Review

Climate change and foodborne transmission of parasites: A consideration of possible interactions and impacts for selected parasites

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ABSTRACT

A changing climate alters the living conditions for almost every species on earth. We recognise that these changes may threaten our environment, our water and food supply, and our health; predicting the likely changes and impacts we try to prepare for different weather conditions. A complicated and perhaps underestimated threat is how climate change may affect foodborne parasites — a subject that tends to be neglected among infectious diseases under any climatic conditions. Here we review some selected examples of these pathogens, and how they may interact and alter with the changing environment: the complexity and variation in their lifecycles mean that different parasites will not necessarily be affected similarly by the same climate changes. To provide illustrative examples we have chosen a couple of parasites from each major group: trematodes, cestodes, nematodes, and protozoans. Even within these groups, different members utilize widely varying routes to complete their lifecycles, exploring new areas together with their hosts, floating from one place to another, or travelling along with their hosts to white spots on their maps. These parasites are very different from each other, but all are influenced by abiotic factors and have a common goal, to reach their next host. This review aims to open the readers mind to how exposure routes and transmission routes may be affected by climate change: realization of the possibilities is the first step towards closing the door to the parasites that are knocking at it.

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1. Introduction

Predicted climate changes will create impacts throughout the globe, and these will vary from region to region. Some areas will experience an overall temperature rise and polar ice is melting; in some countries or regions precipitation is expected to increase, while others are preparing for drier conditions. Overall, sea levels are rising and an increase in the frequency and intensity of extreme weather events is expected in many places. It is generally accepted that these ongoing and predicted climate changes will affect the distribution of infectious diseases (Altizer, Ostfeld, Johnson, Kutz, & Harvell, 2013). Some factors may result in the door opening to new geographical areas for pathogens to explore, while the same, or different, factors may result in other doors closing. The situation is complex and uncertain, and as climate change may affect environmental conditions, making predictions regarding spread of infection due to climate change events must be recognised to include these uncertainties.

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Although most research on climate change and infectious diseases has focused upon viral infections, bacterial infections, and those infections transmitted by vectors, another group of pathogens should also be considered: foodborne parasites. Although foodborne parasites encompass a vast diversity of species with different characteristics, transmission routes and clinical conditions, they are often neglected in comparison with other pathogens. The reasons for this lack of focus on this important pathogen group are diverse, but probably include:

1) many of the parasitic infections that may be transmitted by contaminated food may manifest as a chronic disease progression, rather than acute febrile or gastro-enteric infection; such infections tend to be considered as being of lesser importance or urgency;

2) the relatively lengthy incubation periods between infection and symptoms for several parasites – ranging (depending on the parasite) from a day or so up to months or even years – again reduce the human perception of importance and create problems in ascertaining source attribution;

3) problems in identification of the vehicle of infection and difficulties in diagnosis and detection; these diagnostic and identification challenges hamper both clinical studies and recognition of importance;

4) the range and complexity of foodborne parasites can be off-putting for those without expertise in this subject;

5) there is the mistaken perception in many Western or industrialised countries that parasites are uniquely associated with tropical areas or regions of acute poverty. Although it is true that when infrastructures such as sanitation and water supply are inadequate, then transmission can be exacerbated, outbreaks of foodborne parasitic disease occur globally, including in the wealthiest countries in the world.

Despite parasites being the "poor relation" in terms of perceived pathogen importance, it appears that foodborne parasites are gradually becoming recognised as being serious public health concerns. Not only has *Cryptosporidium* infection been demonstrated as one of the most important causes of moderate to severe paediatric diarrhoea in developing countries (Kotloff et al., 2013), but also in 2010, WHO/FAO were requested by the Codex Committee on Food Hygiene (CCFH) to 'review the current status of knowledge on parasites in food and their public health and trade impact in order to provide the CCFH with advice and guidance on the parasite-commodity combinations of particular concern, the issues that need to be addressed by risk managers and the options available to them'. Part of this review process involved experts evaluating the potential for increases in disease rates (Robertson, van der Giessen, Batz, Kojima, & Cahill, 2013; WHO/FAO, 2014), and thus must consider factors such as climate change that may affect the spread and emergence or re-emergence of these infections.

It should be noted that whereas climate may restrict the range of infectious diseases, it is weather, as a short-term manifestation of climate, which affects timing and intensity of outbreaks; this has been recognised for decades by many parasitologists, particularly those concerned with veterinary infections, and temperature and humidity have long been considered as major factors constraining the geographical range of many of these pathogens. Weather events such as El Niño and La Niña are of relatively short duration and have a greater magnitude and impact on the local environment than the more gradual character of other proposed climate changes. A higher frequency of extreme events will result in parasites that are more tolerant of highly diverse conditions, being able to survive, adapt to the new environments, and perhaps thrive. However, how the dynamics of parasite transmission may alter under conditions of climate change is also dependent on host characteristics (Martínez & Merino, 2011).

Thus, although some modelling has been conducted to provide useful data for some foodborne parasites (e.g. *Fasciola hepatica*; Valencia-López, Malone, Carmona, & Velásquez, 2012) precisely how the predicted climate changes (and also weather events such as El Niño and La Niña, floods etc.) will impact on the distribution and burden of the majority of foodborne parasites is uncertain, as it is for all pathogens.

Nevertheless, it is possible to make some general comments based on our current state of knowledge. Although some assumptions may retrospectively be found to be flawed, by examining what the future may hold for us, it is possible that plans can be made to mitigate increased transmission.

In this review we focus on a few selected parasites from each of the major parasite groups: trematodes, cestodes, nematodes, and protozoa, their various and varied paths to our plates, and how these routes in different regions of the world may alter in the face of climate change. It is not possible to cover all foodborne parasites or include all scenarios, but we hope that this selection provides some insights and suggestions of what may occur.

Slowly the world is waking up to smell the coffee, but are we prepared to drink it?

2. Selected foodborne parasites

2.1. Trematodes

Most trematode parasites, also known as flukes, have relatively complicated lifecycles including one or more intermediate hosts, of which the first intermediate host is almost always a mollusc, usually, but not always, an amphibious snail. It is generally well-accepted that in parasite-host systems in which intermediate hosts or free-living stages are intrinsic to the lifecycle, weather conditions have a considerable impact on transmission (Marcogliese, 2008), and therefore climate change is likely to affect trematodes.

For trematode parasites in general, it has been suggested that a small increase in temperature will lead to a marked increase in cercarial emergence from the first intermediate host (snails), with little if any reduction in their transmission efficiency, and that this may also enhance the local impact of trematodes (Poulin, 2006). Under many climate change scenarios this may result in an increase in local burden in endemic areas, as well as increases or shifts in distribution. The number of generations per year may also increase.

A model trematode to consider in terms of potential effects of climate change on spread and transmission is *F. hepatica*. The final stage of the lifecycle of *F. hepatica* can occur in a range of different mammals, including humans, and is also a disease of veterinary concern, causing disease, sometimes severe or even fatal, in sheep and cattle. The zoonotic aspect also maintains the transmission cycle in the absence of human infection. As with other trematodes, the lifecycle of *F. hepatica* depends on amphibious snail intermediate hosts (infected by the miracidium stage, produced from the parasite eggs), from which the cercariae emerge after a stage of asexual multiplication. The resultant metacercariae (encysted cercariae in the environment) are robust, and final hosts, including humans, are infected by ingesting either plants or water contaminated with these metacercariae.

Climate change may affect transmission of *F. hepatica* not only by affecting the parasite directly, but also indirectly, by affecting the success and distribution of the intermediate host. Snails are cold-blooded animals, so their activity and metabolism are dependent on environmental temperature. In Europe the major intermediate host, *Lymnaea truncatula*, has its northern distribution limited by temperature, and is recognised as a rather stenoecious species (Caron, Martens, Lempereur, Saegerman, & Losson, 2014); higher temperatures may enable northward spread of this intermediate host, and hence northward spread of this parasite.

In the trematodes themselves, temperature has a direct and pronounced effect on crucial lifecycle stages, including the production of cercariae in the snail host, which is a key component of the parasite's success (Mas–Coma, Valero, & Bargues, 2009). An increase of only a few degrees in environmental temperatures may result in marked increases in cercarial emergence; within the range of temperatures in which the snails and parasites can live, an increase in temperature is almost invariably coupled with an increase in cercarial output. This

phenomenon results from two processes: higher temperatures not only trigger the emergence of cercariae from snails, but also accelerate the production of cercariae within snails. The net outcome of increasing temperature will thus be a greater number of cercarial infective stages.

Rainfall, as well as temperature, is also known to have a substantial impact on transmission efficacy for *F. hepatica*, and reduced water availability has also been predicted to reduce infection risk in some areas in the UK (Fox et al., 2011). However, studies on veterinary fascioliasis have provided conflicting results – although high temperatures and droughts may result in the free-living parasites and the snail intermediate hosts succumbing to desiccation, dry summers in the UK have also been associated with high levels of infection in livestock. This is presumably due to stock being forced to graze on metacercaria-infested grass as water levels recede (Fox et al., 2011). Similarly, although wet weather is intuitively associated with increased *F. hepatica* transmission, extensive rainfall may wash away the snail and free-living stages, thereby reducing transmission risk (Fox et al., 2011). However, in terms of transmission to humans it is worth noting that some outbreaks of fascioliasis in Cuba have been associated with flooding of lettuce fields (Rojas Rivero, Vazquez, Domenech, & Robertson, 2010); extreme weather events may bring this parasite into contact with produce in the human supply chain, and such events are expected to rise in frequency in the face of climate change.

One aspect that should be considered is that allopatric combinations of *F. hepatica* and *L. truncatula* are more efficient than sympatric ones (Gasnier et al., 2000), demonstrating the capacity of this parasite to adapt to new environments and new hosts. Another important factor is the lack of host-specificity of the *F. hepatica* miracidium stage; although *L. truncatula* is the most important intermediate host in Europe, in other countries other aquatic snails dominate as the intermediate host. Even in Europe other snail genera (e.g. *Radix* species) that are less fastidious with respect to environmental conditions may serve as effective intermediate hosts (Caron et al., 2014). Thus, *F. hepatica*, due to its capability of adapting to different intermediate hosts and environmental situations, has considerable potential for increased distribution during shifting climatic conditions.

F. hepatica has a global distribution, although with specific hotspots of human infection including the Bolivian Altiplano, but other foodborne trematodes of interest currently have more restricted geographical distributions; one of these is *Opisthorchis viverrini*. *O. viverrini* is one of the most important foodborne trematodes in Asia, with an estimated 10 million people infected (Prasopdee et al., 2013). As with other trematodes, *O. viverrini* has a complex lifecycle; however, unlike for *F. hepatica*, the lifecycle of *O. viverrini* includes two intermediate hosts — providing a further stage where climate changes may exacerbate or limit transmission. The eggs shed by the final mammalian hosts (often humans), are washed into freshwater habitats occupied by snails, the first intermediate host, belonging to the genus *Bithnya*. These snails ingest the eggs and become infected. Following asexual replication, the cercariae are released into the water where they actively seek a fish host belonging to the family Cyprinidae. In the second intermediate host, the metacercarial stages develop, localised in the flesh (skin, fins and musculature) of the fish, such that human and carnivore hosts become infected from consumption of the infected fish.

Climate changes in Thailand have been predicted to include decreased precipitation and consequently drought, increased frequency of extreme weather events, increase in mean temperature, rises in sea level resulting in increased salinity in water sources and higher level of salt in the soil, shortage of freshwater, prolonged flooding, a rise in minimum and maximum temperature, a fall in relative humidity and a decrease in freshwater fish population due to reduction of wetlands and changes in migration patterns (Marks, 2011).

Such effects of climate change may be expected to have a negative impact on the distribution of *O. viverrini*. For example, a study investigating the temperature dependence of *O. viverrini* infection in the first intermediate host concluded that when rainfall was adequate, two

generations could be produced each year with peaks occurring during spring rains and after the fall monsoon floods (Prasopdee et al., 2013). Under drought conditions, a population density of 400–500 snails/m^2 decreased to 5–15 snails/m^2. In addition, snail density was affected by both the level of water salinity and also temperature, with optimal infection rates at 34 °C.

The Lower Mekong River in Thailand, Lao PDA, and Cambodia is recognised as a biodiversity hotspot for gastropod molluscs with over 100 endemic species (Petney et al., 2012). A drought in 2010 resulted in the water level falling to its lowest in 50 years. The ability of *Bithynia* snails to disperse is limited and a prolonged drought beginning early in 1981 resulted in a dramatic population crash (Petney et al., 2012). Although equivalent data from the drought in 2010 is lacking, this drought probably had a similar outcome, resulting in a dramatic reduction in the numbers of the intermediate host of *O. viverrini*. Thus, the success of infection in this snail host depends on several factors, particularly water temperature, duration and amount of rainfall, and sea ingress (salinity). With the climate changes predicted by Marks (2011), these extrinsic factors seem, overall, to change in a less favourable direction for this trematode. Although an increase in temperature may increase snail infection rates, this cannot be considered in isolation, and a reduction in precipitation and change in salinity may over-ride the effects of temperature.

However, with two intermediate hosts, transmission of *O. viverrini* is even more likely to be affected by the environment, including climate change, than transmission of *F. hepatica*. According to Marks (2011), climate change in this region will result in reductions in the populations of freshwater fish due to losses of wetlands and effects on migration patterns. The 2010 drought disrupted fish populations, and local fishermen reported fewer and smaller fish, and the disappearance of some species. This information suggests that local diets may be forced to adapt to the new circumstances, and if freshwater fish are consumed less commonly, then transmission to humans will also be reduced.

These two examples of foodborne trematodes indicate that the potential for climate change to affect distribution and transmission is considerable, largely, but not solely, due to the possible effects on their intermediate hosts. It is important to stress that effects and impacts may vary considerably even in a limited geographic area, and thus decisions regarding trematode infections in food control must be based on local conditions and not on generalized assumptions. It should also be emphasised that there are a range of other foodborne trematodes that may be affected by climate change; these include, but are not limited to, other species of *Fasciola* and *Fasciolopsis buski, Clonorchis sinensis, Paragonimus* species, and other fishborne trematodes such as *Heterophyes heterophyes, Haplorchis pumilio, Procerovum* spp. How climate change is likely to affect each of these will depend not only on their molluscan intermediate hosts, but also other factors concerned with the parasite and host biology and ecology.

2.2. Cestodes

There are several parasitic cestodes, commonly known as tapeworms, which may be transmitted to humans via food. As with trematodes, cestode lifecycles are complicated by being indirect (inclusion of one or more intermediate hosts in the cycle), but are perhaps more simple than that of trematodes as in many species there is no asexual replication; in these species, —reproduction is only sexual.

For some tapeworms, humans are, or can be, the definitive hosts (e.g. *Taenia saginata, Taenia solium, Diphyllobothrium* spp.), with the adult tapeworm residing in the human digestive tract. However, for other tapeworms, humans may act as aberrant intermediate hosts (e.g. *T. solium, Echinococcus* spp.), resulting in infection with much more severe pathology, although onward transmission will probably not occur (the human host is unlikely to be eaten). In this section we discuss how climate may affect two different cestodes, one for which humans may act as an aberrant intermediate host, *Echinococcus multilocularis*, and one for which humans may be the final host,

Diphyllobothrium spp. Despite choosing these two parasites to illustrate this them, it should nevertheless, be noted that other helminths are also of importance and their transmission may be affected by climate change. Although *Echinococcus granulosus* is a parasite of particular concern (the majority of human cases of echinococcosis are caused by this parasite), we have selected *E. multilocularis* as the major focus due to the importance of climate change on survival and spread of the rodent intermediate hosts (Atkinson et al., 2013). Furthermore, although *E. granulosus* infections are more common than those of *E. multilocularis*, the disability-adjusted life-years (DALYs) due to the latter infection have been estimated to be higher (666,000 DALYs) for *E. multilocularis*, (Torgerson, Keller, Magnotta, & Ragland, 2010) compared with around 290,000 DALYs for *E. granulosus* (Budke, Deplazes, & Torgerson, 2006)).

Canids, particularly foxes, are the definitive hosts of *E. multilocularis* and eggs from this parasite are excreted in the faeces of the definitive host. The intermediate hosts are usually rodents, and hydatid cysts form in the rodent organs, particularly the liver. However, if humans ingest the tapeworm eggs, either directly hand-to-mouth or as contaminants of food or water, then the development of the parasite is similar to that in the usual intermediate host. This parasite is particularly associated with northern or temperate regions and climate change scenarios that suggest an increase in humidity in more northern regions may favour the survival of *E. multilocularis* eggs as more humid conditions favour survival (Mas-Coma, Valero, & Bargues, 2008). A study in Slovakia found a significant correlation between prevalence of the tapeworm in red foxes and mean annual precipitation. The highest prevalence was found in the north, where the terrain is mainly mountainous with mixed and coniferous forests, pastures and a high proportion of natural vegetation. The same correlation was also found in France (Miterpáková, Dubinsky, Reiterová, & Stanko, 2006). In Arctic Alaska, the growing season has been observed to be increasing, presumably due to recent warming, and has been accompanied by a widespread advance of trees into tundra ecosystems (Hinzman et al., 2005). Although not all Arctic regions are warming, and not all regions that are warming are doing so at a constant rate (Hinzman et al., 2005), the tendency of tundra regions becoming coniferous forests and pastures means that more areas are starting to resemble the environment of Northern Slovakia. Changing environments in terms of vegetation, have a "knock on" effect on wild fauna, and under the conditions described fox and vole populations may also increase. In individual seasons, a tight relationship between prevalence of *E. multilocularis* in red foxes and the relative density of small mammals has been demonstrated (Miterpáková et al., 2006). Furthermore, the opportunistic feeding behaviour of foxes may result in them consuming almost exclusively grassland rodent species when they are in abundance and this has been considered to result in higher adult worm burdens and thus more eggs dispersed in the environment (Raoul, Deplazes, Rieffel, Lambert, & Giraudoux, 2010). Should this occur near to human settlements or in areas where people collect berries or other produce, microfoci of transmission to humans may result (Atkinson et al., 2013). Taken together these factors may increase the prevalence of *E. multilocularis*, and also elevate the exposure risks for the human population, with infection rates also having the potential to increase, particularly to those populations whose diet regularly includes berries and other wild vegetation.

The intermediate hosts of the related parasite, *E. granulosus*, may also be impacted by climate change. Barrenground and woodland caribou populations in Canada are declining as a result of "knock-on" effects of climate and landscape change (Jenkins, Schurer, & Gesy, 2011). Increased winter precipitation and frequency of extreme weather events in the future will likely contribute to further declines in caribou populations (Miller & Gunn, 2003; Vors & Boyce, 2009). As parasite prevalence is likely linked to the density of intermediate hosts, as with *E. multilocularis*, decreased abundance and even local extirpation of caribou populations might reduce parasite transmission in Arctic regions. However, several cervid species in Canada are competent intermediate hosts for *E. granulosus*; wapiti and moose moving further north in response to climate changes could fill the current role of caribou in the lifecycle of *E. granulosus* at Arctic latitudes. Warming temperatures might push the current southern distribution limit of the cervid strain further north, and increased precipitation in the north would favour survival of eggs of *E. granulosus* in currently moisture-limited environments (Jenkins, Schurer & Gesy, 2011) . However, excessively wet conditions might reduce the availability of eggs for ingestion by grazing intermediate hosts (Schwabe, 1984).

Despite these data suggesting that climate change may affect transmission of *E. multilocularis* and *E. granulosus*, data in humans is scanty, and, because a long time period usually elapses between infection and diagnosis (a period of years), identification of transmission vehicle is usually impossible. Risk assessment studies often give contrasting results, and some suggest that food is infrequently a vehicle of infection (Kern et al., 2004; Stehr-Green, Stehr-Green, Schantz, Wilson, & Lanier, 1988). Nevertheless, the clinical severity of alveolar echinococcosis resulted in it being considered important in the FAO/WHO risk ranking exercise (Robertson et al., 2013; WHO/FAO, 2014).

Tapeworms for which humans are the definitive host are considered to be of relatively minor clinical relevance, causing generally mild pathology. For this reason, cestodes in the *Diphyllobothrium* genus were not ranked highly in the FAO/WHO risk-ranking exercise (Robertson et al., 2013; WHO/FAO, 2014). However, this genus, which contains a vast number of species, many of which are infective to humans, can cause, as well as mild symptoms (diarrhoea, abdominal pain, etc.), severe vitamin B-12 deficiency in a small number of cases. This anaemia may result in subtle demyelinative neurological symptoms; although infection must persist for many years in order to reach the state that neurological symptoms appear, lack of other symptoms prompting investigation and diagnosis means that this manifestation is not impossible.

As well as two intermediate hosts occurring in the *Diphyllobothrium* lifecycle (freshwater crustaceans and freshwater fish), and also paratenic hosts (freshwater fish), there is also a wide range of final hosts, including humans, meaning that there is a significant zoonotic reservoir (Chai, Murrell, & Lymbery, 2005), and thus climate change may impact at several points in the lifecycle. Although the distribution of *Diphyllobothrium* spp. is worldwide, prevalence knowledge is generally fragmented due to the lack of reportability of infection and usually mild clinical symptoms, and this makes assessment of prevalence changes difficult. However, an association between an increase in *Diphyllobothrium pacificum* infection in Chile and the cyclic appearance of El Niño phenomenon in the eastern Pacific has been described (Sagua, Neira, Araya, & González, 2001). This was considered to be due to the event effect on fish populations, migration of sylvatic animals, particularly sealions, as well as environmental contamination. Also, a survey of *Diphyllobothrium latum* in lakes concluded that transmission was optimal during the warm season; thus climate change could favour the *D. latum* lifecycle by warming freshwater systems, thus increasing both the number of infected fish, and the chance of ingesting one (Wicht, Limoni, Peduzzi, & Petrini, 2009). Although the mild pathology associated with *Diphyllobothrium* gives it a less threatening aspect, it also means that a slow increase in prevalence may not be perceived, and under specific conditions it may modify from being a largely sylvatic parasite into being a domesticated annoyance, silently increasing its prevalence until severe cases occur.

Again, other foodborne cestodes may be affected by climate change, and the examples given here should be considered only as illustrative. In particular, *Taenia* infections (*T. solium*, *T. saginata* and *T. asiatica*) may be of particular relevance, especially the effects of climate on the survival of *T. solium* eggs (the cause of neurocysticercosis) in the environment.

2.3. Nematodes

A wide range of nematodes, commonly known as roundworms, are parasites of humans; some are transmitted by vectors (e.g. filarial parasites), but there are also several parasites that may be transmitted by contaminated foodstuffs, although other routes may also be important. In addition, for other nematodes, such as those in the *Trichinella* genus and Anisakids, foodborne transmission is almost the only transmission route (congenital and mammary transmission also may occur for *Trichinella* spp. (Matenga et al., 2006)). *Trichinella* are very special parasites, being the smallest human nematode but the largest intracellular parasite (the transmission stage being a nurse cell-larva complex most commonly located in the striated muscle), and also the parasite for which there is no external transmission stage in the lifecycle. The adults live in the small intestine where larvae are produced that migrate to skeletal muscle and sometimes other tissues. Transmission occurs when these larvae are ingested by the next host; thus only animals that eat meat are infected. For human infection, transmission occurs by consumption of undercooked meat, either domestically produced (usually pork) or game, containing larvae. The most important transmission cycle is domestic, and involves pigs. However, the sylvatic cycle, in which game may be consumed by humans, may be important in some areas of the world. In the far north, infection transmission is particularly associated with consumption of bear, walrus and seal; in some indigenous peoples these animals are the major source of meat (Polley, Hoberg, & Kutz, 2010).

As none of the lifecycle stages of *Trichinella* are usually exposed to the environment (except, perhaps, in carrion), climate change effects on transmission are likely to result primarily from shifts in host faunal structure and trophic linkages, shifts in contacts between wildlife and domestic animals, and, perhaps, through behavioural shifts in the utilization of infected hosts as food (Polley et al., 2010). For example, the decrease in sea-ice in recent years is indicative that climatic warming may have a devastating effect on pelagophilic animals. In response, walruses have become more pelagic, changing their feeding habits and preying more often on ringed seals. This change in diet from molluscs, benthic invertebrates and other soft-bodied animals, to greater consumption of mammals or their remains may result in a higher prevalence of trichinellosis in walrus, and thus increased risk of exposure to people who frequently include walrus in their diet (Rausch, George, & Brower, 2007).

Another tissue-borne nematode infection, anisakiasis, is mostly associated with the genera *Anisakis* and *Pseudoterranova*. In the normal lifecycle, marine mammals or piscivorous birds are definitive hosts, with aquatic invertebrates and fish as intermediate or paratenic hosts. Thus humans are aberrant hosts, infected from consuming raw or undercooked fish (Klimpel & Palm, 2011).

It may be generalized that *Anisakis* and *Pseudoterranova* have a pelagic and benthic lifecycle, respectively (Klimpel & Palm, 2011). *Anisakis* spp. mainly infect toothed whales and a range of pelagic schooling fish worldwide, in contrast to the sealworms of the genus *Pseudoterranova*. The differences in species appear to be related more to geographic distribution and feeding habits of hosts than to behavioural or physiological host preferences of the parasites (Chai et al., 2005; Klimpel, Palm, Rückert, & Piatkowski, 2004), and transmission pathways are habitat-dependent and usually involve a broad spectrum of invertebrates and intermediate or paratenic fish hosts. The complexity of these chains means that environmental factors may play deciding roles in transmission, distribution, and prevalence.

In marine ecosystems, phytoplankton abundance is strongly related to temperature, and large-scale shifts in distribution in response to temperature have been observed (Gibson, Atkinson, & Gordon, 2006). Being at the base of many marine foodwebs, changes in phytoplankton biomass affect all subsequent stages, first impacting on zooplankton abundance and thereafter migratory fish, squid, and other predators further up the foodchain, such as pinnipeds and cetaceans (Gibson et al., 2006). Marine species tend to forage in areas of nutrient-rich oceanic upwellings, and these may change in strength, shift location or become less predictable in the face of climate change (Gibson et al., 2006). Any of these factors may affect the transmission of parasites within the food-web, and hence the probability of Anisakids occurring in fish commonly consumed by humans.

Furthermore, many marine mammals undertake seasonal migrations, defined here as the seasonal movement between two geographic locations that is related to the reproductive cycle, changes in temperature and prey availability (Gibson et al., 2006). With increases in temperatures in some areas of the ocean, migrating marine mammals may have to explore new areas and undertake longer migrations as the polar caps retreat, bringing with them their burden of Anisakid nematodes; in contrast, the migration of other marine mammals may become more restricted or cease entirely. For example, the pygmy sperm whale (family Kogiidae) is expected to increase its migration range (Gibson et al., 2006), and this family is also one of the natural final hosts for *Anisakis physeteridae*. On the other hand, Atlantic white-sided dolphins (*Lagenorhynchus acutus*) are expected to decrease their range of migration (Gibson et al., 2006), thereby also reducing the spread of *Anisakis simplex*.

With their potential to act as indicators of environmental change and host migration, fish parasites may even be useful as bioindicators of climate change (Klimpel & Palm, 2011). Warming of coastal waters may result in a higher number of pelagic fish species following the warmer currents northwards, and resulting in the prevalence and intensity of *Anisakis* spp. infection rising (Klimpel & Palm, 2011). This may again result in greater exposure of the human population.

There is some evidence that the prevalence of *Anisakis physeteris* increased during the El Niño phenomenon in 1997–1998 (Cabrera, Del Pilar, & Altamirano, 2004). Because of the increased temperature, an increased migration towards the coastal areas of a fish species that harbours this parasite (*Coryphaena hippurus*) was registered.

Several nematodes are described as soil-transmitted helminths (STH), including *Ascaris lumbricoides*, *Trichuris trichiura*, and hookworm. Of these, both *Ascaris* and *Trichuris* can also be transmitted by contamination of fruit and vegetable produce consumed raw; although hookworm is an important parasite, its most usual mode of transmission is probably not ingestion, but penetration of the skin. These nematodes are very common in tropical or semi-tropical countries and are good indicators of poor basic infrastructure, such as effective sewage disposal. Although having very different lifecycles, transmission of both *Ascaris* and *Trichuris* is dependent on ingestion of the robust eggs that are not immediately infective but embryonate in the environment. Embryonation is a temperature dependent function, and in areas where temperatures are rising lifecycle speed may increase; indeed, accelerated transmission of *Ascaris* due to increases in global temperatures and ecosystem changes has been suggested (Kim et al., 2012). Additionally, as described earlier for *F. hepatica*, extreme events are more likely to result in contamination of produce in the human supply chain; arid conditions have been demonstrated to limit the transmission of STH (Pullan & Brooker, 2012). Due to their widespread occurrence, their potential clinical impact on infected individuals, particularly children, and the difficulty in eradicating these persistent parasites from endemic areas, these nematodes are of particular importance. However, whether food is the most usual route of transmission is less certain; general persistence in the environment and overall contamination are of particular relevance.

2.4. Protozoans

Protozoans may be considered among the simplest of parasites, being unicellular organisms. However, the lifecycles of many are complicated. Many important protozoa are vector-transmitted (for example, *Plasmodium* spp., causing malaria), but several may also be foodborne

and/or waterborne. *Giardia duodenalis*, *Cryptosporidium* spp. and *Toxoplasma gondii* occur worldwide and are among the most frequently reported parasites of humans and animals. All are widely dispersed and have been associated with outbreaks of infection resulting from drinking contaminated surface water (Fayer, Dubey, & Lindsay, 2004). Although *Cryptosporidium* and *Toxoplasma* are more closely related, both being in the phylum Apicomplexa, it is more usual to consider *Cryptosporidium* and *Giardia* together, as their transmission routes are more similar, and both have been particularly troublesome to the water supply industry. As with most parasites for which waterborne transmission is important, the extensive use of water in the food industry, particularly in the fresh produce chain, means that such waterborne parasites might also transfer to food as vehicles of infection.

Giardia cysts and *Cryptosporidium* oocysts are transmitted by the faecal–oral route from humans and animals. An infected person or animal may shed enormous numbers of (oo)cysts, and relatively few are required to initiate an infection (Fayer et al., 2004). The (oo)cysts are very resistant to environmental and water treatment stresses, a trait only beneficial for their dissemination, and some types have the potential to be transmitted from human to non-human host and vice versa, enhancing the reservoir of infection (Dorny, Praet, Deckers, & Gabriel, 2009).

There seems to be a generally positive association between increases in temperature and rainfall and transmission of both these parasites. For example, a correlation between environmental temperatures and cryptosporidiosis in tropical and temperate regions has been reported (Lal, Baker, Hales, & French, 2013), and also between heavy rainfall and the likelihood of detecting *Giardia* and *Cryptosporidium* in surface and river water (Hunter, 2003; Sterk, Schijven, de Nijs, & de Roda Husman, 2013). Heavy rainfall and subsequent runoff can affect the risk of waterborne disease outbreaks, and it is therefore plausible to assume that increased precipitation will favour pathogen transport (Sterk et al., 2013). Heavy rainfall may lead to changes in the direction of flow of water systems and flow occurring through channels that would not normally occur (Hunter, 2003). The severity of the Milwaukee outbreak has been attributed to the heavy spring rainfall and runoff from melting snow. Similarly, in the Delaware River, an association was found between the amount of rainfall and the number of *Cryptosporidium* oocysts (Patz, Graczyk, Geller, & Vittor, 2000). In the areas where precipitation is expected to rise, waterborne protozoal diseases may also.

Precipitation is projected to increase by approximately 20% in the winter months in the Arctic (Davidson et al., 2011), and in conjunction with milder climatic conditions, this climate change may increase the risk of extreme weather related events such as heavy rain, snowfall, melting permafrost and flooding, which could result in widespread contamination of traditional water sources and damage to community sanitation infrastructures (Parkinson & Butler, 2005). Milder climatic conditions might also facilitate survival of (oo)cysts in the environment.

However, other changes induced by climate change may cancel out such effects. For example, changes in the timing of manure application to soil and subsequent rain events could decrease pathogen input by increasing the period of die-off on land surfaces (Sterk et al., 2013). Summer droughts lowering river discharges could decrease infection risks due to decreased dilution and inactivation of pathogens by increased temperature and residence time (Sterk et al., 2013), at the same time leading to greater effluent concentration of the waterborne pathogens in surface and groundwater sources, and increased runoff from unsaturated land. Subsequent periods of intense rainfall can result in the flushing out of this high pathogen load, resulting in increased disease occurrence (Lal et al., 2013). Droughts also lead to poor hygiene due to scarcity of washing water, and poor hygiene of water generally (Marcogliese, 2008), exacerbating the increased risk of infection. When water supplies are scarce, wastewater is more frequently used as irrigation water thereby increasing contact between pathogens, including parasite transmission stages, in sewage and food crops.

Higher temperatures and reduced snow cover could lead to expansion of the northerly range of different wild and domestic animals. For example, beavers in Alaska are migrating north into areas that have become more habitable by expanding vegetation. As beavers are hosts for *G. duodenalis*, they are possibly making this a novel threat by contaminating pristine drinking water sources and exposing native inhabitants to potentially infective cysts (Parkinson & Butler, 2005).

T. gondii has a more complex lifecycle than either *Cryptosporidium* or *Giardia*. Oocysts from this protozoan, which are excreted from the definitive feline host, and are infective to a wide range of warm-blooded animals, including humans, are likely to be affected by climate change similarly to *Cryptosporidium* and *Giardia*. However, this parasite can also be transmitted by ingestion of cysts in the tissue of infected animals, and this is considered the most common route of human infection in many areas of the world including Europe. Infection of cats is generally through consumption of infected prey animals. Thus there is a complex interaction between these two infection routes and the prevalence of infection in different hosts (including meat animals) and the occurrence and spread of oocysts in the environment. Dissection of how climate change may impact on this interaction between hosts and transmission routes is complicated and probably only generalized statements can be made at present. Nevertheless, it does appear clear that climatic events impact on prevalence and transmission in both intermediate and definitive hosts, and thus on the likelihood of human exposure, either via tissue cysts in meat or oocysts in water or fresh produce. For example, a 10-year study in an urban population of domestic cats in France, demonstrated that prevalence of antibodies against *T. gondii* was related to the interaction between temperature and rain (Afonso, Thulliez, & Gilot-Fromont, 2006) and that cool, damp winters resulted in feline seroprevalence increasing (Afonso et al., 2013). In the USA, the lowest antibody prevalences in cats were encountered in the most arid regions of the country (Vollaire, Radecki, & Lappin 2005). Melting of the tundra makes new habitats arise for the feline definitive host, as well as warm-blooded intermediate hosts. Cats are found almost everywhere on the planet except in the frozen Arctic (Dubey, 2010), but under warmer conditions wild and domesticated felines may place their markings on new areas (Meerburg & Kijlstra, 2009). The seas are also opening up for *T. gondii*, as they are found in numerous migrating marine mammals (Dubey et al., 2003); how they become infected is unclear but at least somewhere in the chain, oocysts from infected felids are probably washed into the sea. A conceptual framework has been developed that suggests melting snowpacks in Canada could result in contamination of the marine environment with *Toxoplasma* oocysts (Simon, Poulin, Rousseau, & Ogden, 2013).

Other foodborne protozoans whose transmission may be affected by climate change include *Cyclospora cayetensis*, *Entamoeba histolytica*, and *Trypanosoma cruzi*. While the first two may be considered as being somewhat similar to *Cryptosporidium* and *Giardia* in the faecal–oral transmission route and the survival of their transmission stages (oocysts and cysts) on food, *T. cruzi* has a more complicated lifecycle in which reduviid bugs have an important role as vectors; how climate change may impact on the spread of these vectors is a further important aspect for consideration.

3. Conclusion

Climate change is a complicated story, and how the different projected changes may interact and impact upon a diversity of foodborne pathogens is almost impossible to predict. Effects of different weather patterns on some parasites may give some clues, but cannot provide the whole picture. It is worth remembering that the success of many parasites is due to a number of factors. These include: the robustness of the transmission stages, their enormous proliferation rate, and their adaptability to different hosts and environments. Thus while other pathogens may suffer under some conditions of climate change,

being unable to locate the "right" host, or incapable of surviving inhospitable conditions, many parasites are likely to persist and adapt. The snap-shot overview provided here, taking just a couple of parasites from each major parasite group as illustrative examples, is intended to show how initial short-term alterations in the weather, as well as predicted long-term changes, may affect parasite transmission and impact. However, it should also be remembered that climate change is not happening in a vacuum; other factors not necessarily related to climate change may also affect the transmission and impact of foodborne parasites. These include development of improved diagnostic tests and new treatments of humans and animals that reduce infection pressure, introduction of interventions and procedures that prevent the contamination of food or inactivate or remove parasites in different types of food, demographic changes and social changes, such as urbanisation or food management practices, and even globalisation that has already been discussed regarding its effect on foodborne parasites (Robertson, Sprong, Ortega, van der Giessen, & Fayer, 2014), and encompasses a range of factors and events. The overall picture is complicated and there are no simple models or descriptions, even for an individual parasite. While beginning to consider how climate change may impact on different foodborne parasites provides no easy answers, we think the first essential step is trying to understand the possible outcomes, assess current and future risks, and thereby identify potential courses of mitigation as necessary.

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