenhouse gases have driven upwards the global mean surface temperature (Hartmann et al., 2013). The characteristic of a greenhouse gas is that it influences 'radiative forcing' towards a more positive value. Radiative forcing is defined as a rate of change in energy per unit area (measured in W/m^2) of the upper atmosphere. As greenhouse gasses (also known as radiative forcing components or climate sensitivities) trap more of the incoming energy from the sun, so the ratio of incoming vs reflected energy gets greater and the radiative forcing value increases (Fig. 1).

The Intergovernmental Panel on Climate Change (IPCC) has adopted several representative climate change scenarios throughout its working history. The aim of these scenarios has consistently been to present policymakers and research scientist possible outcomes associated with specific narratives which have then been modelled using methods summarised later. The first iteration of these scenarios consisted of so-called 'Special Report on Emissions Scenarios' (Nakicenovic et al., 2000). They are known as A1, B1,
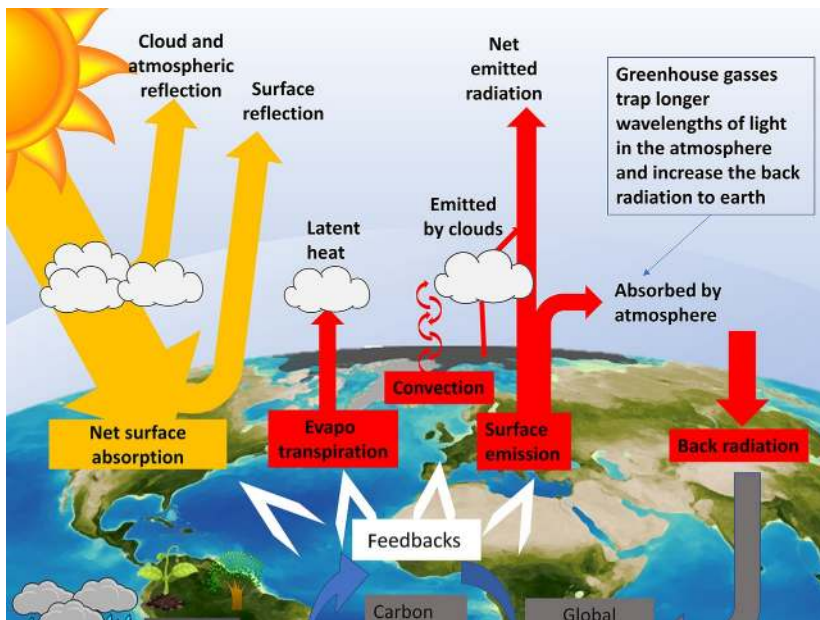

Fig. 1 The role of greenhouses in terms of climate change is to affect the balance between surface and atmospheric energy absorption and emission (the energy budget). Increasing the back radiation will affect global temperature changes, the carbon and water cycles and have both direct and indirect effects at various scales across multiple domains of organisation as illustrated in Fig. 2.

A2 and B2. The A1 scenario predicts a future world that converges in terms of rapid economic growth, and rapid introduction of more efficient technologies. The A2 scenario indicates a more fragmented world with slower rates of development. The B1 scenario describes a convergent world with a static population, and the B2 scenario describes a world with intermediate population growth and technological development.

The so-called relative concentration pathways (RCPs), rather than being based on socioeconomic scenarios, use radiative forcing narratives to project global warming trends over the coming decades. They differ from the SRES family by decoupling climate modelling from scenario development and thereby allow for independent modelling of specific interventions, rather than having them built in at the onset. These scenarios are known as RCP2.6 (van Vuuren et al., 2011a), RCP4.5 (Thomson et al. 2011), RCP6 (Masui et al., 2011) and RCP8.5 (Riahi et al., 2011). The nomenclature of these pathways corresponds specifically to the anticipated change in the global average level of radiative forcing in the year 2100 compared to preindustrial levels. So, for example, RCP2.6 represents a change of $2.6 \ \mathrm{W/m^2}$ over this time period.

The RCPs have been developed over several years by research teams that modelled changes to the atmosphere based on projected anthropogenic drivers of greenhouse gasses. Each RCP imagines a particular future where levels of CO_2 and other gasses are either reduced or increased by changes in the drivers of emissions. For example, RCP2.6 is the output of models that combine reforestation programmes, reduced methane emissions and moderate population growth. Conversely, RCP8.5 considers a future where methane emissions increase substantially, there is considerable population growth and continued heavy reliance on fossil fuels. RCP2.6 is considered to be 'reversible' and in the underpinning models it is suggested that emissions will peak in 2050 before returning to historically normal values by 2100. Conversely, RCP8.5 summarises a future of no climate policies and no possibility of return to historic levels of emission.

RCPs are associated with integrated assessment models (van Vuuren et al., 2011b) to produce time series data of emissions that act as inputs into more complex Atmosphere-Ocean Global Circulation models (AOGCMs). The next step in producing state-of-the-art projections is to develop earth system models (ESMs) that include both land and ocean biogeochemistry. Combining AOGCMs and ESMs leads to multimodel 'experiments' that project global temperature, precipitation and other variables over coming decades. The experiment known as CMIP5 is capable of producing dozens

of different simulated output variables (Taylor et al., 2012) including snow-fall flux, zooplankton carbon concentration, near-surface wind speed, evapo-ration, soil temperature and water content. The spatial and temporal resolutions of these outputs can be specified depending on need and within the limits of the available IT infrastructure. Daily estimates of precipitation and temperature are now available, for example through the NASA Earth Exchange Global Daily Downscaled Projections (NEX-GDDP) at a temporal resolution of 1 day and a spatial resolution of 0.25 degree (approximately $25 \times 25\,km$). One of the crit-icisms of highly detailed models is that as they become more realistic, they become more uncertain (Maslin and Austin, 2012).

4. CROSSCUTTING ENVIRONMENTAL AND ANTHROPOCENTRIC ISSUES

Evidence suggests that recent climate change is already affecting the phenology of a wide range of organisms across the globe (Walther et al., 2002). From the relatively simple concept of climate forcing springs a hugely complex and interactive web of interacting ecosystems that might impact on the ecology of hosts, parasites and vectors over both time and space. This idea has been previously and commonly referred to as chaos theory, or the but-terfly effect, originally proposed by Lorenz (1963) in terms of long-term weather prediction. Below I summarise some important elements of antici-pated change that evidence suggests may impact on NTD ecology.

4.1 Asynchrony

Life cycles of several parasitic infections, particularly those with a life cycle involving a vector or intermediate host, rely on circadian rhythms to ensure that transmission stages are available at the same time as the host is exposed to the intermediate host or vector. For example, it has been long established that malaria parasites exhibit circadian patterns in emergence from red-blood cells (Mideo et al., 2013), and also well known that schistosome cercariae exhibit a circadian pattern of emergence from snail hosts (Mintsa-Nguéma et al., 2014). Less well known is that humans excrete eggs of schistosome par-asites in a circadian pattern, with peak excretion late morning (Doehring et al., 1983; Hawking, 1975). Climate change has the potential to create asynchrony by either changing host behaviour (e.g. time of faecal expulsion change as a result of abiotic and biotic pressures on host behaviour), or by disrupting the availability of hosts at the time required to complete the life cycle (e.g., by forcing a range shift). Evidence for this occurring already

has emerged from studies of livestock carrying *Nematodirus battus* (Gethings et al., 2015).

The net result of asynchrony may be to reduce disease in the short term, but it may also place a selection pressure on the parasites, selecting those variants that induce the host to expel transmission stages at a time appropriate to the new system. Variation in the timing of peak output of schistosome cercariae from snails has been recorded across different species of definitive host (Théron, 2015)—indicating that selection pressures can alter circadian emergence patterns. It remains to be seen whether the selection pressure will be sufficiently strong to produce new timing peaks in the future, and whether the potential for reducing disease will be offset by increased abundance of both vectors and hosts.

4.2 Scale

NTD is so called because their geographical distribution is bounded by environmental conditions normally encountered between the lines of latitude denoted as the tropic of Cancer and Capricorn. There is some evidence that the width of the tropics, or at least the arid tropical edge, is increasing northwards and southwards at a rate of between 0.5 and 1 degrees latitude in each direction each decade (Lucas et al., 2014), possibly in part due to stratospheric ozone depletion at the poles (Kang et al., 2011). What remains unclear is not just how best to measure changes in the area constituting the tropics and subtropics (reviewed by Lucas et al., 2014), but also how individual vegetation and other zones within the geographic tropics will vary locally in their biotic and abiotic characteristics.

Climate change is likely to have an effect at every scale of biological, social, ecological and geographical organisation (Fig. 2). Local scale considerations are important in terms understanding the effects of climate change on NTDs because the life history traits of many species of organism involved in NTD life cycles are tied to a particular environmental envelope. Ecologists continue to debate whether or not heterogeneity in abiotic resources at a particular scale is associated with diversity of organisms (Lundholm, 2009), but it remains true that microclimatic variation is a driver of species abundance at a very local level. The availability of specific habitats is a requirement for many vector and intermediate host species. For example, eggs of helminth species require specific abiotic and biotic conditions to thrive. Intermediate snail hosts require vegetation that is anchored in a substrate that will supply appropriate nutrients.
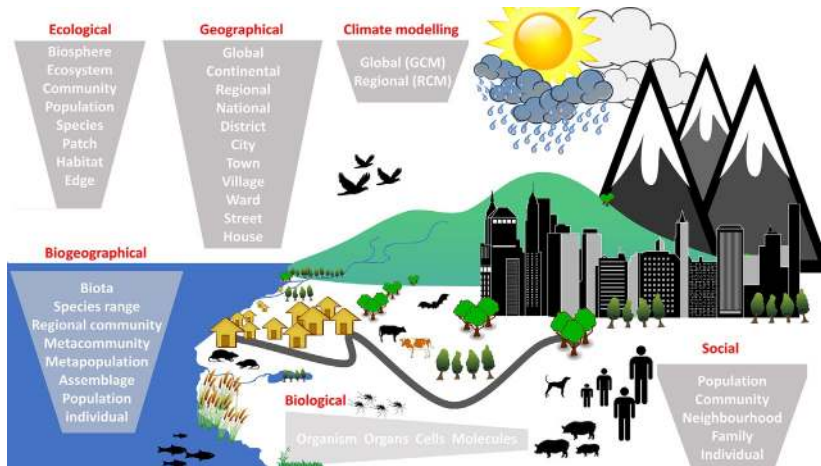
Fig. 2 Illustration of the range of scales within ecological, biogeographical, social and geographical domains of organisation that will be affected directly or indirectly by climate change. The terms 'macro' and 'micro' are relative to each domain.

The relationship between spatial diversity in abiotic, biotic resources, host availability and parasite distribution remains poorly understood in the NTD context. Studies of wildlife populations offer some insights into the drivers of current relationships (Ellis et al., 2015), pointing to a complex system of host–switching and localised adaption driven by host availability at specific locations.

As the local soil and water chemistry alters as a result of changes to the local climate, it can be expected that current patterns of heterogeneous transmission will change in the future. Areas that are currently unsuitable for transmission, perhaps because of a lack of suitable vegetation to support an intermediate or zoonotic host, may become more suitable at some point in the future.

4.3 Population Movement, Urbanisation and Growth

While considering the effects of changing temperature and precipitation patterns is a vital component of understanding climate change and NTDs, it is also necessary to take a step sideways to consider other anthropocentric aspects of global environmental change that are directly or indirectly connected to climate change.

Population movement for reasons ranging from tourism to labour migration is an important component in the epidemiology of several NTDs

(Aagaard–Hansen et al., 2010). Urbanisation, as a major subdomain of population movement is now considered to be not just a driver of climate change (Kalnay and Cai, 2003), but also a consequence of climate change (Barrios et al., 2006). As people move to the cities because of, e.g., failing crops due to prolonged drought (Barrios et al., 2006), they will contribute to increased emissions and potentially expose themselves to NTDs that thrive in urban situations, including Dengue (Were, 2012).

Water demand. Global water demand is projected to increase significantly, particularly in terms of water needs for irrigation (reviewed by Wang et al., 2017). Globally, water scarcity is expected to increase (Gosling and Arnell, 2016). The fragmented nature of the change (van Vliet et al., 2013) may lead to selective national or international population migration from at risk areas, as has been observed in various countries (reviewed by Obokata et al., 2014), including Ethiopia (Gray and Mueller, 2012), Mexico (Nawrotzki et al., 2015) and South Africa (Mastrorillo et al., 2016). Fig. 3 illustrates known international movements attributable to water-based climatic factors such
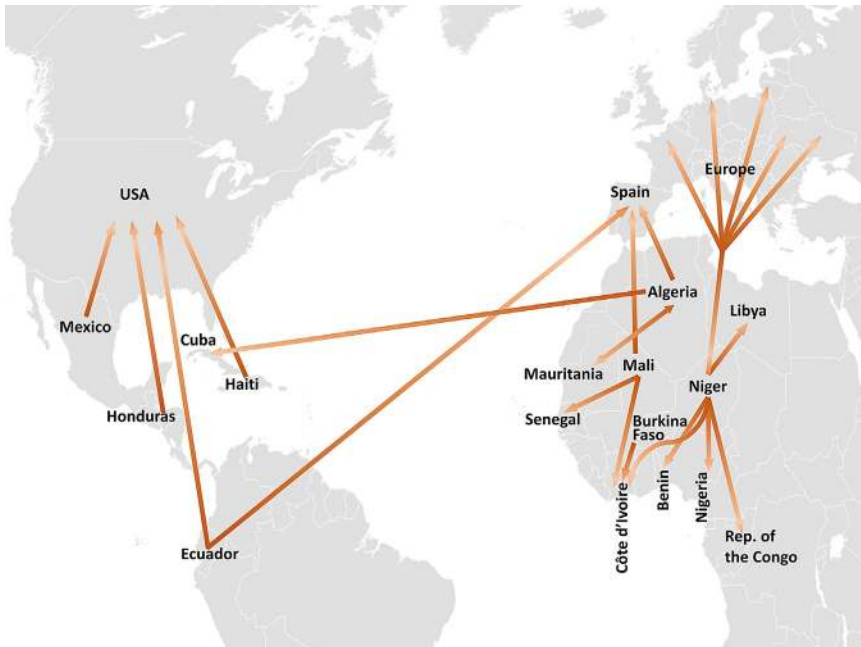

Fig. 3 Known population movements attributable to climate-based issues including drought and natural disasters. Points of departure and destination are country level and based on table 2 of Obokata et al. (2014).

as drought and flooding. This occurs alongside and in addition to internal and crossborder migration, often temporary, which has a multitude of environmental causes (Reuveny and Moore, 2009). Understanding the role of climate-associated migration is important as individuals who migrate may carry parasites and cause new outbreaks, as has been observed recently in Corsica, where *Schistosoma* hybrids have been observed and attributed to the mixing of imported *Schistosoma haematobium* and local *Schistosoma bovis* (Boissier et al., 2016).

Urbanisation is associated with population growth (Cohen, 2006), but not necessarily in a readily predictable or linear manner. Within Africa alone, the population is expected to double to 2 billion by 2050 (United Nations, 2015), but several models and observations suggest complex patterns of migration and countermigration depending on the motives and opportunities (Geyer and Geyer, 2015). Increasing levels of urbanisation associated with population increase (Satterthwaite, 2009) is nonetheless likely to impact on the climate substantially—e.g., as land-use changes are enacted (Pielke, 2005), as habitats are altered and fragmented (Haddad et al., 2015), as biodiversity decreases (Mooney et al., 2009). Human–wildlife interactions in both rural (Aryal et al., 2014) and urban (Becker et al., 2015) locations will inevitably change over the coming decades as a result of these and other changes.

4.4 Agriculture and Farming

A large fraction of people exposed to NTDs is smallholders or subsistence farmers dependent on natural water cycles to support crops and/or livestock. Evidence suggests that climate-associated events such as prolonged drought, delayed onset of rains, or above normal precipitation can adversely affect a range of livelihood assets (Ziervogel and Calder, 2003). Small holders and poorer farmers are more likely to be concerned about heavy rainfall, but may have no livelihood response due to a lack of assets and entitlements (Cooper and Wheeler, 2017). This effect may not be universal, as there is also evidence that farming communities have adapted to harsh environments over many generations (Kassie et al., 2013; Mortimore and Adams, 2001) to include allocating labour differentially across seasons to mitigate unpredictable precipitation patterns, increasing biodiversity and diversifying livelihoods.

Food demand and production are likely to change considerably in coming decades due to population growth, direct and indirect effects of

climate change (Valin et al., 2014). Various large-scale effects have been speculated including risks to global food security (Wheeler and von Braun, 2013) through, e.g., loss of freshwater for irrigation (Elliott et al., 2014). Simultaneously, the demand for water for aquaculture is rising, bringing the potential for food-borne diseases to become a major issue in coming decades. Almost 60 species of fish-borne trematode have been described (Hung et al., 2013). Infections among farmed fish have been associated with aquaculture practices in several SE Asian countries (reviewed by Lima dos Santos and Howgate, 2011). Concerns have also been raised regarding potential spillover from wildlife populations into tilapia productions in China (Li et al., 2013). The encroachment of wildlife into human communities is also expected to increase with increased urbanisation, habitat encroachment, loss and fragmentation (Hassell et al., 2017.)

For NTDs with a zoonotic life cycle that can involve domesticated animals, the potential effects of climate change cannot be ignored. Livestock is a driver of climate change due to the emissions of greenhouse gasses within the system (Gill et al., 2010). Thornton et al. (2009) consider various potential effects including change in quality and quantity of feed, heat stress and water security. Potential effects on transmission of infections in livestock animals have been reviewed by Baylis and Githeko (2006), who suggest that climate change is likely to have been responsible for the introduction of several infectious diseases into new areas including bluetongue virus in the United Kingdom, but also suggest that *Fasciola* infections in the United Kingdom may decline due to lower levels of summer rainfall.

4.5 Exposure, Vulnerability and Risk

This review concentrates largely on the ecology and natural history of infections, as this where most of the literature on NTDS and environmental change is located. In the IPCC framework on vulnerability and adaptation (IPCC, 2014), the information contained herein would contribute to understanding future hazards, as distinct from exposures or vulnerability. The term 'Hazard', quoting directly from IPCC (2014), refers to 'The potential occurrence of a natural or human–induced physical event or trend or physical impact that may cause loss of life, injury, or other health impacts, as well as damage and loss to property, infrastructure, livelihoods, service provision, ecosystems, and environmental resources'. The term 'Exposure' refers to 'The presence of people, livelihoods, species or ecosystems, environmental functions, services, and resources, infrastructure'. The term

'vulnerability' refers to 'The propensity or predisposition to be adversely affected. Vulnerability encompasses a variety of concepts and elements including sensitivity or susceptibility to harm and lack of capacity to cope and adapt'. The term 'Risk' refers to the '… probability of occurrence of hazardous events or trends multiplied by the impacts if these events or trends occur. Risk results from the interaction of vulnerability, exposure, and hazard …'. Fig. 4 illustrates how these issues are connected and interact in the context of climate change and NTDs.

Vulnerability is a contested term in the risk–reduction community (Füssel, 2007) but has its roots in geography and social sciences, often referring to indicators such as socioeconomic status, the political economy, human agency and social capital. In relation to infectious diseases, vulnerability has been historically assessed in these contexts for HIV, TB and Malaria in Europe (Bates et al., 2004). The EU funded Healthy Futures programme (www.healthyfutures.eu) adopted the IPCC vulnerability–hazard-risk framework to produce risk maps related to decadal climate change in the context of Rift Valley Fever, Malaria and *S. mansoni* in East Africa (Taylor et al., 2016). In that project, stakeholder analysis and expert consultation were deployed to provide weighted indicators that could be included in the vulnerability domain. A comparative approach to estimating vulnerability that compared the expert-weighting approach to statistical modelling found high concordance in the context of modelling vulnerability to Dengue (Hagenlocher et al., 2013).

5. ENVIRONMENTAL PHASES

5.1 Soil

Soil is the upper covering layer of the earth, consisting of three subphases (water, gas and solids) which combine to describe the overall mechanics and other properties. Typically, soil properties vary in terms of texture (particle size and distribution), chemical and mineralogical properties, surface area and particle aggregation (related to aeration, compaction, temperature and water retention). The overall structure, mechanics and properties of a soil matrix are also influenced by a range of other factors such as the amount and properties of organic matter (detritus), oxides, clays, living vegetation, bacteria and fungi.

Recent theoretical and empirical studies have improved understanding of soil processes, mainly from the viewpoint of ensuring 'soil security' (Amundson et al., 2015). However, there are still many gaps in knowledge
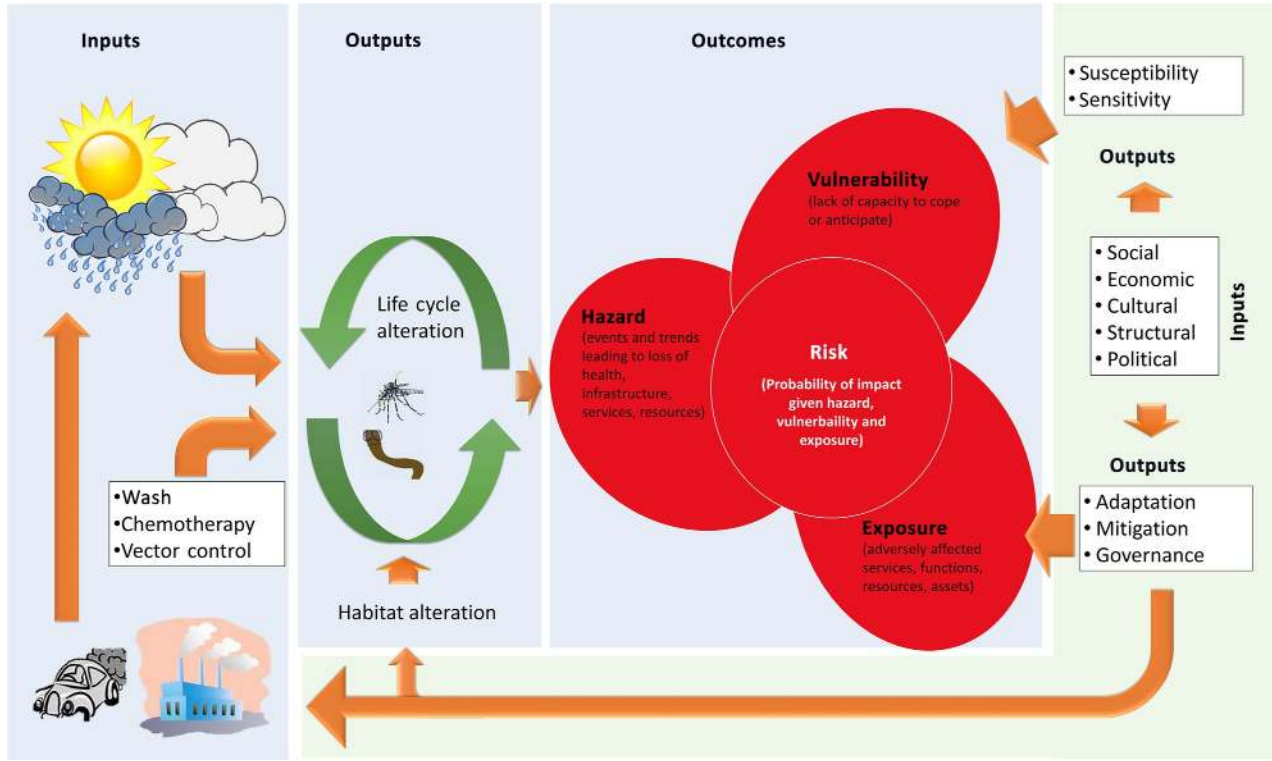
Fig. 4 A core concept of the IPCC (2014) report on vulnerability and adaptations is that risks to populations are formed by interactions between sources of hazard, vulnerability and exposure. In the context of NTDs, natural and anthropogenic inputs—including interventions such as WASH and vector control—combine to affect the life cycles of climate-sensitive stages (the hazard). Simultaneously a wide variety of societal inputs can affect vulnerability and exposure levels, and can lead to mitigations that modify emissions and habitats to affect the NTD-associated hazard. A lack of adaptive inputs is likely to lead to higher exposure, vulnerability, hazards and risk.

of how a changing climates might affect 'soil health'—defined as 'the capacity of a specific kind of soil to function, within natural or managed ecosystem boundaries, to sustain plant and animal productivity, maintain or enhance water and air quality, and support human health and habitation' (Doran and Zeiss, 2000).

Soil is essential to the natural history of many parasites and/or their vectors; examples include eggs of geohelminths (Steinbaum et al., 2016), larvae of Tsetse flies (Leak, 1999) and burrows of mammals fed on by triatominae insects (Miles et al., 1981). An understanding of how changes to the soil phase will affect the survival of these and other life stages is an essential component of understanding the wider impact of climate change on transmission. Part of this process is likely to include a better understanding of how microgeographical variation in soil chemistry affects herb-layer vegetation (Bruelheide and Udelhoven, 2005).

5.2 Water

A central tenet of climate change is rising temperatures in the water phase, including freshwater and marine domains (see above). Temperature change, combined with population growth, and many other factors related to future aspects of landscape, hydrology, human behaviour, water and sanitation infrastructure, water- and land-use, is likely to have profound effects on many aspects of the water budget. The global hydrological cycle is thereby expected to undergo potentially profound changes (Held and Soden, 2006). Here I summarise some of the key aspects that are relevant to NTD natural history.

5.2.1 Precipitation

It is likely that anthropogenic influences differentially affected precipitation during the 20th century depending on region—with increase precipitation in (very broadly speaking) northern latitudes and decreased precipitation in southern latitudes (Zhang et al., 2007). Projecting precipitation patterns into the 21st century has proved more challenging than temperature (Schaller et al., 2011). Consensus is emerging that extremes of precipitation are likely to increase in frequency (Knapp et al., 2015). Also of concern is increased frequency of drought (Dewes et al., 2017) and flooding (Hirabayashi et al., 2013), although there is still considerable debate on the role of anthropogenic drivers underpinning these changes (Kundzewicz et al., 2014). This alteration in hydrological stability may nonetheless impact on not just aquatic habitats (Marino et al., 2017), groundwater and streamflow

(Taylor et al., 2013) but also the carbon cycle (Haverd et al., 2017), soil moisture and vegetation phenology (Richardson et al., 2013). Effects may include fragmented changes to freshwater systems, due to, for example, changes to location-specific river discharges (Schewe et al., 2014) and recharges (Hartmann et al., 2017).

Increased precipitation in urban areas without adequate capacity to adapt or mitigate the situation has been associated with outbreaks of Dengue in several countries, including India (Mutheneni et al., 2017) and Bangladesh (Karim et al., 2012). Similarly, abundance of freshwater snails acting as intermediate hosts in the schistosome life cycle, as well as transmission of the parasite, are known to peak at specific times of year, depending on location (reviewed by Rollinson, 2011) and driven by climatic factors including rainfall (e.g. Moser et al., 2014).

Climate change-driven changes to the water balance, such that affect soil moisture conditions, are also likely to affect suitability of specific habitats for soil–transmitted helminths. Seasonality of hookworm transmission in several countries including South Africa (Mabaso et al., 2003), Nigeria (Nwosu and Anya, 1980) and Timor Leste (Wardell et al., 2017) has been at least partly attributed to seasonal precipitation.

5.2.2 Thermal Tolerance

Thermal tolerance may be a critical issue for many water-based, or semi-aquatic organisms involved in the life cycles of NTDS—including insects, freshwater snails, fish, crabs, copepods, crayfish and insects. Poikilothermic ectotherms such as these consume oxygen based on the water or temperature until some threshold temperature where ATP supply and demand is over-whelmingly disrupted and the organism dies (Poertner, 2001). Tropical species may have relatively wide tolerances, but may also be more vulnerable to increases in temperature due to already inhabiting water bodies with temperatures close to their thermal limits (Sunday et al., 2012). Whether mean increases in temperature are more important than changes in diurnal variation is being debated in the literature (Vasseur et al., 2014).

5.2.3 Stratification

The life cycles of several NTDs including *Schistosoma*, the food-borne trematodes and *Dracuncula* involve intermediate hosts that may inhabit and reproduce in water bodies with thermal stratification, such as lakes. Analysis of historic data indicates that global warming is associated with changes to lake stratification that are dependent on lake morphometry (Kraemer et al., 2015a). How the intermediate hosts will respond over the coming

decades is unclear, but evidence suggests evolution may have led to divergent populations of copepods that have adapted to warmer or colder conditions (Wallace et al., 2014).

5.2.4 Sea Levels

Rising sea levels are expected to impact significantly on coastal areas, not just in terms of flood risk but also in terms of the influx of salt water into coastal fresh water systems. Evidence of the effects on ecosystems is emerging in the literature. For example, saltwater intrusion into tropical rivers can affect the bacteria of floodplain soils by altering both the salinity and pH (Nelson et al., 2016). Increase in the influx of brackish water in coastal areas due to sea level changes has been implicated as the reason behind an increase in the abundance of salinity-tolerant *Aedes* mosquitoes in the Sri Lankan context (Ramasamy and Surendran, 2012).

5.2.5 Mitigation

Mitigating the challenges outlined above through providing sustainable water resources forms part of SDG Goal 6—the other key component for NTDs being access to sanitation and hygiene 'for all' by 2030. This latter aspect, commonly termed water, sanitation and hygiene (WASH) is considered crucial in reducing transmission of STH (Freeman et al., 2013), trachoma (Stocks et al., 2014), schistosomiasis (Grimes et al., 2014) and *Entamoeba* (Speich et al., 2016).

   Our warning from history on this subject is quite clear. Development projects with all good intentions, related to water infrastructure in particular, have themselves been associated with increased transmission of parasitic infections including malaria in unstable areas (Ijumba and Lindsay, 2001; Kibret et al., 2017), filariasis (Erlanger et al., 2005) and schistosomiasis (e.g. N'Goran et al., 1997). In the latter case, concerns have been raised recently about how a large-scale water conservation project could translocate *Oncomelania hupensis* (an intermediate host snail of *S. japonica*) in China (Liang et al., 2012; Zhu et al., 2017), how migration of seasonal workers related to dam construction might have led to admixture of *S. mansoni* populations in Senegal (Van den Broeck et al., 2015), how dam construction could affect the transmission of *Schistosoma mekongi* in Laos (Attwood and Upatham, 2012) and prevent the migration of snail-eating prawns across sub-Saharan Africa (Sokolow et al., 2017). These and other examples remind us of the importance of implementing health in all policies (Rudolph et al., 2013) when undertaking sustainable development projects.

5.3 Air

The central tenet of climate change is the forcing effects of so-called 'greenhouse' gasses including CO_2 and aerosols. Forcing in this context means the impact that production of these gasses has on the balance of energy in the atmosphere. As greenhouse gasses increase in density, they tip the energy balance positively and positive forcing ensues. All climate models derive from this process and then simulate how varying degrees of forcing will affect global air and land surface temperatures.

Tropical climates are typically governed by the Intertropical Convergent Zone (ITCZ). The ITCZ is a belt of low pressure surrounding the earth close to the equator that moves between the tropics of cancer and capricorn at different times of year. It is this movement that generates the characteristic dry and rainy seasons in countries located within the tropics (for animation click here): http://www2.palomar.edu/users/pdeen/animations/23_weatherpat.swf.

The dynamics and positioning of the ITCZ are highly sensitive to small changes in the global energy balance (Sachs et al., 2009; Schneider et al., 2014). Models struggle to predict the future dynamics of the ITCZ (Bony et al., 2015), and until the models can project the future of the ITCZ in relation to climate scenarios it will be challenging to model the transmission of NTDs effectively.

The relationship between surface air temperature (as predicted by climate projections) is generally assumed to be correlated, over decadal scales, with the ground surface temperature, but over shorter time scales there may be considerable variability. Soil acts as a heatsink and conducts heat from the air on a daily timescale, resulting in some level of phase shifting that depends on location and other variables including precipitation (Smerdon et al., 2004). Abiotic changes to the soil as a result to changes in air temperature may affect the natural history of a wide range of NTDS as diverse as trypanosomes and cestodes.

6. CROSSCUTTING MODELLING ISSUES

6.1 Scale

Downscaling is a recently developed process, derived from subnational weather forecasting, to improve the spatial resolution of GCMs over limited areas (Dickinson et al., 1989). A broad and accessible overview of the methodologies is available elsewhere (USAID, 2014). Here I summarise some of the key methods.

Statistical downscaling is a two-step process that involves understanding statistical relationships between observations at one point over time and GCM outputs at that location over the same time period, and correcting the GCM output to more closely resemble the observations (also known as bias correction). Statistical downscaling is computationally inexpensive but has low utility if the observations are scarce over time and space, and/or if the relationship between GCM and observations changes over time.

Dynamical downscaling (also known as generating regional climate models or RCM) is a process whereby a GCM is run and the lateral boundary outputs at the edge of the RCM region are used as the initial conditions of an RCM using the same physics-based model as the GCM but at a higher spatial resolution and over a relatively small area. The output of this computationally intensive process is a climate model at relatively high spatial resolution compared to the GCM (typically less than 0.5 degree).

In the context of understanding how climate change might affect local scale transmission of NTDs, RCMs arguably have greater utility than statistical models as they can be run on relatively sparse observations. Their disadvantage, apart from computing costs, is that each individual model can output widely differentiated products in regions with complex climates and widely varying but sparse observations (e.g. the tropical regions). For this reason, RCMs are often combined into ensembles with multiple outputs summarised into a single model that represents the average of all models in the ensemble. RCM ensembles, made available through the coordinated regional climate downscaling experiment have been used to model future precipitation over the African continent (Nikulin et al., 2012).

Despite recent advances, none of the current models predict or project temperature at a microgeographical scale, which is considered a major limitation in estimating how a particular organism may be vulnerable to a future climate (Scheffers et al., 2014; Storlie et al., 2014). Furthermore, the choice of RCP tends to be arbitrary as there are many possible future climate scenarios (Fuss et al., 2014), and a more objective approach is therefore needed when selecting a particular scenario (Casajus et al., 2016). Estimating precipitation continues to challenge the modelling community, due partly to the complex interaction between temperature and rainfall (Zhang et al., 2007), including the influence of fine-scale drivers of cloud formation and rainfall.

6.2 Absence vs Missing Data

All models are limited by the absence of data. There is a need to distinguish between absence and missing data in order to reduce potential bias. In their attempts to address this issue when working on leishmaniasis, Carvalho et al. (2015) tested several ecological niche modelling algorithms and concluded that the inclusion of absence data improved model performance. A range of modelling approaches benefit from inclusion of absence data (Li and Guo, 2013) if a survey has been undertaken in the area and the absence has been confirmed by direct observation. If there has been no survey in a particular area the data are missing and cannot be used in place of absence data. This is one of the major factors preventing accurate mapping of several NTDs or their vectors. The Maxent approach, as used by authors researching various parasites including leishmaniasis Peterson and Shaw (2003) and lymphatic filariasis (Slater and Michael, 2012) is a valuable tool for analysing presence-only data. Process–based mapping issue, as used by Stensgaard et al. (2016), can ameliorate the problem to an extent by predicting where the environment may be suitable for a vector or intermediate host based on the results of experimental observations.

6.3 Uncertainty and Bias

Uncertainty is a fact of climate projections from which it is difficult to escape. It is not possible to draw data from the future and there are many possible intermediate scenarios as depicted in Fig. 5. We could end up in 2100 at any one or none of the points on this chart. The RCPs offer useful touch points for comparative purposes, but every projection of the impact of climate change must acknowledge the inherent uncertainty.

To illustrate the uncertainty regarding estimating the potential impact of climate change on NTDs, consider Fig. 6. As surface temperatures warm there may be differential effects on transmission of NTD infections depending on regional environmental changes. For example, in some places the regional climate may become too extreme to support vectors or zoonotic hosts, whereas in others an extreme flooding event may translocate vectors or zoonotic hosts from one part of a river system to another. This level of uncertainty places additional challenges on modelling future scenarios of not just schistosomes but all NTDs due to their tight association with specific environments.

Bias is another universal feature of climate models. Future trends in warming and precipitation are based on simulations of historic events. Simulations of those past events produce results that are different to observations.
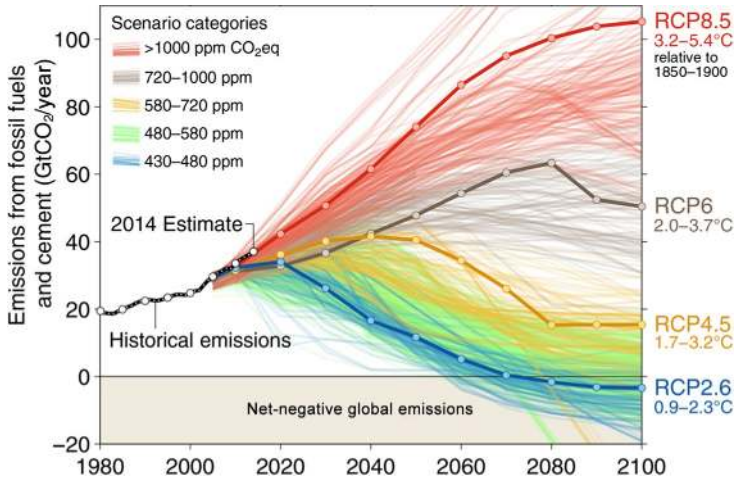
Fig. 5 Historical and potential future CO_2 emission scenarios to the year 2100, with four representative concentration pathways (RCP2.6, RCP4.5, RCP6 and RCP8.5). *Reproduced with permission from Fuss, S., et al., 2014. Betting on negative emissions. Nature Climate Change 4 (10), 850–853. Nature Publishing Group, a division of Macmillan Publishers Limited. All Rights Reserved. Available at: https://doi.org/10.1038/nclimate2392.*
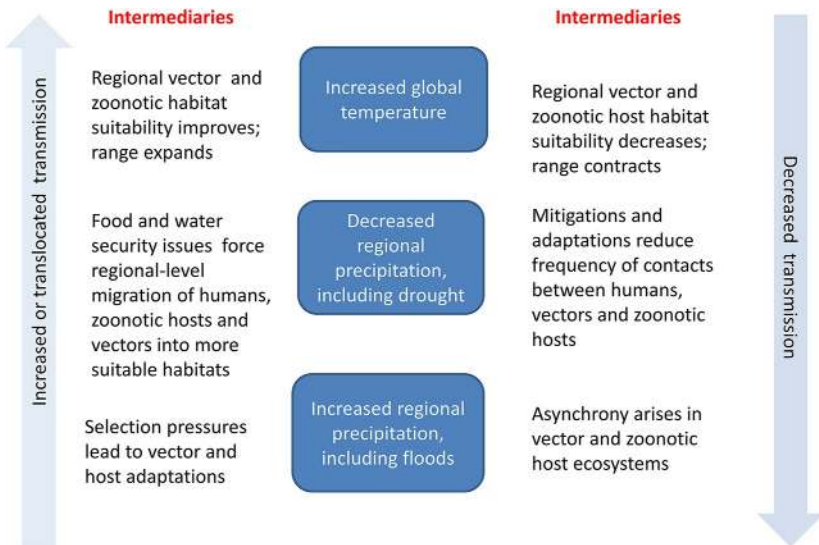
Fig. 6 Generalised framework of how increases in global temperatures and regional changes to precipitation patterns may lead to increased, translocated or decreased transmission of NTDs. *Central column* describes particular temperature and precipitation changes associated with climate change. *Left column* describes intermediary steps that might be expected to increase or translocate transmission. *Right column* describes intermediary steps that could lead to reduced transmission.

This is referred to as bias, and the bias is then carried over into future projections. Bias correction involves correcting the future simulations so that they more accurately predict the future. The simplest method is the so-called 'delta' method (e.g. Hay et al., 2000). This approach requires calculating the difference between observed and simulated climate from the past and applying the difference to simulations of the future. There are several different types of bias correction available, which are detailed elsewhere (e.g. Teutschbein and Seibert, 2012).

7. CROSSCUTTING VECTORS AND ZOONOTIC HOSTS

7.1 Mosquitoes

Several genera of mosquitoes are involved in the life cycles of vector-borne NTDs. Here, I briefly describe factors affecting the life history traits of three of the main vectors—*Aedes*, *Culex* and *Anopheles*. For a more comprehensive review of oviposition, see Day (2016).

7.1.1 Aedes

This urban dwelling mosquito is perhaps the most sensitive indicator of how environmental change can affect transmission of vector-borne diseases. Many different NTDs are transmitted by various species of *Aedes*. Two of the most prominent *Aedes* species in terms of the number of diseases that can be transmitted via their feeding mechanism are *Aedes albopictus* and *Aedes aegypti*. *A. albopictus* has been observed to carry Yellow fever virus (YFV), Chikungunya viruses, West Nile virus, Eastern equine encephalitis, Japanese encephalitis. It can also transmit dog heartworm. *A. aegypti* can transmit both Dengue and YFV as well as Chikungunya, Zika virus and Mayaro virus.

Some information is available on how *Aedes* mosquitoes respond to pressures exerted by short-term environmental change. For example, it is now known that gene flow is higher in wet than dry seasons due to transient selection pressures (Sayson et al., 2015) and that interaction between vectors and viruses that alters the carrying capacity of the mosquito to vary over time and space also likely to be important determinants of future transmission in particular locations (Lambrechts et al., 2009; Yee et al., 2012).

A second important factor may be diapause (Jia et al., 2016, 2017). This feature of *Aedes* mosquitoes natural history allows them to suspend development during adverse environmental conditions, such as cold weather (Brady et al., 2013). Both temperature and photoperiodicity affect the length of dormancy (Yee et al., 2012). Photoperiodicity in particular has been

identified as a target for potential intervention, with efforts underway to identify genes that produce potential targets for genetic or chemical disruption (Huang et al., 2015).

A number of reasons have been cited as responsible for the lack of effectiveness of campaigns to eradicate *Aedes* mosquitoes historically, even after initial success. *Aedes* spp. oviposit in a wide range of man-made containers (Tun-Lin et al., 2009), adapt oviposition rates to local water conditions (Wong et al., 2012) and rest after feeding in places that are difficult to reach with insecticides, including storm drains (Paploski et al., 2016), and on dark wall surfaces across different rooms of houses (Chadee, 2013; Perich et al., 2000). From a climate change perspective, it will be important for modelling efforts to accommodate these extremely successful adaptations of the target mosquitoes to available environments. One of the key challenges will be to consider how future rates of urbanisation and climate change connect with issues such as precipitation, water collection and drainage (Moore et al., 2016; Semadeni–Davies et al., 2008).

7.1.2 Culex

As with other mosquito vectors, Culex spp. all life stages are ectothermic and therefore climate sensitive. Species of *Culex* are currently distributed across the globe. *Culex pipiens* complex is the most widely distributed, with mosquitoes inhabiting latitudes as far apart as Northern Europe and the South Island of New Zealand (Farajollahi et al., 2011). In terms of the NTDs covered within this chapter, *C. pipiens* complex is responsible for transmission of Rift Valley fever and lymphatic filariasis. *Culex quinquefasciatus* is distributed across the tropics and subtopics and is responsible for the transmission of lymphatic filariasis and possibly Zika virus (Diallo et al., 2014).

The development of *Culex* mosquitoes has been demonstrated to correlate with temperature in a number of studies. Gunay et al. (2011) observed that body size of inbred *C. quinquefasciatus* decreased with increasing temperature (covering the range 20–27°C). This result echoed earlier work by Rueda et al. (1990) who also observed *C. quinquefasciatus* body size parameters (including head capsule width, larval body widths and weight) decreased with temperature (covering the range 15–34°C). The parabolic nature of the relationship between temperature and survival was demonstrated also in that study, with the peak emergence occurring at temperatures between 20 and 30°C and high levels of mortality recorded at 15 and 34°C. A more comprehensive review of the relationship between

temperature and *Culex* life history traits is available elsewhere (Ciota et al., 2014).

Observations on the relationship between temperature and development of Culex mosquitoes have been used to inform investigations into the possible effects of climate change on the geographic distribution of *Culex* species. Morin and Comrie (2013), focusing on the southern United States, applied their dynamic mosquito simulation model (Morin and Comrie, 2010) to project the distribution of the mosquitoes up to 2050 under a down-scaled A2 climate scenario. The results of their analysis suggest a pattern of regional changes that reflect the complex topography of the location under study, but also an overall trend towards a lengthier mosquito breeding season combined with a lower abundance in summer months.

Focusing on a more global picture, Samy et al. (2016) combined observed occurrence data of the contemporary distribution of *C. quinquefasciatus* with climatic projections of temperature based on the RCPs (covering RCP2.6, RCP4.5, RCP6.0 and RCP8.5) and a set of biolimactic variables containing monthly temperature and rainfall data. Current potential distribution of the mosquito was then estimated by first estimating, using an ecological niche model, which bioclimatic variables were contemporaneously associated with the distribution of Culex. From this model, it was then possible to predict how different RCP scenarios may affect future geographical distribution. The conclusion from this work was that the limits of the geographical distribution would increase by up to 4.9% in the future (no specific date given) between RCP2.6 and RCP6.0 and then decrease under RCP8.5.

7.1.3 Anopheles

Mosquitoes of the *Anopheles* genus are responsible for the transmission of malaria and as such have been studied relatively extensively in terms of their biology and life history. Information on this vector is included here due to its role in transmission of *Wuchereria bancrofti* and *Brugia malayi* (Bockarie et al., 2008), but with the caveat that species–specific observations may not translate across species.

Anophelene mosquitoes generally lay their eggs singly onto water, and on hatching the larvae float horizontally to allow breathing. Exceptionally, viable *Anopheles gambiae* eggs have been observed in both moist soil (Minakawa et al., 2001), and dry soil (Bier et al.,) and treeholes (Omlin et al., 2007). The larvae are amphibious and will move towards water (Miller et al., 2007).

As all stages of all species are poikilothermic, the life history traits of the organism are tightly controlled by environmental conditions from egg laying onwards (Davies et al., 2016; Lyons et al., 2013). Several other environmental factors including pH, water flow and presence of algae are also important drivers of egg, larval, pupal and adult stage survival, larval feeding behaviour, larval—adult development time, gonotrophic cycle rate and population abundance (e.g. Araújo et al., 2012; Gouagna et al., 2012; Kamara et al., 2015).

Understanding the individual life history traits of individual species is necessary but not sufficient for modelling purposes. For example, a study in Nigeria by Lenhart et al. (2007) established that in Nigeria the relative contribution of *A. gambiae*, *Anopheles arabiensis* and *Anopheles funestus* to *Wuchereria bancrofi* transmission is likely to vary over a 12-month period. Competition between sibling *Anopheles* species (Paaijmans et al., 2009) may be partly responsible for the dominance of particular species at different times, combine with changes to water and/or soil phases that favour the development of one species over another.

Taking into account all the possible abiotic and biotic factors that influence *Anopheles* life history, understanding how climate change might affect the populations of Anopheles mosquitoes and transmission of filarial infections is therefore challenging. Evidence is nonetheless emerging that a mixture of anthropogenic activities related to land cover change, combined with increased temperatures, is shifting the species range in specific areas (e.g. Fuller et al., 2012; Kulkarni et al., 2016) and may either cause local extinction (Escobar et al., 2016), or an overall increase in environmental suitability combined with seasonal and range shifts (e.g. Ryan et al., 2015).

7.1.4 Bats

Bats are either known, or suspected, to be vectors of many zoonotic infections (Olival et al., 2017) including several filoviruses and hepanaviruses (Moratelli and Calisher, 2015; Olival and Hayman, 2014). Infections of humans via bats infected with filoviruses have tended to occur in outbreaks, which has been hypothesised to occur as a consequence of within–host dynamics (Plowright et al., 2016). Outbreaks of emerging viral infections, including filoviruses, have been increasing in recent decades (Smith et al., 2014) correlating with global environmental change.

Like many nonhuman mammals, bats are acutely susceptible to the impacts of environmental change, including climate change (Aguiar et al., 2016; Sherwin et al., 2013). The direction of travel is less certain than the

anticipation of change. Published species–distribution models suggest that the fruit bat *Pipistrellus kuhlii* has extended its range over recent decades as global temperatures have increased (Ancillotto et al., 2016). Extreme temperatures (>42°C) have been identified as fatal to flying foxes (Welbergen et al., 2008). A more complex, and localised, situation may exist across all species, given evidence that the call frequency is affected by temperature and humidity (Mutumi et al., 2016) and that efficiency of echolocation (and hence foraging success) is affected by temperature in a convex manner (Luo et al., 2014).

Known bat vectors of filoviruses include flying foxes and fruit bats (Table 1). An attempt to predict which of the other existing 1116 bat species could possibly host filoviruses suggests that candidate species tend to produce more than 1 L per year of relatively large neonates, inhabit relatively large geographic ranges of high mammal density and live in larger roosts (Han et al., 2016). One of the challenges in identifying bat vectors is the lack of pathology attributable to the viruses themselves, a situation that has led to the hypothesis that metabolic and internal temperature increases caused by flight may have led to the evolution of tolerance (O'Shea et al., 2014).

8. DIRECT LIFE CYCLE PARASITES

8.1 Goehelminths

At the time of writing this chapter, there were no original research articles retrievable through PubMed specifically referring to climate change and hookworm infections, climate change and geohelminths, climate change and *Ascaris lumbricoides* infections or climate change and *Trichuris trichiura* infections. I therefore summarise here what is known about the climate-sensitive stages of their life cycles to inform future efforts at statistical and/or dynamic modelling.

8.1.1 Trichuris

The climate-sensitive stages of the *Trichuris* spp. life cycle are eggs deposited onto the ground within faecal matter. Embryonation occurs at a pace dependent on temperature (Beer, 1973), with an optimum rate of development at approximately 34°C. At this temperature, embryonation and development to infective stages take approximately 2 weeks. These and other experiments of temperature on embryonation of *Trichuris suis* indicate a lower threshold of 20°C and an upper threshold of approximately 40°C for development of

the organism (Beer, 1973; Vejzagic et al., 2016). Typically, the soil needs to be moist (Spindler, 1929). Increasing the pH of the soil can reduce the survivorship of eggs (O'Donnell et al., 1984), in a temperature-dependent manner with a rapid reduction in survivorship under alkaline conditions (Ghiglietti et al., 1995).

Egg survival periods of 2–6 years have been suggested in temperate conditions (Beer, 1973). The upper temperature boundary of approximately 40°C for development to infective stages is similar to that reported in prevalence studies among school-aged children, where evidence of transmission has been observed in communities with land surface temperatures up to 45°C (Brooker et al., 2004). Other factors related to soil chemistry, including the level of quartz, may also be important in determining egg survival and viability—sandy soil channels may form down which the eggs fall to become incorporated into the subsoil and protected from environmental hazards (Brooker et al., 2004).

8.1.2 Ascaris

A. lumbricoides eggs, deposited onto soil within faecal matter, are the climate-sensitive stage of this roundworm parasite. They are more robust to environmental perturbation than either *Trichuris* spp. eggs or hookworm larvae due to being coated in chitin (Meng et al., 1981). Some studies have suggested the eggs may survive for several years in soil (Rudolfs in Storey and Phillips, 1985). Statistical analysis of bioclimatic data suggests that relatively moderate amounts of rain are associated with peak infection (Schüle et al., 2014).

Changes in relative humidity (RH) under experimental conditions reflect expected seasonal changes at certain latitudes, with much greater mortality under simulated field conditions that combined prolonged periods of simulated sunlight and dry soil conditions (Gaasenbeek and Borgsteede, 1998).

In experimental studies, a major determinant of egg longevity has been reported to be the level of ammonia in the faecal matter (Jensen et al., 2009; Pecson et al., 2007). A combination of ammonia, temperature and pH is also deterministic, with the majority of eggs able to survive at pH 7 in low ammonia conditions at 20°C for several 100 days, whereas conditions combining high pH with high ammonia at 40°C kill the eggs within minutes (Pecson et al., 2007). In separate studies, it has been reported that egg survival is also sharply determined by relative survival, with a fall from almost 100% 8-week survival at 100% RH to almost 0% 8-week survival at 7.5% humidity (Gaasenbeek and Borgsteede, 1998).

8.1.3 Hookworms

The climate-sensitive stages of hookworm infection are the eggs and larval stages. Much of our current understanding of how abiotic and biotic variables affect the natural history of these stages comes from research undertaken many decades in the past (e.g. Chandler, 1929). Like the other geohelminths the picture is still very incomplete, but nonetheless yields some relevant information.

The presence of hookworm infection is associated with particular bioclimatic variables related to temperature and moisture. Soil types are important with larvae thriving in particularly sandy soils (Mabaso et al., 2003). Efforts to map the ecological niche suggest arid areas and minimum temperatures of <20°C are inhibitory (Mudenda et al., 2012), as are temperatures above 30°C (Udonsi and Atata, 1987). The dependence on environmental cues for the behaviour of the juvenile worms indicates that a changing environment which is predisposed to longer periods of dryness is likely to be detrimental. Under stable and ideal soil conditions, the larvae may live for several weeks (Augustine, 1923). If the soil becomes more clay like due to perturbation the larvae are not likely to survive (Payne, 1923). If there is rapid alteration of drying and moistening, the larvae will likewise not thrive (Beaver, 1953).

8.1.4 Toxocara

Eggs of *Toxocara* species are deposited onto land by canids and other animals upon excretion of faecal matter. The eggs are therefore directly sensitive to climate factors. Like eggs of other soil-transmitted nematodes, the eggs of *Toxocara* spp. have evolved to withstand a range of changes in the abiotic and biotic features of the soil phase. Specifically in the case of *Toxocara canis*, the eggs are able withstand extremes of temperature ranging from below freezing (O'Lorcain, 1995) to over 30°C (Azam et al., 2012). *Toxocara leonis*, which rarely affects humans, has been historically present in artic foxes at very high latitudes of the Canadian Artic (Elmore et al., 2013), indicating how this species of this genus have adapted to extreme environmental conditions before through selection pressures.

The microgeographical distribution of *Toxocara* eggs is affected by conditions including soil texture (Mizgajska, 1997) and oxygenation. Lower temperatures, lower humidity and low levels of oxygenation slow development times (Azam et al., 2012; Gamboa, 2005) leading to diversity in the rate of maturation depending on geographical location—typically maturation

times are lower in tropical regions with all year transmission as a result (Macpherson, 2013).

Evidence for changing patterns of *Toxocara* infection globally is emerging from studies of zoonotic infections in northern latitudes lying well beyond tropical regions. North–west Canada is sited at the southern limit of the discontinuous permafrost zone, overlapping with the Arctic circle (>60 degree latitude). High levels of parasitic infection in Artic regions, excluding *Toxocara*, have been historically recorded (Hotez, 2010). This changed in 2006 when a survey of dogs recorded a prevalence of 5%—up from a prevalence of 0 in previous surveys at the same latitude (Salb et al., 2008). More recent studies have confirmed that the prevalence of *Toxocara* in adults living in regions above 60 degree latitude is below 5% (Messier et al., 2012). In Northern Saskatchewan, however, the prevalence of *T. canis* in humans was recently recorded at 13.4% (Schurer et al., 2013).

Northern Canada is facing a disproportionate increase in temperature changes and is therefore considered as a sentinel site for understanding how climate change might affect parasitic disease transmission (Jenkins et al., 2011). In that review, Jenkins and colleagues suggest that a combination of migrating animal populations, including arctic fox, combined with increased survival of eggs over the winder period will result in a net increase in transmission despite the potential for higher summer temperatures to affect the eggs negatively. There are no published studies that have projected how climate change may affect transmission and this issue remains to be investigated further through a combination of epidemiological surveys and modelling projects.

8.2 Bacterial

8.2.1 Leprosy

The cause of leprosy, *Mycobacterium leprae*, is another example of an organism of public health importance for which there is a paucity of information available on its association with environmental factors (Franco-Paredes and Rodriguez-Morales, 2016). Long considered to be transmitted directly among individuals through nasal discharges and droplets, the role of the wider environment, including vector-borne transmission, remains cryptic (Franco-Paredes and Rodriguez-Morales, 2016). Some climate-sensitive factors are considered below.

8.2.1.1 Soil

M. leprae bacteria survive in soil under specific laboratory conditions (Desikan and Sreevatsa, 1995) and have been found in soil in the natural environment close to human habitation (Turankar et al., 2012). It is therefore important to consider how soil conditions may be affected under conditions of a changing climate (see above).

8.2.1.2 Water

M. leprae have been detected in water samples, using PCR, in India (Matsuoka et al., 1999). The same study also reported an association between the presence of leprosy in water and the prevalence of leprosy in the population.

At the time of writing, there were no original research articles available on how climate change might affect future incidence of Leprosy.

9. PARASITES WITH INTERMEDIATE HOSTS

9.1 Trematodes

9.1.1 Schistosomes (S. mansoni, S. haematobium)

The breadth of research undertaken on each aspect of this lesser-neglected NTD is sufficient to fill several books (Evans, 2015; Mahmoud, 2001; Secor and Colley, 2004). Here, I focus on describing recent research relevant to modelling decadal climate change.

The complex life cycles of schistosome species contain several climate-sensitive stages (miracidia, sporocysts, cercaria and intermediate host snails). Each of these components is affected temperature (reviewed by Kalinda et al., 2017) and a wide range of other environmental and physiochemical factors, depending on species, but which includes substrate type, flow velocity, water turbidity, metal content and chlorophyll content (Monde et al., 2016).

An early attempt at modelling the future transmission of Schistosomiasis in the African context used a deterministic model of the entire life cycle, suggesting that higher temperatures (>30°C) could substantially reduce both prevalence and intensity of transmission (Mangal et al., 2008). While it is clear that the temperature and the state of the aquatic ecosystem are a critical factor for snail and parasite development (Morley and Lewis, 2013), the question of whether climate change alone will have a noticeably existential impact on the future transmission of schistosomiasis is still very uncertain (McCreesh and Booth, 2013; Stensgaard et al., 2016).

Pedersen et al. (2014) and Stensgaard et al. (2013) used an ecological niche model to estimate potential changes to the macrodistribution of two snail species (*Biomphalaria pfeifferi* and *Biomphalaria sudanica*) in the African context. The results of their studies hinted at the both the underlying complexity and uncertainty of this type of projection. Assuming all else remains equal; Stensgaard et al. (2013) predicted that snail range of *B. pfeifferi* could either contract by 43% by 2080 under the SRES A2 scenario while the range of *B. sudanica* could increase by 14% under the same scenario. Their conclusion, that climate change is unlikely to have a uniform and unilateral effect, was borne out in a later study of *S. mansoni* in East Africa (McCreesh et al., 2015). Functional relationships drawn from the literature on *B. pfeifferi* were first used to model how a long-term trend towards warmer water may affect snail population biology (McCreesh and Booth, 2014). Virtual miracidia were added into the model, with the output being virtual cercariae. Using this output as a measure of 'infection risk', combined with downscaled climate change projections for specific RCP scenarios allowed for mapping future transmission potential up to 2050 in Tanzania, Kenya, Uganda, Rwanda, Burundi and Zambia (McCreesh et al., 2015). Owing to the nature of the functional relationships contained within the model it was observed that some areas are likely to become unsuitable either for the parasite or the host, whereas other areas would become more suitable. A later collaboration that combined the ecological niche and functional trait modelling reached a similar conclusion (Stensgaard et al., 2016). Fig. 7 summarises the steps taken in this project, which represented an application of a generalisable approach to assessing the effect climate change through considering how abiotic changes may affect functional traits of both intermediate hosts and parasites (Cizauskas et al., 2017).

9.1.2 *Schistosoma japonicum*

Early models of the potential for transmission of *S. japonicum* transmission to be altered by climate change focused on how projected changes in average temperature with China may affect the potential transmission area (e.g. Yang et al., 2005). A later effort extended this approach to include statistical modelling of the relationship between temperature and snail natural history to produce risk maps that illustrated the potential range shift in 2030 and 2050 (Zhou et al., 2008). An assessment by Moore et al. (2012) of the degree–day modelling approach used by Zhou et al. (2008)—as well as other publications (see table 2 Moore et al., 2012) cautioned against the use of the
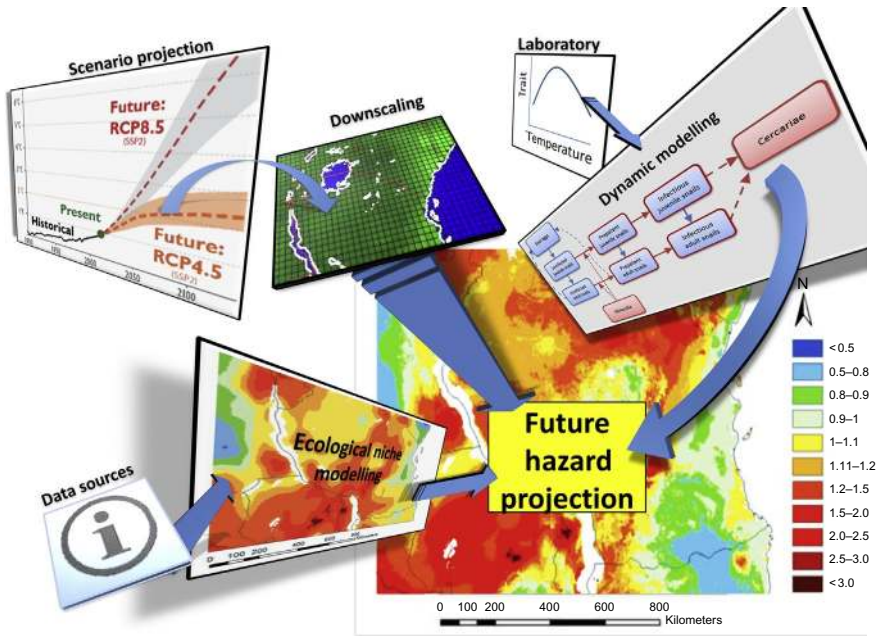
Fig. 7 Illustration of the steps taken to map future transmission potential of *S. mansoni* in East Africa, combining functional trait knowledge on the relationship between temperature and *Biomphalaria* fecundity with dynamic agent-based models, downscaled climate projections and ecological niche modelling. The results of combining the outputs of these models and experiments resulted in a high-resolution hazard map which was then used to underpin a risk map that incorporated a vulnerability layer as observable in the Healthy Futures Atlas. *Elements of the figure reproduced from McCreesh, N., Booth, M., 2014. The effect of increasing water temperatures on Schistosoma mansoni transmission and Biomphalaria pfeifferi population dynamics: an agent-based modelling study. PLoS ONE 9 (7). doi: 10.1371/journal.pone.0101462; Stensgaard, A.-S., et al., 2016. Combining process-based and correlative models improves predictions of climate change effects on Schistosoma mansoni transmission in eastern Africa. Geospatial Health 11 (1 Suppl), 406. doi: 10.4081/gh.2016.406.*

use of degree–day models due to their inability to deal effectively with parametric uncertainty.

9.2 Food-Borne Trematodes

This is an important group of zoonotic trematodes transmitted to humans via poorly processed food, particularly fish, crustaceans and plants. Included in this group is Clonorchiasis, Fascioliasis, Opisthorchiasis and Paragonimiasis (Keiser and Utzinger, 2009). The epidemiology, pathology and control of

the parasites causing the first three diseases in the above list have been reviewed, in the SE Asia context, elsewhere (Sripa et al., 2010). For Paragonimiasis, a recent comprehensive review is available (Blair, 2014), and aspects of the evolution and phylogeography of all four genera have also been reviewed (Attwood, 2010). At the time of writing, there was little published literature regarding decadal climate change and transmission of these infections. The discussion below summarises what is known about the relationship between environmental change and the climate-sensitive stages of the life cycles.

9.2.1 Clonorchiasis and Opisthorchiasis

The life cycles of *Clonorchis sinensis* (endemic in Asia), *Opisthorchis viverrini* (endemic in SE Asia) and *Opisthorchis felineus* (endemic in Europe and Asia) involve open defaecation by a definitive host into fresh water, typically small ponds, containing vegetation and compatible snail hosts. There are numerous species of snail that support the infections (Tang et al., 2016), each of which may be restricted to specific habitats and possess its own set of attributes affected by abiotic and biotic characteristic properties of the water body (Petney et al., 2012). Water temperature is crucial in terms of snail population size and dynamics—e.g., *Parafossarulus manchouricus* abundance–temperature relationship follows a convex curve, with the highest seasonal abundance associated with temperatures of between 24 and 26°C, and lowest abundance below 10–13°C (Chung et al., 1980).

The second intermediate host is a freshwater (often a cyprinid) fish or crustacean that predates on the snail host. Again, there are multiple species of fish or crustacean involved, depending on location (Tang et al., 2016). The natural history of cyprinid fish, which are poikilothermic, is also affected by water temperature and hence likely to be affected by climate change (Ficke et al., 2007). Research into the effects of climate-induced changes suggest that population turnover (Buisson et al., 2008), recruitment into rivers (Nunn et al., 2007), species range (Comte et al., 2013), body size and growth rates (Ruiz-Navarro et al., 2016) are all likely to be affected depending on species and habitats (Buisson and Grenouillet, 2009).

The natural histories of both miracidia, cercariae and metacercariae of *Clonorchis* and *Opisthoricis*, and their relationship with snail and fish intermediate hosts, are acutely affected by the abiotic properties of the water bodies they inhabit. For example, field and experimental observations of the *Opisthorchis* intermediate host, *Bithynia siamensis goniomphalos*, indicate that infection rate by miracidia of *O. viverrini* is minimised at water temperature

of 16°C, maximised at 30–34°C, declines rapidly thereafter, and is more common in relatively small snails (Echaubard et al., 2017; Prasopdee et al., 2015). The convex nature of infectivity and survival of both snails and free-living parasites indicates that water bodies which exceed the upper temperature threshold over the coming years may become unsuitable habitats, whereas those water bodies that move from below 16°C towards 20°C or higher may become more suitable.

Evidence of the downstream effect of warmer waters on transmission of the infections to humans is very limited, but one published study on Clonorchis from Guangzou city, China suggests a link (Li et al., 2014). In that study, annual average 1°C increase was associated with an average 1.18% rise in monthly incidence from 2006 to 2012, a 1 mm change in rainfall was associated with 0.03% increase in incidence, and 1% rise in RH was associated with a 1.5% decrease in incidence. In contrast, projected impacts over several decades have been explored for Opisthorchis, specifically in Thailand (Suwannatrai et al., 2017), where Maxent was used to model a potential future hazard distribution, using IPPC A2 scenarios to 2070. The conclusion from that study was that northern regions may become unsuitable for transmission.

9.2.1.1 Fascioliasis

Fasciola hepatica is an important food-borne parasite with a global distribution (Mas-Coma et al., 2009). Although mainly an infection among livestock, human cases are regularly reported (World Health Organisation. Foodborne Disease Burden Epidemiology Reference Group, 2015). Risk factors include a list of anthropogenic behaviours that lead to ingestion of contaminated vegetation (Ashrafi et al., 2014).

The parasite life cycle is similar to other food-borne trematodes and schistosoma with one main difference. The snail intermediate hosts are air-breathing freshwater mollusks of the 'fossarine' group (family *Lymnaeidae*), most importantly Galba (formerly *Lymnaea*) *trunculata*, from which metacercaria emerge onto vegetation. This vegetation is ingested by the definitive host, which may include humans. The snails typically inhabit slow-moving or standing water bodies, often within marshy or muddy habitats, where they feed and lay eggs. They can aestivate by burying into the substrate to survive drought conditions, with the period of aestivation decreasing with altitude (Goumghar et al., 2001).

The global spread of the infection has been attributed to anthropocentric activities, related to domestication and transport of livestock, stretching back

thousands of years (Mas-Coma et al., 2009). Habitats with temperatures as low as 10°C have been recorded as suitable for several intermediate host species including *Fossaria bulimoides* (Cruz-Mendoza et al., 2004) and *G. trunculata* (Rapsch et al., 2008). Adaptations of snails and parasite to conditions associated with high altitude (~4000 m) have also been observed (Mas-Coma et al., 2001). Temperature above 30°C is associated with rapid reduction in egg survival, with the 'lethal' temperature depending on species (Harris and Charleston, 1977).

Miracidial development and hatching have been observed to depend on temperature of the water body, with early studies indicating that no development was possible at temperatures lower than 9°C or above 30°C (Kendall). Cercarial shedding is also temperature dependent, with minimal shedding at 9°C (Kendall and McCullough, 1951). There is some disagreement over the optimal temperature. The studies of Kendall and McCullough (1951) suggested ongoing shedding at 26°C. Subsequent observations have suggested not just that 20°C may be optimal, but also that the magnitude of the shedding may depend on susceptibility of the snail species and the degree of diurnal variation in temperature (Rondelaud et al., 2013).

As a zoonotic infection affecting livestock of economic importance, *Fasciola* has received relatively more attention, in terms of environmental change research, than the other food-borne infections. It is known, for example, that contemporary weather patterns shape exposure among cattle in the European context, with the number of relatively warm days per annum, combined with relatively high average levels of within-farm precipitation (excluding within-year spikes) are positively associated with milk-seropositivity (Charlier et al., 2016; Munita et al., 2016). Within-country spatial clustering is thereby associated with spatial variation in these meteorological factors (Selemetas and de Waal, 2015). Enhanced vegetation (assessed remotely) has also been associated with increased risk of transmission in areas as regionally distant as Colombia (Valencia-López et al., 2012) and Pakistan (Afshan et al., 2014).

Soil type, slope and treatment, along with the characteristics of the underlying water budget contribute significantly to determining spatial distribution. In the tropical US context, hydric soils with poor drainage (Malone et al., 1992) or chenier soil with accumulated water that seeps out to provide a habitat for snails (Zukowski et al., 1993) is positively associated with exposure. In the tropical African context, arid and/or acidic soils (<5.5 pH) are negatively associated with endemicity (Malone et al., 1998).

Exposure within human communities is also associated with seasonal variation, as observed in Pakistan (Qureshi et al., 2016). Historic climate data have been used to map risk of human fascioliasis in Iran (Halimi et al., 2015), with conclusions on the role of rainfall, temperature and vegetation that align with studies of the parasite in animal populations.

The wide window of available temperatures and habitat characteristics, as well as anthropocentric activities such as global travelling, highlights the potential for continued transmission of *Fasciola* infections under many climate change scenarios. At the time of writing, the majority of literature related to environmental change consisted of articles as described earlier, mapping spatial heterogeneity in exposure or levels of infection through analysis of environmental covariates. In terms of future projections, only a few articles have been published. These include modelling snail habitat suitability in Zimbabwe up to 2099 using the SRES A1B scenario (Pedersen et al., 2014); modelling decadal exposure up to 2089 in the United Kingdom based on the SRES 1B scenario (Fox et al., 2011) and modelling infection risk in New Zealand up to 2090 using SRES A1B, A2 and B1 scenarios (Haydock et al., 2016).

9.2.1.2 Paragonimus

This food-borne parasite consists of over 40 species that infect a wide range of intermediate and definitive hosts (Blair et al., 1999). Nine species or species–complexes are known to affect humans (Blair, 2014; Chai, 2013). The main focus of infection with species of the *Paragonimus westermani* complex is SE Asia, where multiple individual species within the complex infect intermediate hosts with low specificity (Doanh et al., 2013). Other foci, consisting of highly distinct parasite species are located in West Africa (*Paragonimus africanus* and *Paragonimus uterobilateralis*) and (sub)–tropical parts of North, Central and South America (*Paragonimus mexicanus* and *Paragonimus kellicotti*).

In common with the other food-borne trematodes, the climate-sensitive stages of the Paragonimus life cycle are those contained in the water phase. The first intermediate hosts are freshwater snails from the super families *Rissoidea* and *Cerithioidea*, but the full range is still unknown (Attwood, 2010). The second intermediate hosts are decapod crustaceans consisting drawn from several genera, depending on location and including *Cambraoides* crayfish (Kim et al., 2009), the freshwater crabs *Liberonautes* and *Sudanonautes* (Aka et al., 2008) and *Tehuana* (Vargas–Arzola et al., 2014). This is not an exhaustive list, as many other genera have been

identified specific to regions including Ecuador (Calvopiña et al., 2014) and the United States (Fischer et al., 2011). The list of susceptible hosts in these and other papers point to the extreme generalisation of this parasite, and thus indicate a major challenge to modelling future trends in transmission.

In the absence of available literature on climate change and paragonimiasis per se, it is nonetheless plausible to suggest that the contemporaneous distribution of *Paragonimus* species is shaped by a wide range of factors as described in previous sections. Future transmission of the infection may also be affected by climate-related changes to local ecosystems, food webs, zoonotic reservoirs, farming practices, consumption patterns, human behaviours related to sanitation and translocation of humans, intermediate and zoonotic hosts. Long-distance translocation may have occurred to bring the parasite into South Africa, for example (Appleton, 2014).

9.3 Nematodes
9.3.1 Guinea Worm
Although scheduled for eradication due to the low number of recent cases, guinea worm may reemerge as a public health problem in the future due to the recent observations of infections in various animal hosts including dogs, fish and frogs (Eberhard et al., 2016; Ruiz-Tiben et al., 2014). The climate-sensitive stages of *Dracuncula* are the L1 larvae released by the adult female worm, along with the L2 and L3 larvae contained within the poikilothermic copepods of the *Metacyclops*, *Mesocylops* and *Thermocylops* genera that act as the intermediate host.

There were no published papers available on climate change and guinea worm at the time of writing. Historically, guinea worm infections are known to occur seasonally (Bloch and Simonsen, 1998), with peak infection tied to rainy seasons in countries at the southern fringe of the Sahara desert, and tied to dry seasons in those countries close to the Gulf of Guinea (reviewed by Ruiz-Tiben and Hopkins, 2006). In both regions, this has been attributed to the presence of stagnant freshwater used for drinking purposes rather than the population biology of the copepods or changes in ambient water temperature.

The thermal tolerance of warm-water copepods was established several decades ago. For example, the eggs of *Thermocyclops* spp. develop at a linear rate from 15 to 30°C, after which point there is a rapid downturn until 40°C, whereupon development ceases (Burgis, 1970). Studies on the phenology of warm-water copepods suggest that increased temperatures can lead to increased fecundity and thereby increase population size at specific times

of year (Gerten and Adrian, 2002; Wagner and Adrian, 2011). Concern has been raised that the frequency of diurnal changes in the physiochemical environment could overwhelm the adaptability of copepods (Almén et al., 2014), and freshwater scarcity (see above) may also play a role in determining future abundance.

Given that cases among humans are an historically low point, but that copepod populations may be put under stress by environmental change, it is challenging to speculate how climate change will affect future *Dracuncula* transmission. History tells us that reduced efforts at controlling parasites can cause increases in transmission of parasites previously controlled (Ekwanzala et al., 1996). Calls have been made for continued financing into field-based research (Molyneux and Sankara, 2017). This will need to be accompanied by continued awareness of the potential dangers of drinking copepod-infested water to ensure sustainable interruption of the parasite life cycle.

9.4 Cestodes

9.4.1 Echinococcosis

Key to understanding how climate change might affect the distribution of *Echinococcus* spp. in the future is a detailed understanding of all climate-sensitive stages of the life cycle. The life cycle of *Echinococcus* spp. involves homeotherm mammals (including humans). Only one life stage—the eggs deposited with faecal matter from the definitive host—is essentially poikilothermic. Typically, these eggs are deposited onto soil through open defecation of dogs and other canidae. Eggs are therefore most likely to be directly affected by abiotic or biotic factors that affect the soil.

Echinococcus multilocularis is confined to northern latitudes and its eggs can survive freezing temperatures, with an optimal temperature range of 0–10°C and are viable only for a few hours at temperatures >25°C (Veit et al., 1995). *Echinococcus granulosus* is responsible for the majority of morbidity in humans and has a wider distribution including tropical and temperate regions (McManus et al., 2003). It is clear from this latter fact alone that the eggs of *E. granulosus* must have historically adapted to a wide range of temperatures above 0°C. This has been reported by a very small number of studies at the time of writing. Wachira et al. (1991) tested the viability of *E. granulosus* eggs under various conditions in a semiarid region of Kenya. After placing eggs in suspension, samples were positioned on open ground, near a house or near a water hole. Only the eggs near the water hole were observed to be viable after 10 days, where the average temperature was approximately 29°C. Most recently, Thevenet et al. (2005) observed that eggs of the

parasite kept outdoors on deposited stool samples from canines were viable after 41 months exposure to the elements in an arid region of Pategonia. During the exposure period, the eggs were subject to a temperature variation of −3 to +37°C and low rainfall (<300 mm per annum). At the end of the exposure period, the eggs were still viable in terms of producing cysts in *Texel ovines*. Together, these studies, combined with a few earlier studies cited by Wachira et al. (1991), suggest that eggs of *E. granulosus* may be viable when deposited onto the ground at temperatures not yet reached by more temperate areas.

At the time of writing, there have been no published studies in terms of modelling the potential future transmission of Echinococcus spp. under specific climate change scenarios. Atkinson et al. (2013) offer a wide-ranging narrative review of how environmental change, including climate change, might affect future transmission. Much research has covered the myriad environmental factors that shape the contemporary geographic distribution (Atkinson et al., 2013). It is also made clear in that review that there is a lack of evidence on the role of anthropogenic factors.

Anthropogenic changes that are likely to affect the contemporary transmission of Echinococcus are those which modify the habitat, range and/or behaviour of predator and prey animals. Atkinson et al. (2013) review the possibilities regarding urbanisation, deforestation and land use change. The modifying effects of climate change on anthropogenic influences presents a further, as yet unexplored, challenge.

9.4.2 Taeniasis–Cysticercosis

Cysticercosis is a disease, mainly endemic in low-to-middle income countries (LMICs), which is considered to be responsible for approximately 30% of all epilepsy cases in endemic countries (Ndimubanzi et al., 2010). The primary risk factor is consumption of pigs infected by *Taenia solium*. The WHO updated its map of *T. solium* distribution in 2015 (Donadeu et al., 2016), highlighting how the import of infected pigs leads to cases in countries without comprehensive screening protocols.

The life cycle of *Taenia* parasites includes a climate-sensitive stage and its future transmission potential may therefore depend partly on how soil phases change in the future. At the time of writing, there have been no papers published that model future transmission scenarios. This review is therefore restricted to reviewing existing literature that has explored how environmental variables affect the survival and viability of the eggs shed by the definitive hosts.

In common with other parasites, the majority of work related to the natural history of taenid eggs was comprehensively investigated several decades ago (reviewed Lawson and Gemmell, 1983; see also Willis and Herbert, 1984 regarding *Taenia multiceps*). The aim of these studies was to understand the abiotic and biotic factors that affect the survival of eggs either under in vitro or field conditions, covering a range of species including *Taenia pisiformis*, *Taenia ovis*, *Taenia hydatigena* and *T. multiceps*. The in vitro experiments examined the effects of varying temperature and/or humidity or surface moisture on egg survival. Field experiments have focused more on the distribution and survival of eggs (e.g. Wachira et al., 1991) and uptake of eggs by animals under controlled conditions.

In terms of temperature, eggs have recorded to withstand freeing conditions of up to −20°C without any effect on hatching (Willis and Herbert, 1984), while surviving for just 4 days at 21°C (Gemmell, 1977) and for just a few hours, if at all at 37°C (Coman, 1975; Gemmell, 1977). In terms of humidity and surface water, the evidence suggests that conditions of low RH can dramatically affect the survival of eggs. Laws (1968) reported that only *T. hydatigena* eggs could survive RH levels below 60%, while Gemmell (1977) observed that a lack of surface moisture reduced hatching to almost 0% after 4 days, irrespective of species and storage temperature. Similar observations were made by Sánchez Thevenet et al. (2017) who again concluded from laboratory studies of *T. hydatigena* that low RH values are inimical to eggs of this parasite. The inferences from all these studies are that dryer environments cause higher rates of mortality, possibly due to the desiccation of the keratin shell leading to shrinkage and increased hydrostatic pressure on the embryo, leading to its demise (Laws, 1968).

Risks to humans as a result of climate change are currently challenging to estimate. There are two routes to infection—either the consumption of infected pork or ingestion of eggs, e.g., by eating food stuffs fertilised with contaminated faeces. Pigs can be treated and meat can be screened to prevent that particular route of infection (Gabriel et al., 2015), and there is no a priori reason to expect that would be directly affected by a changing climate.

It is more likely that changing climate conditions will affect the ingestion of eggs. Changes to the soil phase that supports the eggs may have localised effects depending on a combination of soil temperature and soil moisture. Given the evidence from the studies summarised earlier, it is possible only to speculate that areas where a combination of increased humidity and only

moderate increases in temperature may experience a greater percentage of egg survival. This may translate into a localised hazard function for modelling purposes, but this function will need to be modified by other risk factors associated with the vulnerability of associated human populations that may or may not alter depending on which climate change scenario is realised.

Another factor that will need to be considered is the potential for insects to distribute the eggs over extended distances through coming into contact with contaminated faecal matter. It has been previously suggested that blow flies could distribute eggs (Lawson and Gemmell, 1990) but this has not been demonstrated other than experimentally with dead flies being ingested by lambs (Lawson and Gemmell, 1990). More recently, *Ammophorus rubripes*, a dung beetle, has been implemented as a potential carrier through experiments that demonstrated carriage of viable eggs by the beetles for up to 24 days (Gomez–Puerta et al., 2014). A broad range of synergistic and competing factors is likely to affect the ecology of any organism capable of dispersing eggs, leading perhaps to localised extinction (Brook et al., 2008), among other effects related to anthropogenic disruption of established ecosystems (Cable et al., 2017).

10. ZOONOTIC VIRUSES

10.1 Coronoviruses

Middle East respiratory syndrome coronavirus (MERS–CoV) and severe acute respiratory syndrome (SARS) are two coronaviruses on the list of WHO priority diseases due to the lack of preparedness for future outbreaks. Bats are the major suspects in terms of zoonotic origin of both SARS and MERS–CoV (Anthony et al., 2017; Drexler et al., 2014).

Person-to-person transmission of aerosolised virus is the predominant risk factor for infection post-spillover. As with all other respiratory viruses, a range of environmental factors facilitate or inhibit the transmission, including temperature, precipitation, RH and airflow (reviewed by Pica and Bouvier, 2012). Relatively few investigations have been undertaken on SARS or MERS–CoV specifically. From the available literature, it is possible to deduce that both SARS and MERS–CoV persistence in the environment decreases at temperatures $>20°C$, at a rate dependent on a convex humidity–temperature interaction (Casanova et al., 2010; Chan et al., 2011; van Doremalen et al., 2013).

At the time of writing, there were no original research papers available on the potential for climate change to affect transmission. Given the earlier observations, it may be possible to speculate that both MERS-CoV and SARS are likely to be less common in tropical and tropical areas in the future.

10.2 Henipavirus

10.2.1 Nipah and Hendra

Nipah henipavirus is a recently discovered member of the Henipavirus genus and is closely related to *Hendra henipavirus* (Ksiazek et al., 2011). Both Hendra and Nipah are on the WHO list of priority diseases, are highly pathogenic, affect populations in southeast Asia and are zoonotic. Fruit bats have been confirmed as the main zoonotic hosts of Nipah (Yob et al., 2001) and Hendra (Halpin et al., 2000). Food-borne transmission is possible given observations of cases who reported drinking palm sap from containers previously accessed by fruit bats in Bangladesh (Islam et al., 2016; Luby et al., 2006).

At the time of writing, there were no original papers in the literature on the potential for decadal climate change to affect Henipavirus transmission. Some environmental cues are nonetheless available. Under experimental conditions, both Nipah and Hendra can tolerate conditions with pH of 3–4 to 11, can survive more than 4 days in bat urine kept at 22°C, but are rapidly inactivated under conditions of desiccation (Fogarty et al., 2008).

In epidemiological studies, seasonality of Nipah spillover into human populations has been observed in Bangladesh (Luby et al., 2009) outside the typhoon season. In terms of understanding which environmental factors are associated with Nipah spillover risk, Walsh (2015) identified bat density and a derived variable termed 'human footprint' as key factors, but excluded vegetation cover and pig density. Seasonality has also been observed in terms of viral antibody dynamics in bats (Baker et al., 2014). Taken together, these observations hint that the risk of spillover events is determined by an interacting combination of bioclimatic factors and bat ecology.

10.3 Filoviruses

10.3.1 Ebola and Marburg

The filoviruses (Ebola and Marburg) are highly pathogenic NTDs (MacNeil and Rollin, 2012) that affect human populations in outbreaks associated with a spillover event from zoonotic hosts. Bats are speculated to be primarily responsible for these spillover events, where the infections persist, possibly due to biannual birth pulses (Hayman, 2014). Epidemiological evidence of

spillover phenomenon comes from observations of seasonal variation in the prevalence of Marburg virus coinciding with the onset of outbreaks (Amman et al., 2012). The majority of human infection after the spillover is through direct contact with cases.

At the time of writing, there were no original research papers available that have modelled future climate change-related projections of either of these filoviruses. All attempts at modelling the risk of infection has instead focused on the near term. Bats have received some attention in the literature in relation to both Ebola and Marburg, particularly in terms of modelling interactions between bat ecology and environmental factors. Taken together, the current models suggest that infected bats migrate to resource rich areas (Buceta and Johnson, 2017) but are limited in their geographic distribution by a combination of temperature, evapotranspiration and elevation (Pigott et al., 2014, 2015). Areas that combine relatively high human population density with high vegetation coverage are at relatively high risk of outbreak (Walsh and Haseeb, 2015), presumably as this increases the rate of contact between bats and humans. It remains to be seen whether climate change will significantly alter the interactions between these risk factors.

10.4 Arenaviruses

10.4.1 Lassa Fever

Lassa mammarenavirus (the aetiological agent of Lassa Fever) is a member of the *Arenaviridae* family of viruses (Yun and Walker, 2012). Up to 37 million people, mainly living in West Africa, may currently live in areas where the environment is suitable to support the main zoonotic host of Lassa Fever, the Natal multimammate rat, *Mastomys natalensis* (Fichet-Calvet et al., 2009; Mylne et al., 2015). Human-to-human transmission is considered to be account for between 5% and 20% of all cases, possibly due to 'super-spreaders' (Lo Iacono et al., 2015). Transmission occurs when humans come into close contact with the mouse specifically through ingestion or inhalation of mouse urine, faeces or blood. Risk factors include living in close proximity to the mice, butchering and consumption (Bonwitt et al., 2016, 2017).

As with other zoonotic NTDs, a consideration of the life history traits and population biology of the zoonotic host is essential to understanding how climate change may affect future transmission patterns. *M. natalensis* is an endotherm and as such its gestation period is not directly affected by external temperatures. In contrast, the population abundance of this organism is characterised by clearly definable and high-amplitude fluctuations.

Published field studies have consistently observed that these fluctuations are predictably associated with seasonal rainfall patterns (Coetzee, 1975; Makundi et al., 2007; Sluydts et al., 2007; Stenseth et al., 1997). Typically, *M. natalensis* breed during rainy seasons and are most abundant in the proceeding dry season (Christensen, 1993). Specific rainfall events, including so-called 'short rains' have been associated with rapid growth in population, termed outbreaks (Mwanjabe et al., 2002). This phenomenon is the result of more rapid development of the pups (Leirs et al., 1990), a process triggered by the rains and the consequential lifting of food restrictions (Christensen, 1993), and leads to both parents and their offspring breeding within relatively short periods of time.

Although known as an opportunistic species able to occupy a wide range of habitats, several natural environment factors nonetheless limit the spatial distribution of *M. natalensis*. The type of soil appears important, with higher abundance observed in regions with high vegetation cover and sandy (Massawe et al., 2005, 2008). Both these environmental factors can be naturally and anthropogenically determined, thus farming practice and land use are also likely to affect the population biology of the rodent (Massawe et al., 2007).

Survival of the virus in the environment is also key to completing the transmission cycle. Once an infected mouse has urinated or defecated, there is a finite period over which the virus is viable. Laboratory investigations indicate that aerosolised virus is inactivated within 60 min at temperatures >24°C (Stephenson et al., 1984) and that dark, dry conditions (Sagripanti et al., 2010) are associated with rapid decay of the virus.

The potential effects of climate change on the transmission of Lassa fever to humans have so far received limited attention in the literature. Given the well-known propensity of the mouse to undergo population outbreaks, historic attention has been given to either mapping contemporary risk (Fichet-Calvet et al., 2009) or forecasting over short periods (Leirs et al., 1996). One study has focused on the issue of estimating the effect of global change, including climate change (Redding et al., 2016). In that particular study, the authors created a spatially stratified mechanistic model for West Africa and modelled the effects of three climate change scenarios drawn from the HADGem3 AOGCM. The results of this simulation suggest that more extreme scenarios of both temperature increase and land-use change are likely to increase the rate of spillover events from animals to humans.

10.5 Lyssavirus

10.5.1 Rabies

Dog-transmitted rabies are present in 150 countries including all of Africa, parts of Latin America and all of Asia (Hampson et al., 2015). As a vaccine preventable, zoonotic disease, most research is focused on contemporary issues related to these two domains of enquiry. Efforts to understand the environmental component of transmission are geared towards operational aspects of vaccine delivery, e.g., in relation to landscape features (Russell et al., 2006), the delivery of vaccines to wildlife (Rupprecht et al., 2004). There is little attention in the literature on how environmental change (including climate change) might affect transmission decades in to the future. To date, the focus on climate change and rabies has been confined to arctic areas (Huettmann et al., 2017; Kim et al., 2014).

11. VECTOR-BORNE INFECTIONS

In contrast to direct life cycle infections, there has been more attention given to the vector-borne diseases (e.g. Parham et al., 2015; Rogers and Randolph, 2006). This reflects both the larger number of actors working in the field of vector-borne disease, and a relatively early realisation that climate can have a profound impact on the distribution of vector species, particularly mosquitoes.

11.1 Helminths

11.1.1 Lymphatic Filariasis

W. bancrofti, the parasite that causes LF, is transmitted by mosquitoes of the *Anopheles*, *Culex* and *Aedes* genera. The potential effects of climate change on the transmission of this infection (assuming all else remains equal) therefore depends primarily on how the vectors respond to the biotic and abiotic shifts associated with changing climates. See sections earlier for more information on each of these species.

The potential impact of climate change on the parasite itself has not been comprehensively studied. There is some evidence that ambient temperature can affect the density of the symbiotic Wolbachia density (Mouton et al., 2007), particularly in terms of the interaction between host genotype and Wolbachia strain. This may reflect local adaptability to changing temperatures over short timescales. A less direct effect may be possible through

competition for resources as the availability of food changes over a longer period of time (Ross et al., 2016), with evidence that certain Wolbachia strains (wMel, wMelPop and wAlbB) can reduce the survival times of Aedes larvae under starvation conditions. In the context of using *Wolbachia* to control populations of Aedes mosquitoes, high temperatures (e.g. 30–40°C over several days) have been observed to reduce bacterial levels, at least in the short term (Ulrich et al., 2016). Again, this points to adaptability but tells us little about how a sustained pressure will shift the host–symbiont relationship. Such information may emerge from longer-term studies over multiple generations of vector kept at constantly higher temperatures.

11.1.2 Onchocerciasis

Onchocerca is transmitted by the blackfly *Simulium damnosum* complex and is therefore a parasite with a life cycle that is sensitive to climate change. Reviews of blackfly ecology and the relation between vector and parasite are available in specific contexts (e.g. see Cheke et al., 2015 for a modelling perspective; Takaoka et al., 1982 for a review specific to Guatemala). Here I summarise work that has been conducted on the potential impact of climate change in particular.

The fact that over 60 sibling species or cytoforms have been identified (Adler et al., 2010), each with different life history parameters, makes any attempt at projecting the effects of climate change highly challenging. Nonetheless it has been possible, as with other NTDs, to estimate how changing temperatures can affect the development of each stage of the vector, the development of *Onchocerca* within the fly, fly fecundity and the mortality rate of the fly (Cheke et al., 2015; Takaoka et al., 1982). Unlike some other vector species, there appears to be no threshold temperature (within the range 15–32°C) at which point either fly mortality increases or the rate of development of the parasite decreases (Cheke et al., 2015). Fluctuations in daily temperatures may affect the overall development time, corresponding to seasonal fluctuations in fly abundance (Zarroug et al., 2016).

Importantly, temperature is not the only driver of the ecology of *Simulium*. A crucial feedback mechanism may lie in the phenomenon of aggregated oviposition, which is the process by which gravid *Simulium* females select existing egg masses to lay their eggs upon (McCall et al., 1994). The stabilising effect on the population of the vector possibly comes from a higher rate of egg mortality with increasing egg mass (Kyorku and Raybould, 1987). When incorporated into a mathematical model, this

feedback produced a sharply convex curve when plotting temperature against the abundance of both parous and nulliparous flies, peaking at 29°C (Cheke et al., 2015).

At the time of writing, there were no original research publications available that considered the potential for long-term climate change to influence future transmission of this NTD.

11.2 Viruses

11.2.1 Dengue

Of all the NTDs, Dengue infections have been considered more often in terms of climate than all other infections, with over 200 publications available at the time of writing. A recent review on the subject by Ebi and Nealon (2016) revealed that most of this literature is concerned with identifying risk factors for contemporary transmission, with only a handful of studies devoted specifically to estimating the effects of decadal–scale climate change on Dengue transmission. These studies have employed a range of modelling techniques (reviewed by Messina et al., 2015), with varying results in terms of where in the world Dengue infections are likely or not to be transmitted under particular scenarios. Messina et al. (2015) attempted to unify the field by writing a statistical modelling framework for future projections that relies on capturing spatially explicit information at high spatial resolution to map the contemporary distribution before replacing the existing values of covariates (e.g. temperature, precipitation) with projected values based on different RCPs.

Most of the existing models project that Dengue is likely to increase its range in the coming decades as global temperatures rise. Where they differ is the amount of uncertainty in their outputs (Messina et al., 2015). Neither the individual projects nor any unifying frameworks consider the possibility that selection pressures acting on the *Aedes* vector or the dengue virus itself could affect future transmission. General evolutionary features of the dengue virus in relation to climate change and urban vs sylvatic cycles of the *Aedes* mosquitoes are reviewed elsewhere (Tabachnick, 2016), with the conclusion that past evidence of evolution warns us to expect future adaptation.

Studies of how temperature change affects host–virus interactions are few in number, with most evidence emerging in the context of investigating how *Wolbachia* bacteria may be used to control populations of

dengue-transmitting mosquitoes. In that context, ambient temperature has been observed to affect DENV infection rate in *A. aegypti* mosquitoes (Sgrò et al., 2016).

11.2.2 Yellow Fever

YFV is a member of the *Flaviviridae* family, closely related to Dengue and also transmitted by *Aedes* mosquitoes. It is predominantly observed in Africa and South America. Unlike other most other VBDs, yellow fever has been historically partially controlled through successful vaccination campaigns (Rogers et al., 2006), combined with visa restrictions on travellers who have not been vaccinated. Control efforts have not been entirely successful, with recent estimates putting the death toll at approximately 78,000 in Africa during 2013 alone (Garske et al., 2014).

Outbreaks of yellow fever have highlighted a number of issues, predominantly related to lack of vaccination campaigns in East and Central Africa, and large-scale urbanisation (Kraemer et al., 2017). One expressed fear is that this outbreak will facilitate world-wide distribution of the virus due to the establishment of direct air travel routes from east Africa into areas with susceptible mosquito populations (Wasserman et al., 2016). Notable in this regard is the recent observation that Australian strains of *A. aegypti* are susceptible to YFV infection (Higgs et al., 2011) that European populations of *A. albopictus* can carry YFV (Amraoui et al., 2016), and that either *A. albopictus* or *A. aegypti* is present in numerous US states (Kraemer et al., 2015b).

The reasons for the absence of YFV in SE Asia are unknown. Hypotheses have been established that include a lack of carrying capacity among Asian strains of *Aedes*, an historic lack of travel from endemic areas to Asia, cross-immunity related to Dengue infection, a lack of a sylvatic cycle in Asia and the lack of a slave trade in Asia (Cathey and Marr, 2014; Rogers et al., 2006; Wasserman et al., 2016). Given uncertainty about current reasons for lack of transmission, it is even more uncertain how climate change might affect future transmission of YVF in Asia. *Aedes* mosquitoes are susceptible to selection pressures as a result of climate change (see above), and may therefore disseminate due to certain environments becoming more suitable. The establishment of susceptible *Aedes* from Australia into parts of SE Asia where the environment has become more suitable is possible through international trade (Benedict et al., 2007).

The same hypothesis can be applied to other areas where the environment may become suitable for species or strains of *Aedes* that are capable of carrying YFV, contemporaneously with the transport of the virus through globalised air travel of people and cargo. For example, as the tropics expand (see above), it may be expected that some areas will become more humid and vegetative cover may increase.

Like Dengue, YFV transmission may be affected by climate change due to the fact that Aedes mosquitoes are the vectors. It cannot be assumed, however, that the direction of change will be the same for all these infections. This is due to the fact that each virus has at least two types of transmission cycle involving partly overlapping combinations of vectors or nonhuman hosts (Rogers et al., 2006; Tabachnick, 2016). The sylvatic cycle is particularly important in YFV epidemiology, contrasting with the urban cycle being predominant in terms of Dengue transmission. Thus, we have to consider how the different cycles of each infection may be affected by global environmental change.

Rogers et al. (2006) offer some insights into the differential effects of environmental variation on transmission of Dengue and YFV. They attempted to map the global risk of Dengue and YBF by considering which environmental variables (including land surface temperature and normalised difference vegetation index) are associated with known outbreaks. They concluded that YFV transmission is predominantly associated with changes in vegetation cover and humidity, whereas Dengue virus transmission is more closely associated with changes in temperature. The maps produced by Rogers et al. (2006) also suggest that environmental conditions are suitable for transmission for YFV in SE Asia despite an absence of the virus in that region.

The effects of climate change on sylvatic cycles of either Dengue or Yellow fever transmission have not been directly studied. Again, we must infer the likelihood of climate having a significant impact based on what is already known about the ecology and the natural history of the organisms within each cycle. For example, toque macaques (*Macaca sinica*) are known hosts of Dengue in Sri Lanka. The genus *Macaca* is also known for its plastic characteristics in terms of its ability to adapt to changing food availability caused by anthropogenic activities (Riley, 2007). The macaques adapt their foraging strategy by moving beyond their home range if food becomes scarce in one particular area. This range extension could occur as a result of decreasing availability of natural foodstuffs in areas with altered patterns

of agriculture, forcing the monkeys into new areas (including urban settings) where food is more available. Toque macaques are already found in urban settings in Sri Lanka and are exploited in a number of ways—as pets, performer and for ritual activities (Radhakrishna et al., 2014).

11.2.3 Rift Valley Fever (RVF)

RVF is a vaccine preventable, epizootic and zoonotic disease that has a complex natural history involving dozens of mosquito species as vectors (Pepin et al., 2010). *Aedes* and *Culex* spp. have been implicated as the main vector genera, with the former acting to transmit RVF in the interepidemic period and the latter acting as an amplifier species during epidemics (Pepin et al., 2010).

Epidemics of RVF are closely associated with excessive rainfall and El Nino events (Linthicum et al., 1999). Additional large-scale determinants include the presence of irrigation schemes, a high level of cultivation, higher population density (Redding et al., 2017). At a local scale, a critical factor is the nature of the local habitats—they must be suitable for supporting mosquito populations. In this context, Sang et al. (2010) collected both *Aedes* and *Culex* mosquitoes associated with RVF from a diverse range of habitats in Garissa, Kenya, including human settlements near flooded wetlands, mixed forest close to mangrove swamps and livestock holding areas. Elsewhere, *Culex tritaeniorhynchus*—a vector of RVF in Saudi Arabia, prefers wet, muddy substrates with a low total dissolved salts content (Sallam et al., 2013).

Mathematical models of RVF typically focus on identifying factors that can be used to forecast or mitigate the next epidemic (e.g. Leedale et al., 2016; Mpeshe et al., 2011; Pedro et al., 2016). The repeated observation of the importance of precipitation and water availability at specific locations, combined with the differentiated natural history of the main vectors, means that attempting to predict longer-term transmission of RVF under projected climate change scenarios is inherently more challenging than for a disease that has only one vector. Additional to the bioclimatic variable of importance are other factors related to the overall vulnerability of a population. This aspect of disease has been explored by Taylor et al. (2016) who constructed an overall risk map of future RVF outbreaks in East Africa that comprised the deterministic RVF model of Leedale et al. (2016), downscaled RCP projections and several expert-weighted indicators of social vulnerability.

Like all attempts to capture future transmission potential of an NTD, a number of assumptions have to be made. In the case of Taylor et al. (2016), one of the main assumptions was that the weight of certain social indicators (e.g. the relative importance of the percentage of homes with a mobile phone as an indicator of capacity to anticipate) would remain constant over the coming decades. It was also assumed that neither the mosquito vectors nor the virus itself will evolve as a result of selection pressures from climate change.

11.2.4 Crimean Congo Haemorrhagic Fever (CCHF)

A tick-borne infection, the CCHF virus is a member of the *Bunyaviridae* family. Many tick species, especially members of the *Hylalomma* genus, can act as vectors. Both domestic animals and wildlife, particularly birds, can act as reservoir populations.

The geographic distribution of infection is currently limited to the countries within Africa, the Middle East, Southern-Eastern Europe and Southern Asia (Dreshaj et al., 2016; Ergönül, 2006). Not all populations within each country affected by CCHF are at risk due to factors such as limited environmental suitability for the ticks (Messina et al., 2015) or the restricted distribution of zoonotic reservoirs including cattle and goats (Mostafavi et al., 2013). Concerns have been raised that countries such as Turkey and those in former Yugoslavia can act as portals for exporting cases into neighbouring countries (Mahzounieh et al., 2012; Mild et al., 2010), due to the ability of the vectors to be transported across boundaries.

Retrospective analyses of incidence data from human cases in Europe have observed distinct seasonality and correlations with environmental factors including increased vegetation (grass, scrubland and herbaceous) cover, medium–high level fragmentation of landscapes and warmer temperatures (Vescio et al., 2012). Similar conclusions regarding high temperatures were reached in a study of cases in Pakistan (Abbas et al., 2017).

Efforts to estimate the potential impact of climate change on future transmission of CCHF have, to date, focused on the role of migratory birds spreading the infection further into livestock of Europe (Gale et al., 2012). In that context, it has been concluded that climate change will not have a substantial impact by 2084.

The absence of a contribution from birds does not preclude other organisms from affecting potential future transmission. The role of climate in affecting tick ecology is likely to be highly significant given the sensitivity of tick development and mortality to temperature, water availability and vapour deficit (Estrada-Peña et al., 2015). In common with other infections

included in this review, the relationship between success of the organism and temperature is nonlinear due to the differential effects on development, transovarial transmission, egg survival and mortality of the adult ticks (Estrada–Peña et al., 2013).

11.2.5 Severe Fever With Thrombocytopenia Syndrome (SFTS)

SFTS is caused by a phlebovirus from the *Bunyaviridae* family, first reported in 2009 in China (Yu et al., 2011). *Haemaphysalis longicornis* ticks are reservoir hosts of SFTS (Luo et al., 2015). Antibodies to the virus have been detected in goats, cattle, dogs and chickens (Ding et al., 2014; Zhao et al., 2012). The virus is on the list of WHO priority diseases. Elderly agricultural workers inhabiting rural, shrub or forested areas are at the greatest risk at specific times of year, according to epidemiological surveys (Liu et al., 2014).

At the time of writing, there were no original research publications on the potential for climate change to affect transmission in the future. A current hypothesis is that ticks have historically distributed the infection around China, South Korea and Japan by attachment to migrating birds (Li et al., 2016; Zhang and Xu, 2016).

11.2.6 Zika Virus

Zika virus is an arbovirus of the Flaviviridae family, known to be transmitted to humans through the bite of *Aedes* mosquitoes (Marchette et al., 1969). *Culex* has been assessed as a vector but appears refractory (Huang et al., 2016). Historically, the infection has been known to be endemic in parts of Africa (particularly Nigeria) and parts of southeast Asia (including Borneo and the Philippines). It was the emergence of Zika virus as a public health problem in Latin America in 2015 that created disquiet among global public health practitioners. The potential importance of the infection was recognised by WHO, which declared a public health emergency in February 2016 as the infection was observed to spread across 69 countries and territories, causing thousands of cases of microcephaly (World Health Organisation, 2016b). The designation was removed in November 2016, with WHO maintaining that Zika was a high priority issue. At the time of writing, Zika virus was placed on the list of priority diseases for research and development to prevent epidemics.

It has been speculated that climate variation was partly responsible for the rapid expansion of Zika during 2015 (Ali et al., 2017; Paz and Semenza, 2016). The reason for the rapid rise from 2015 onwards has been attributed

to the El Nino event of 2015 (Caminade et al., 2017), due to the rise in temperatures increasing the biting rate of the mosquito vectors.

A few modelling studies have been published to estimate the contemporary risk of transmission of Zika virus, using ecological niche models to estimate environmental suitability for the two main vectors, *A. albopictus* and *A. aegypti* (Messina et al., 2016); or estimates of R0 for South America (Perkins et al., 2016). At the time of writing, there were no published original research studies on the potential for decadal changes in climate to affect transmission of Zika virus on a local or global scale. As with other vector-borne diseases, a key factor will be the effect of environmental change on the ecology of the vectors (see above), modified by the vectoral capacity of the two vectors (Gardner et al., 2017).

11.3 Bacteria

11.3.1 Trachoma

There have been several papers published that have considered whether or not transmission of trachoma (*Chlamydia trachomatis*) is associated with abiotic factors including temperature, rainfall, RH and sunshine fraction (reviewed by Ramesh et al., 2013). Of the various factors considered, rainfall and temperature (or altitude as a proxy for temperature) were most consistently reported (in mainly cross-sectional studies) to be associated with variation in the prevalence of active *Trachoma*. None of the eight papers reviewed by Ramesh et al. (2013) modelled prospective transmission under specific climate change scenarios. Clements et al. (2010) incorporated land cover and land use in a geostatistical model with the conclusion that transmission is higher in savannah and grassland compared to areas with higher precipitation or high water-table (wetlands).

C. trachomatis can be transmitted directly from person to person or through fomites. From a climate change perspective, it will be important to identify all potential fomites and consider how they may be affected in the future. The most widely implicated are fabrics that can come into contact with faces—towels, bedlinen, etc. But exudates from the eyes are often wiped away with fingers which then come into contact with a wide range of surfaces and objects touched by others. Some of these may be associated with climate-sensitive factors in ways that are poorly understood.

For example, there is a known link between inclusion conjunctivitis and genital chlamydia (caused also by *C. trachomatis*), whereby contaminated genital secretions are transferred by hand to the eye either through auto-inoculation or from a partner. Contaminated fingers may or may not be

washed depending on the availability of water. Water availability is a climate-sensitive issue. In areas of water scarcity, hand washing is likely to be less frequent. Blinding trachoma is a major problem in countries with a high level of desertification, including Egypt and Chad. Although speculative, it is possible that blinding trachoma in such areas is partly associated with both the presence of genital chlamydia and lack of water for hand washing.

An understanding of the ecology of the vector-borne route is of critical importance when considering climate change. *Musca sorbens*, a major vector of trachoma, lays its eggs on (preferably human) faeces (Emerson et al., 2001). The larvae develop and emerge if conditions are suitable. Factors affecting the probability of emergence include whether or not the environment around the faeces leads to crust formation (making it harder to emerge), whether or not the faeces is removed by dung beetles, or whether fly predators such as the dermapateran *Labidura riparia* or histerid beetles such as *Atholus rothkirchi* Berkhardt, predate the larvae prior to emergence (Toyama and Ikeda, 1981). When considering how climate change may affect trachoma transmission it is therefore necessary to consider how dung beetles, and arthropod fly predators will also be affected. Furthermore, although *M. sorbens* appears to prefer human faeces, the fly will also settle and lay eggs on dung of animals such as cows. So it also important to consider how humans and animals will deposit faeces, and what happens to the faeces once deposited, under conditions of a changing climate which may include increasingly long periods of extreme conditions.

In a recent attempt to understand better how climate affects trachoma transmission, Ramesh et al. (2013) reviewed studies of abiotic factors associated with *M. sorbens* ecology. First implicated as a vector at the turn of the 21st century (Emerson et al., 2000), the fly is known to be affected by temperature and humidity, but the limited number of relevant studies makes modelling of the future transmission potential highly challenging (Ramesh et al., 2013).

The lack of empirical data to support dynamic models is of particular concern. The WHO strategy of combining mass antibiotic distribution, facial cleanliness and environmental hygiene (known as SAFE), has been scaled up in recent years, and blinding trachoma is one of the conditions scheduled for global elimination by 2020. Given the paucity of information on the epidemiology of blinding trachoma, its links to genital chlamydia, water insecurities, land use change and other potential ecological variances, it is still an uncertain future.

11.3.2 Buruli Ulcer

Buruli ulcer is a debilitating and disfiguring infection of tropical regions caused by *Mycobacterium ulcerans*. For a recent review of the pathology of Buruli ulcer, see Yotsu et al. (2015). Within that review is a list of known or suspected vectors of *M. ulcerans* that includes insects, mammals, fish and shellfish. One of the key suspects is *Naucoridae* water bugs (Portaels et al., 2008), which have been demonstrated to be able to transfer the bacterium to mice through biting—the bacterium being located in the salivary glands (Marsollier et al., 2002). There is also evidence that certain types of water body (e.g. swamps) are associated with increased risk of exposure to the bacterium, but no evidence that direct water contact is a risk factor (Williamson et al., 2012). The reason for proximity to water being a risk factor may be partly due to the presence of the water bugs. Linking the abundance of water bugs to the risk of infection has proven challenging—various studies have identified that carriage of the bacterium in in the mouthparts of the water bugs changes at specific times of year (Marion et al., 2010), but also that unidentified environmental factors can better explain spatiotemporal variation in disease when compared to spatiotemporal variation of *M. ulcerans* presence in the environment (Garchitorena et al., 2016).

Cases of the Buruli ulcer are predominantly found in West Africa (Yotsu et al., 2015), but also in other tropical countries including Japan (Yotsu et al., 2012) and northern parts of Australia (Lavender et al., 2012). Anthropocentric activities such as dam building have been implicated in terms of establishing new sites of infection (Marion et al., 2011). A recent case report suggests the bacterium is also found in Honduras (Southern, 2016). Buruli ulcer is classified as an emerging disease. The number of cases per country fluctuates and there is no clear temporal trend over the previous decade (Yotsu et al., 2015).

Evidence is emerging of landscape factors driving spatiotemporal variation in abundance of *M. ulcerans* cases—(Aboagye et al., 2017—presence of bacterial DNA in the environment; Landier et al., 2014; Merritt et al., 2010). At the time of writing, there were no original research articles on the potential for decadal climate change to affect transmission patterns.

11.4 Protozoa

11.4.1 Leishmania

For a review of papers published on this subject before 2008, see Ready (2008).

Several species of *Phlebotomus* and *Lutzomyia* sandflies, distributed and segregated geographically across the tropics, have been identified as major vectors of leishmanial parasites (Bates, 2007). Each species of sandfly occupies a specific ecological niche and has a climate-sensitive life cycle and population biology governed by a mixture of abiotic and biotic factors acting independently and through interactions. While it has been recognised since the turn of the century that climate change may have a significant impact on the distribution of both the vectors and the disease (Peterson and Shaw, 2003), the general direction of travel is less well specified due to the fact that sandfly populations are affected on a microgeographical scale.

In the European context, it has been demonstrated that the density of *Phlebotomus ariasi* at a particular sampling location is affected by both minimum and maximum temperatures and to some extent by RH (Prudhomme et al., 2015). South facing slopes, wall vegetation, soil type and neighbouring land cover precipitation may also be important factors in determining local abundance of this and other species (Ballart et al., 2014). Effects of individual explanatory factors disaggregate among species of sandfly, indicating a need to consider not just how climate change might affect individual ecological drivers of abundance and site-specific vector density, but how individual species of vector might be affected.

In the South American context, the relatively early models of Peterson and Shaw (2003), using a combination of ecological niche modelling and a general circulation model, predicted that by 2055 conditions in parts of Brazil may become more favourable for transmission due largely to anticipated increases in temperature. A more refined conclusion was reached by Carvalho et al. (2015), working with an ensemble of ecological niche models and downscaled ($344 \, \text{km}^2$) general circulation models, projected to 2041–60. In that study, the simulations indicate that southern and eastern parts of Brazil are likely to become more suitable in terms of the environment a simulation model of climate change scenarios on the distribution of leishmanial vectors in the Colombian context, it was suggested that spatial range could decrease under minimally disruptive scenarios through to maximally disruptive scenarios (González et al., 2014).

11.4.2 Chagas Disease

The organism responsible for Chagas disease is *Trypanasoma cruzi*. This protozoan parasite is distributed widely across Latin America and is estimated to infect 6–8 million people of all ages (Rassi et al., 2010). The climate-sensitive

stage of the parasite is in the insect vector, members of the Triatominae subfamily.

The evolution, natural history and ecology of many Triatominae vectors are described in detail elsewhere (Abad-Franch et al., 2015; Galvao and Justi, 2015; Teixeira et al., 2009). What has emerged from these and other studies is that many *Triaotominae* species have evolved to be closely associated with specific natural environments involving vertebrates such as birds, bats and rodents (Galvao and Justi, 2015) from which they derive blood meals. The large number of species means that there are a corresponding large number of potential niches, each of which may respond differently to changing climates.

It is becoming increasingly apparent that these traditional niches are being disturbed by anthropogenic changes affecting life history traits, species composition in specific locations and habitat availability (Gottdenker et al., 2012). Several studies have reported that normally sylvatic species are increasingly invading urban domestic properties, for example in Bolivia (Rojas-Cortez et al., 2016) and Brazil (Ribeiro et al., 2015). Reasons for expansion of the vector range into human habitations have speculated to include the increasing availability of electrical light. Many insect species are attracted to the blue light fraction of electrical light and several studies have observed clustering of Triatomine species around artificial light sources, both in sylvatic (Castro et al., 2010) and urban (Pacheco-Tucuch et al., 2012) settings. Economic activities associated with the availability of electric light have also been suggested to underlie recent epidemics of *T. cruzi* in new areas.

The anthropogenic influences above demonstrate that Triatominae adapt rapidly to new opportunities and/or pressures. The potential for climate change to affect transmission patterns of *T. cruzi* over much longer periods, through long-term effects on the soil and water phases, is less well understood but has received some attention in the literature, specifically through attempts to model the future suitability of habitats to support vectors. Two separate studies have focused on how projected warming scenarios may affect the geographic distribution of *Rhodnius prolixus* and *Triatoma infestans* in Venezuala and Argentina (Medone et al., 2015), and the geographic distribution of *Eratyrus mucronatus*, *Panstrongylus geniculatus*, *R. prolixus*, *Rhodnius robustus* and *Triatoma maculata* in Venezuela (Ceccarelli et al., 2015).

A common output of these studies was that the distribution of infection is likely to change over the coming decades. Specifically, the distribution of infection is expected to reduce in the countries studied due to

environments becoming unsuitable for the vectors. Neither of these studies considered other changes to the niches that will be affected by climate change. Palm trees, bromeliads, bird and rodent nests, hollow trees and mammal burrows are among the sylvatic ecotopes occupied by the vectors of *T. cruzi*. Climate change is likely to impact on each ecotype in ways that we do not yet fully understand and which will be challenging to project given the potential for multidimensional interactions among biotic and abiotic domains.

11.4.3 Human African Trypanosomiasis (HAT)

The life cycle of HAT involves humans, wildlife and over 20 species of *Glossina*, the Tsetse fly. The most climate-sensitive stage of the lifecycle is in the flies. It is well established that Tsetse natural history dynamics are shaped by environmental factors—as far back as 1940 studies were being undertaken into the role of humidity on the population of *Glossina pallidipes*, *Glossina austeni* and *Glossina brevipalpis* in Kenya (Moggridge, 1949). Readers are referred to Leak (1999) for a comprehensive overview of Tsetse biology and ecology, and Rogers (2000) for an introduction into the use of satellite imagery to map the distribution of Tsetse flies.

More recently, Pagabeleguem et al. (2016) have investigated the fecundity and survival of three strains of *G.p. gambiensis* under conditions of varying temperature at constant RH (25–35°C at 60% RH) and varying RH at constant temperature (40%–75% RH at 25°C). From these two experiments, it was observed that temperature was more important than humidity at affecting survival. The effect of changing temperature on the survival was dramatic. Peak survival of all three strains was estimated to occur at 25°C, with rapid declines thereafter and a median survival time of less than 5 days at 32°C.

In terms of the potential for climate change to alter current transmission patterns, there has been one published study. Moore et al. (2012) used a deterministic model based on a series of ordinary differential equations that described the rate at which tsetse flies become susceptible, exposed, infected and recovered. The effect of changing temperature on the basic reproductive rate (R0) was then estimated from published studies on the effect of temperature change on mortality, biting rate, parasite-biting rate and population growth rate. Changes in temperature over future decades were drawn from the IPCC scenarios B1 and A2 to 2090. Population was assumed to remain constant.

Moore et al. (2012) predicted that rather than expansion of the tseste fly population under conditions set by the IPCC scenarios, there may be a shift

of up to 60% in the geographical extent of the range. Under the A2 scenario, there is likely to be range contraction by 2090 due to some regions of eastern Africa becoming too hot to support the fly population.

In recognising the limits of their study, Moore et al. (2012) highlight a point relevant to all modelling studies—namely that the modelling exercise itself sets a framework for future projects rather than making any definitive statements.

12. CONCLUSIONS

In writing this review, I examined the published peer-reviewed literature for articles that represent interests in climate change and NTDs. Climate change in this context primarily concerns forward looking, decadal-scale changes and is therefore distinct from near or mid-term forecasting which typically concerns within-decade timescales.

It is clear from reviewing the published literature that there is a relative abundance of literature from previous decades, as well as more recently, regarding the environmental factors that underpin the natural history of several NTDs. In contrast, there is a paucity of forward-looking research being conducted on the decadal timescale for the majority of infections. This document therefore serves as a gap analysis as much as a review of the state of the art.

One conclusion that is nonetheless shared among all research outputs is that a changing climate is associated with spatiotemporal variation in exposure and transmission of each species of infection. Along with other aspects of global change (reviewed by Cable et al., 2017), it can be concluded that there are likely to be profound yet hard-to-discern changes to global patterns of NTD transmission in the near, mid- and long term. Some of these changes may be extreme enough to cause elimination or extinction of parasites, vectors and zoonotic hosts in localised, regional or global contexts (Cable et al., 2017; Cizauskas et al., 2017).

The future can only be imagined and modelled, as we cannot draw data down from the future. No model can capture every potential interaction, and the increasingly fragmented nature of ecosystems (Haddad et al., 2015) is an ongoing challenge in terms of providing mitigation and/or adaptation (Villard and Metzger, 2014).

In the absence of sureties regarding the future, combined with recognition of the inherent complexities facing humanity, a viable response may be to increase intersectoral collaboration so that, e.g., emerging knowledge in one domain can be assessed for its utility in another domain. The 'One

Health' concept is a potential avenue down which colleagues working on NTDs from many disciplines could travel together (Webster et al., 2016). One Health joins several other attempts to synthesise an integrated, multi-disciplinary, multisectoral framework, including blue marble health (Hotez et al., 2016) and planetary health (Horton et al., 2014). A complementary approach may be to improve surveillance and adaptation efforts (Ebi et al., 2013; Parham et al., 2015; Wilby and Dessai, 2010). It has been advocated that these new approaches should be community-based (Ebi and Semenza, 2008) and combine capacity building in modelling with decision support tools that are sufficiently flexible and adaptive to emerging conditions (Booth and Clements, 2018).

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