Review

Parasite zoonoses and climate change: molecular tools for tracking shifting boundaries

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For human, domestic animal and wildlife health, key effects of directional climate change include the risk of the altered occurrence of infectious diseases. Many parasite zoonoses have high potential for vulnerability to the new climate, in part because their free-living life-cycle stages and ectothermic hosts are directly exposed to climatic conditions. For these zoonoses, climate change can shift boundaries for ecosystem components and processes integral to parasite transmission and persistence, and these shifts can impact host health. Vulnerable boundaries include those for spatial distributions, host–parasite assemblages, demographic rates, life-cycle phenologies, associations within ecosystems, virulence, and patterns of infection and disease. This review describes these boundary shifts and how molecular techniques can be applied to defining the new boundaries.

The importance of climatic factors

Climate change is one of many anthropogenic factors linked to the disruption of ecosystems around the world. According to the Intergovernmental Panel on Climate Change, the long-term trend for the current episode includes warmer temperatures, altered patterns of precipitation, increased frequency and severity of extreme climatic events (e.g. hurricanes), and rising sea levels [1]. Parasite zoonoses are among many infectious diseases of people, domestic animals and wildlife for which occurrence is linked to climatic factors and, not surprisingly, some are proving sensitive to climate change [2]. The mechanisms generating this sensitivity are not fully understood, however, and are usually interwoven with other drivers of change (Figure 1). Depending on trajectories for future climate and for societal responses, climate change could become an increasingly important determinant of the health impacts of infectious diseases, particularly in areas of the world with limited resources for disease mitigation [3].

Parasite zoonoses, disease ecology and climate change

The life cycles of many parasite zoonoses are complex. Several host species from several taxa might be involved, as well as terrestrial and/or aquatic environments. Life-cycle stages of several of these parasites are widely distributed among ecosystem components, and this distribution varies with place and time [4]. For parasite zoonoses, climate change has the potential to shift boundaries for spatial distributions, host–parasite assemblages, demographic rates, life-cycle phenologies, associations within ecosystems, virulence, and patterns of infection and disease. There is likely to be considerable variability in these responses, however, because the reactions of both parasites and hosts to the stimuli differ with species, individual, and other biotic and abiotic features of the ecosystem.

Because of biological, logistical and analytical complexities, there are few robust data defining the linkages between climate change – as opposed to climate – and the ecology of parasite zoonoses (Table 1). Indeed, multifactorial aetiologies have been identified for some shifts in disease occurrence believed initially to be driven primarily by the changing climate (e.g. tick-borne encephalitis in the Baltic countries) [5].

New spatial distributions

For many birds, ectotherms and plants, but (to date) few mammals, there are well-documented examples of shifts in geographic distributions related to climate change [6]. These shifts are latitudinal and/or altitudinal, and most are expansions and/or contractions of pre-existing distributions. They often reflect new spatial boundaries for temperature, and perhaps other environmental factors, supportive of host and parasite life cycles. The extent of these shifts, and the numbers of hosts and parasites affected, vary with place and time depending on the nature and force of the drivers involved. Climate change also has the potential to shift migration patterns for hosts [7]. Other shifts in distribution result from translocations, which can be either deliberate or inadvertent (as with invertebrates or small vertebrates), to non-contiguous areas. Translocations provide escape from inhospitable habitats (perhaps because of climate or its effects on food supply or other crucial resources) and/or bring benefits, and possibly parasites and other pathogens, to the new locations.

New host–parasite assemblages

Changing geographic distributions generate new footprints for hosts and their parasites and sometimes gen-

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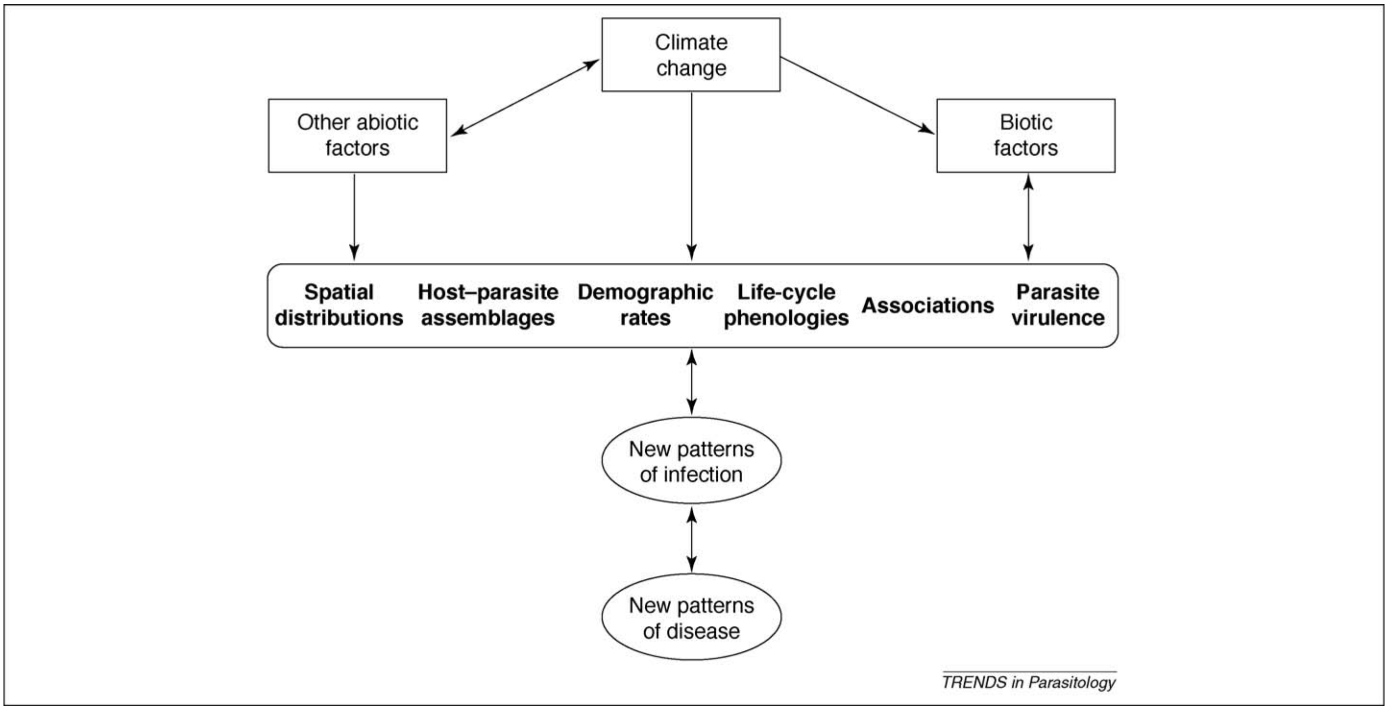

Figure 1. Key linkages between climate change and new patterns of infection and disease. The flow chart shows linkages between climate change, other abiotic and biotic factors, and new patterns of infection and disease. The central box shows the potentially interdependent sensitivities through which drivers of change shift boundaries for hosts, parasites, infection and disease. Molecular techniques can be used to explore all these sensitivities. Note that for some linkages, flow can be in both directions.

erate new sympatries for individuals and species [8]. As a result, parasites might switch between established and newly arrived hosts and/or host species, and first-time exposure of hosts in the absence of specific immunity might result in deleterious health impacts. In addition, immigration or emigration of hosts and/or host species not susceptible to a parasite can influence parasite transmission [9]. Finally, shifting boundaries for spatial distributions for hosts and parasites, with altered patterns of sympatry, can affect food webs, including predator–prey linkages that are crucial for hosts and parasites.

New demographic rates

For parasite life-cycle stages in the environment or in ectothermic hosts, and for these hosts, development and mortality rates can be affected by changes in temperature and precipitation. Within an ‘optimal’ range for each species, rising temperatures increase development rates, and these rates might result in altered parasite generation intervals. For larval trematodes in snails, warming also enhances parasite amplification [10]. The effects of the new climate on mortality rates are more complex. In assessing these potential impacts of climate change, the scale of response is important. For example, in laboratory studies, 3°C increases between 21°C and 30°C shortened the prepatent period of *Schistosoma japonicum* in *Oncomelania hupensis* from 110 to 65, then 50, then 40 days [11]. Less well defined are the effects of new patterns of precipitation, alone and in combination with other drivers of change, on demographic rates. It is possible that different elements of the new climate, acting together, will have opposing effects on these rates.

For parasite life-cycle stages in homeothermic hosts, the effects of climate change on demographic rates are indirect and mediated through the hosts. Shifts in parasite recruitment, development, amplification and mortality are possible. These can result from altered host contacts with infective stages, as might occur with fluctuating abundance of parasites and/or hosts in the environment, changes in host behaviour, or altered ability of the host to prevent, delay or abbreviate parasite establishment. Possible consequences include shifts in the prevalence and intensity of infection, in host morbidity and mortality, and in the basic reproductive number of the parasite (R_0). There might also be shifts in the species composition of host and parasite faunas, leading to a cascade of change in the ecosystem.

New life-cycle phenologies

The timing of many events in the life cycles of both parasites and wildlife hosts is sensitive to the effects of climate and climate change [6]. In particular, reproduction by many host species is governed by temperature, precipitation and/or the availability of food. For hosts that have seasonal reproductive cycles, climate change might shift mating and birthing and disrupt any beneficial synchronies of the life cycle with food supply [12]. In addition, shifts in precipitation might affect life-cycle success for hosts, including, particularly, arthropods and gastropods that require a humid environment or access to standing water for development. For parasites with seasonally variable abundance of infective stages, climatic and/or temporal shifts in the seasons (e.g. warmer winters or earlier springs resulting from climate change) might disrupt synchronies between host and parasite life cycles and the timing of peaks in transmission. Possible consequences include altered magnitude and timing of health impacts for hosts.

Table 1. Some reported approaches to the exploration of linkages between climate change and altered patterns of parasite, host and disease ecology

Type of study, parasite and location	Climatic factor(s)	Effects and/or linkages	Refs
Prospective *Leishmania* species Southern Brazil and adjacent areas	Predicted climate change scenario model predictions for temperature and precipitation	Shifts in distributions and significance of vector species	[47]
Retrospective *Leishmania* species Costa Rica	El Niño/Southern Oscillation (ENSO)	Cyclical temporal correlation between climatic factors and incidence of cutaneous leishmaniasis	[48]
Retrospective *Leishmania* species North Eastern Colombia	ENSO and La Niña	Increase in visceral leishmaniasis cases linked to ENSO and decrease linked to La Niña	[49]
Prospective *Leishmania* species Portugal	Climate change scenario model predictions	Shifts in risk of leishmaniasis for people – varying with climate scenario and location	[50]
Prospective *Trypanosoma cruzi* United States	Climate change scenario model predictions for 2030 of 1°C increase in minimum temperatures	Increases of 15% to 23% in areas at risk for *T. cruzi* transmission	[51]
Prospective *Trichinella nativa* Arctic	Decreasing extent of Arctic sea ice	Shifts in diets of walrus and bearded seals and, potentially, in risk of trichinellosis in people	[52]
Retrospective *Fasciola hepatica* East Anglia, England	Increased summer rainfall, probably coupled with translocations of infected sheep and marshland conservation project	Increased incidence of fasciolosis in cattle	[53]
Retrospective *Fasciola hepatica* Ecuador	ENSO effects on precipitation patterns	Potential for increased incidence of fascioliasis in people in the two years after ENSO event	[54]
Prospective *Schistosoma japonicum* China	Climate model predictions for 0.9°C increase in ambient temperatures in 2030 and 1.6°C increase in 2050	By 2050, 8.1% increase in areas at risk for *S. japonicum* transmission, but limited by freezing line (margin of area with mean January temperature $\leq$0°C)	[55]
Retrospective *Schistosoma japonicum* Yangtze River Valley, China	Periodic flooding of river and collapse of restraining embankments	Increases in areas with snail and infected snail intermediate hosts, and in prevalence and incidence of schistosomiasis in people	[56]
Retrospective *Schistosoma mansoni* Western Uganda	Possibly climate change, including increased ambient temperatures, and other climatic and non-climatic factors	Altitudinal extension of distribution of *S. mansoni* in people	[57]
Prospective *Schistosoma mansoni*	Predictions from model for temperature effects on features of transmission	Within a specified range, temperatures positively correlated with parasite abundance and disease; also shifts in transmission dynamics and efficacy of control measures	[58]
Prospective Ticks Mediterranean region	Climate-based models for tick distributions	Overall northward extension of areas of habitat suitable for some tick species	[59]
Prospective *Ixodes scapularis* Canada	Predicted scenarios for climate change	Overall northward increases in areas of habitat suitability for *I. scapularis* and increased tick abundance	[60]

New associations within ecosystems

Ecosystem change brought about by the new climate is leading to new associations involving hosts, parasites and other biotic components of the ecosystem [13,14]. Examples include new assemblages of host species, parasite species, parasites and other pathogens [15], as well as new associations resulting from altered host and parasite behavior [16,17], and altered ecological networks. For parasite zoonoses in people, the key associations are those that lead to human infection. Among abiotic ecosystem components, water is the most important. In particular, quantity, type (rain or snow), rate of precipitation, spatial distribution, persistence, quality and contacts between hosts, parasites and water all influence the ecology of hosts and parasites, particularly those with crucial dependence on water for specific life-cycle stages or transmission [18].

New parasite virulence

Through progressive selection or seasonal shifts in predominant genotypes (e.g. in the case of *Vibrio cholera*), climate and climate change can alter temporal and spatial patterns of infection and/or disease [19]. Although these effects have been little studied in parasites, protozoans seem likely to be the most susceptible.

New patterns of infection and disease

For many parasite zoonoses, climate change has the potential to generate new patterns of infection and disease in people, domestic animals and wildlife. Possibilities include new geographic distributions, host species infected and affected, epidemiology (including seasonal patterns), prevalence and intensity, virulence, clinical features, and efficacy of treatment and control. These new impacts might be regional, affecting many hosts over a wide area, or

Table 2. Molecular detection and/or identification of zoonotic parasites[a]

Parasite	Parasite in definitive host	Parasite in food products from definitive host	Parasite in intermediate and/or paratenic host	Parasite on foods	Parasite in potable water and drinks	Parasite in terrestrial environment	Parasite in aquatic environment	Arthropod intermediate host identification	Gastropod intermediate host identification
Vector-borne meta-zoonoses									
Leishmania	✓	N/A	✓	N/A	N/A	N/A	N/A	✓	N/A
Plasmodium knowlesi	✓	N/A	✓	N/A	N/A	N/A	N/A	✓	N/A
Trypanosoma brucei	✓	N/A	✓	N/A	N/A	N/A	N/A	✓	N/A
Trypanosoma cruzi	✓	N/A	✓	N/A	N/A	N/A	N/A	✓	N/A
Filarioids	✓	N/A	✓	N/A	N/A	N/A	N/A	✓	N/A
Schistosoma	✓	N/A	✓	N/A	N/A	N/A	✓	N/A	✓
Food-borne meta-zoonoses									
Trematodes[b]	✓	N/A	✓	✓	N/A	N/A	✓	✓	✓
Trichinella	✓	✓	N/A	✓	N/A	N/A	N/A	N/A	N/A
Water-borne zoonoses									
Cryptosporidium	✓	✓	N/A	✓	✓	N/A	✓	N/A	N/A
Giardia	✓	✓	N/A	✓	✓	N/A	✓	N/A	N/A
Toxoplasma	✓	✓	✓	✓	✓	N/A	✓	N/A	N/A
Sapro-zoonoses									
Toxoplasma	✓	✓	✓	✓	✓	N/A	✓	N/A	N/A
Ancylostoma	✓	N/A	N/A	N/A	N/A	✓	N/A	N/A	N/A
Ascarids	✓	✓	N/A	N/A	N/A	✓	N/A	N/A	N/A
Direct and cyclo-zoonoses									
Echinococcus	✓	N/A	✓	✓	N/A	✓	✓	N/A	N/A
Taenia	✓	✓	✓	✓	N/A	✓	✓	N/A	N/A
Trichinella	✓	✓	N/A	✓	N/A	N/A	N/A	N/A	N/A

[a] Abbreviations and symbols: ✓, available; N/A, not applicable.

[b] Intestinal, hepatic and pulmonary trematodes.

local, affecting only a few individuals or communities. Furthermore, some shifts in patterns of infection and disease are likely to be gradual and others very sudden, in some instances precipitating epidemics.

Using molecular tools to study climate change and parasite zoonoses

In the examples that follow, 'molecular tools' refers to PCR-based procedures that enable the amplification of specific gene sequences that have been found to be of value in the characterization of parasite stages to species and/or genotype level. Such techniques can be applied to clinical and environmental samples containing minute quantities of parasite stages that could not be identified without genetic characterization because of the lack of discriminatory morphological features (Table 2).

Vector-borne meta-zoonoses

There is considerable evidence that climate change has, and will increasingly have, a direct influence on the distribution of vectors of parasitic diseases (particularly arthropods), either directly or indirectly, by impacting on the distribution and availability of hosts and, thus, parasite transmission, leading to changes in both the distribution and the incidence of disease [20]. Most research has concentrated on mosquitoes and anthroponotic malaria, but there is increasing evidence that other vector-borne parasite zoonoses such as leishmaniasis, Chagas disease and anthropozoonotic simian malaria will be greatly affected in terms of their distribution [20–22]. This is already being demonstrated with the expanding distribution of *Leishmania infantum* in the Mediterranean [23]. Fortunately, a variety of molecular tools have proved effective for *Leishmania* characterization and surveillance, as well as for monitoring the infection in vector populations, and these need to be applied in areas at risk of leishmaniasis emergence or re-emergence. For example, confirmation and characterization of a novel species of *Leishmania* in kangaroos in Australia [24] was only possible as a result of the application of appropriate PCR-based procedures. As a consequence, questions remain about the origin of this form of *Leishmania*: has it been introduced recently, or is it a previously unrecognized endemic form? This discovery indicates that there are vectors for *Leishmania* in Australia that could also transmit other species of the parasite. Pathogenic species of *Leishmania* regularly enter Australia in infected people or dogs from endemic areas of the world [25]. Until recently, it has been assumed that such infections represent a minimal biosecurity risk because Australia was thought not to have vectors capable of transmitting *Leishmania*. The discovery of the parasite in kangaroos demonstrates that imported cases of *Leishmania* pose a risk of being transmitted to people and their pets and to wildlife. Wildlife could, thus, become a important reservoir of zoonotic leishmaniasis, as well as suffering the potentially serious clinical consequences associated with exposure to a novel introduced pathogen, likely to be of human origin in view of the increasing number of introduced cases in immigrants to Australia [26,27]. More recently, PCR-based molecular tools proved crucial in the identification of an emerging focus of leishmaniasis in Southeast Asia and, furthermore, suggest that the causative agent is a new species [28].

In addition to *Leishmania*, there is evidence that two other vector-borne protozoa are being impacted by climate change. The spatial distributions for *Trypanosoma cruzi* and its vectors are expanding as a result of climate change [29], and as the disease becomes endemic in new regions, there is a need to identify potential new reservoir hosts. As with *Leishmania* spp., appropriate PCR-based molecular tools have been developed that can be used for the characterization and surveillance of parasite and vector populations [30], and these need to be increasingly applied in molecular epidemiological investigations. Finally, the application of PCR-based procedures was pivotal in the recent discovery of *Plasmodium knowlesi* in people [21] and in subsequent studies on the expanding distribution of this potentially fatal zoonosis [22].

Food-borne meta-zoonoses

The influence of climate on the distribution and transmission of *Fasciola hepatica* has been well understood for decades, and models have been developed that accurately forecast risk of transmission based on climate data [31,32]. As such, predicted climate changes are expected to lead to increases in outbreaks of human fascioliasis [31,32]. A variety of DNA techniques have been shown to be useful for parasite diagnosis and characterization, particularly for the differential diagnosis of *F. hepatica* and *Fasciola gigantica* in people in areas of overlapping range. Simple and rapid PCR-restriction length polymorphism assays can be applied directly to faecal samples from people and animals in endemic areas to identify and discriminate between the morphologically identical eggs of the two species [31].

As with *Fasciola* parasites, the transmission of fish-borne flukes to humans and intermediate hosts is influenced by climate and human behaviour [33]. The distribution of human infections corresponds well with the availability of snail and fish intermediate hosts and the food consumption habits of local populations. There is a need for the surveillance of human populations in endemic and potential new endemic regions. This can be a problem with parasites such as *Clonorchis* and *Opisthorchis* that produce morphologically identical eggs, yet it is important to differentiate between the two species because of differences in clinical presentation and prognosis in humans. Direct characterization from faecal samples is now possible using PCR-based procedures, which are being applied in different geographical regions and have recently identified (for the first time) the presence of *Clonorchis sinensis* in Thailand [34], where previously only *Opisthorchis* was thought to occur. It remains to be determined whether this extended distribution reflects more discriminatory surveillance procedures, the influence of climate change and/or other ecological factors on the parasite and its hosts.

Anisakiasis is an emerging zoonosis in which the causative agents have complex multi-host aquatic life cycles that are very sensitive to environmental factors, including temperature. There is an urgent need for molecular epidemiological studies to determine the identity of the various anisakid parasites, as well as the full extent of the geographical distributions, host ranges and prevalence rates of the zoonotic species in definitive, intermediate and paratenic hosts [35,36]. Various causes of habitat disturbance, including global climate change, adversely influence the trophic webs involving different species of marine mammals, fish and invertebrates that act as definitive and intermediate hosts of anisakid nematodes, which could adversely affect the population size of these nematodes and, consequently, their genetic diversity [37]. These authors suggest that anisakid nematodes and their levels of genetic diversity could be indicators of the integrity of marine food webs and of the general biodiversity of a marine ecosystem.

Water-borne zoonoses

Among the zoonotic parasites, those with infective stages that are exposed directly to the environment for prolonged periods are very susceptible to the effects of climate change. These include the water-borne protozoa *Giardia, Cryptopsoridium* and *Toxoplasma*. The application of molecular epidemiological tools for their detection and characterization has been of enormous value, particularly the direct application of PCR-based tools to characterize parasite stages from faeces, tissues and environmental samples. These tools have demonstrated a much greater degree of genetic variation than was previously thought to exist, reflected at both species and intraspecific levels [38]. For *Giardia* and *Cryptosporidium* in particular, their wide host range, and the increasing evidence of host specificity between morphologically identical species and genotypes of both parasites, has meant that molecular tools provide the only effective approach to surveillance and determining the risk factors associated with finding cysts or oocysts in water.

Sapro-zoonoses

Sapro-zoonotic agents, such as the ascarids, hookworm and coccidians (e.g. *Toxoplasma*), all produce resistant stages that require a sojourn in the environment to embryonate or sporulate and are capable of prolonged survival under suitable conditions of temperature and humidity. Climate change will impact all these parasites, potentially in different ways, and there is a need for appropriate molecular tools to identify and characterize those environmental stages that do not exhibit interspecific morphological differences. In the case of hookworm, the recent development of PCR-based techniques for differentiating between species in dogs and cats has demonstrated the presence of *Ancylostoma ceylanicum* in dogs in Australia [39]. This is the first report of this emerging zoonotic hookworm in Australia and raises the question of whether this is a result of the parasite extending its range – possibly because of climate factors – or purely a result of more accurate surveillance.

Direct and cyclo-zoonoses

Climate change will, directly or indirectly, lead to changes in the distribution of hosts, especially wildlife. This will influence the zoonotic transmission of parasites such as *Echinococcus* and *Trichinella*, which are characterized by their low host specificity. For both parasites, a range of molecular tools are available for the detection and characterization in definitive and intermediate hosts of the numerous species and strains or genotypes that have been identified in both genera. For example, *Echinococcus multilocularis* is extending both its geographic and its host range, particularly in Europe [40]. In addition to the fox, dog and cat, the raccoon dog (*Nyctereutes procyonoides*), a known definitive host for *E. multilocularis* in Japan, has been identified recently as a suitable definitive host for *E. multilocularis* in Europe [40]. This is important because the distribution of the raccoon dog in Europe is expanding rapidly and is likely to exacerbate the already worsening *E. multilocularis* problem caused by the spread of the fox in Europe [41]. Although the raccoon dog occupies a similar ecological niche to that of foxes, particularly in terms of diet and urbanization, competition between these hosts has not been observed [42]. However, the raccoon dog has a greater reproductive potential than the fox, and this could increase with the effects of global warming. This is because climate is likely to have a marked effect on the abundance of raccoon dogs [42,43], potentially providing opportunities for this host to increase its numbers and continue to extend its range in Europe. For *Trichinella*, the role of wildlife in the perpetuation of the parasite is an increasing problem in many regions of the world [44]. Climate has been shown to play a part in the distribution of the different species and genotypes, some of which can use both mammals and poikilothermic vertebrates as hosts. Thus climate, especially temperature and rainfall, is likely to have an increasingly important role as a selection factor determining parasite and host distribution. Surveillance for these shifts is greatly facilitated by the use of molecular techniques.

Concluding remarks

Despite strong evidence for impacts of the new climate on global ecosystems [45], rigorous assessment of the data on which these impacts are proposed is crucial [46]. For parasitic diseases, we are currently in the early stages of penetrating the ecosystem–new-climate–host–parasite matrix and are focused primarily on endpoints, often patterns of disease in human, domestic animal or wildlife hosts. As our scientific compass becomes more clearly visible and our investigative capabilities strengthen, however, we will discover an astonishing array of more subtle effects of climate change on this matrix and, thus, develop a better understanding of the linkages between the new climate and parasite zoonoses and the mechanisms determining patterns of infection and disease. These advances are crucial for effective mitigation and prevention of disease and can be achieved only with an understanding of the breadth and complexity of the possible effects of climate change on hosts and parasites and a capability for accurate detection and identification of the parasites in many ecosystem components.

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