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Climate Warming's Alteration of Host-Parasite Dynamics

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Cover Page Footnote

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Climate Warming's Alteration of Host-Parasite Dynamics

Abstract:

Parasites and pathogens have significant roles in host population control, and thus host-parasite interactions affect biodiversity. The important question reviewed in this paper is how changes in temperature due to climate change affect host-parasite interactions. There is mounting evidence that elevated temperatures have both beneficial and detrimental effects on parasites and independently on hosts. These independent changes result in altered host-parasite dynamics through various mechanisms. If elevated temperatures enhance parasite survival, risk of disease transmission among hosts is enhanced as well. This enhancement is dependent on temperature-induced shifts in the host lifecycle, as asynchrony in host and parasite development can result in decreased infection rate and disrupted disease transmission regardless of the increase in parasite survival and density. Host species differ in their responses to temperature elevation. Increased temperature can alter their susceptibility to parasites through changes in their immune functions. Climate shifts also result in host range shifts. As host ranges expand, they may encounter novel pathogens, increasing the risk of spillovers and resulting in a greater mortality rate. From the point of view of native species, newly arriving host species present the potential danger of introducing novel parasites and diseases, which can be detrimental to native species. For seasonally migratory species whose parasites typically decrease during their absence, any climate-induced increase in their parasites' survival prior to their return may decrease the effectiveness of migration, shift their lifestyle to become more sedentary and thus reshape host-parasite dynamic. Altered balance of host-parasite interactions produces changes at higher ecological levels, and the efforts to conserve parasites should thus have the same priority as the need to conserve host species.

Key words: Climate change, parasite range, host range, host-parasite interactions, invasive species, temperature elevation

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Introduction

Climate change remains one of the biggest threats to our ecosystems. Past predictions of climate change, including extended drought, increasing flood, increasing acidity of ocean water, intense heat waves, extreme shifts in temperatures, etc., can be seen occurring across the world today (Hoegh-Guldberg et al., 2007; Whetton, Fowler, Haylock, & Pittock, 1993). Scientists predict that the average surface temperature of the earth is likely to increase by approximately 0.3˚C to 4.8˚C by 2100 (Stocker et al., 2013). Seasons are expected to change with respect to timing and intensity, yet not all seasons will be impacted in the same way. For example, relative to summers, winters in northern regions show double the rate of warming (Ibelings et al., 2011).

Arctic regions are set to become more humid as temperatures rise (Thomas et al., 2018). By 2007, permafrost layer temperature in the Arctic region was observed to have increased up to 3˚C (Gregory et al., 2007). Thawing permafrost has been projected to alter vegetation through changes in soil (Van Hemert et al., 2015), and the shrinkage of ice is likely to influence freshwater organisms as it facilitates elevation of water temperatures (Ibelings et al., 2011). Acidic ocean water brings potential complications to marine ecosystems (Constable et al., 2014). These environmental changes may strongly impact our current biodiversity.

It is also important to recognize that not all species respond to the changes in the environment equally, and this is especially true of hosts and their parasites. As the crucial role parasites play in biodiversity is discovered, understanding how they are impacted by climate change, directly or indirectly, is even more critical to protect ecosystems and species' diversity. Host-parasite interactions change to varying degrees as a result of the effects of environmental and climatic stressors. For instance, nematodes *Trichostrongylus retortaeformis* and *Graphidium strigosum* share identical free-living stages, transmission methods, and face similar environmental stressors, yet under elevated temperature, *T. retortaeformis* exhibited higher egg hatching rate than *G. strigosum.* Variation in success that is seen in these two species may be due to the differences in their interactions with their European rabbit hosts, *Oryctolagus cuniculus* (Hernandez, Poole, & Cattadori, 2013), but more studies are required to form a more definitive conclusion. Though many studies have focused on the ramifications of climate change for various species, the underlying mechanisms at play are not well understood (Van Hemert et al., 2015). For future studies, it is not sufficient to simply observe the consequences of changed stressors on various species; understanding the mechanisms behind these changes can be helpful in predicting how further environmental damages will influence selective pressures on species residing in different regions.

The objective of this paper is to review the effects of rising temperatures on hosts, parasites, and their interactions. In the subsequent sections, this paper will highlight our current understanding of threats and benefits of rising temperatures on:

(1) parasite survival and development,

(2) host resistance and tolerance to the changing environment, and

(3) interaction between hosts and parasites.

The final section highlights important directions to pursue.

Climate warming and parasites

Parasite survival and development in external environments

As the average global temperature continues to elevate, parasites with free-living stages will experience changes in their life cycles and survival rates. Infective free-living stages of parasites are reliant on environmental conditions including temperature and humidity (Dobson, Kutz, Pascual, & Winfree, 2003). Studies have reported that higher temperatures enhance rates of egg hatching and larval development in some species of helminths (Hernandez et al., 2013; Macnab & Barber, 2012; Shields & Tidd, 1968). Reduction in time necessary for development and growth in turn may reduce time spent in external environment, decreasing risk of predation, and increasing the number of life cycles that can be completed per season (Barber, Berkhout, & Ismail, 2016; Marcogliese, 2008). However, rising temperatures may not always be beneficial for parasite development, and the benefits of shortened time of development for parasite eggs are negated when the numbers of eggs developing into free-living larvae are significantly reduced (Van Dijk & Morgan, 2008). For instance, higher temperature promoted earlier hatching of *Lacistorhynchus tenuis*, but decreased coracidia survival (Sakanari & Moser, 1985).

Previous work has shown that temperature elevation does not always affect all stages of parasite life cycle equally. Temperature plays a critical role in the rates of egg hatching and transformation of larvae for anchor worms (*Lernaea cyprinacea*), but not during the remainder of their life cycle (Shields & Tidd, 1968). Indeed, faster development does not always guarantee survival or quality of parasites in their adult forms. Carryover costs from shortened development time may interfere with functions such as reproduction of adult parasites and parasitoids (Colinet, Boivin, & Hance, 2007; O'connor, Norris, Crossin, & Cooke, 2014). For parasitoid *Aphidius colemani*, faster development due to reduced development and growth period resulted in smaller adult body size and higher rate of mortality (Colinet et al., 2007). As insect body size is positively correlated with fat storage, smaller body size has implications for decreasing fecundity as energy is directed away to sustain other life functions, e.g., energy spent on flights (Ellers, Van Alphen, & Sevenster, 1998). Conversely, faster development strengthens opportunities for access to food, mates, etc. for adult parasitoids (Pandey & Singh, 1999).

In addition to pathogenic parasites with free-living stages, climate warming may also impact mutualistic symbionts. For southern green stink bugs *Nezara viridula*, mutualistic gut bacteria are exposed to the external environment when the mother smears her gut secretion over her eggs, so the larvae can consume the bacteria (Birceanu, 2017). Experimental work has shown that a 2.5˚C increase in temperature is positively correlated with bacteria mortality (Birceanu, 2017; Kikuchi et al., 2016). On the other hand, climate warming can indirectly benefit microorganisms that are found in oceans in lower latitudes by decreasing sea ice cover, hence providing more nutrients to support the growth of these bacteria (Kirchman, Morán, & Ducklow, 2009). Although not well documented, ectosymbionts of birds such as mites have been reported to face decreases in density under elevated temperatures (Meléndez et al., 2014). Gaps in our understanding of the changes in symbiotic relationships under climate change pose challenges for predictive work in the future.

Higher winter temperatures have the potential to preserve parasite eggs, thus increasing abundance when spring comes. Because the processes of egg hatching and development are very often dependent on temperature, they can be interrupted if conditions are not to the point of elimination and resume when temperatures are favorable. For different species, different optimal ranges of temperature are necessary for success in egg hatching and survival. When hatching eggs of nematodes *Nematodirus battus* were placed at temperatures outside of the optimal range (i.e., 11˚C to 15˚C), hatching stalled until they were placed back within the optimal range and hatching resumed (Van Dijk & Morgan, 2008). With more eggs able to survive overwinter, more parasites are ready for the initiation of infections when season changes and temperature rises (Ford & Smolowitz, 2007). Vulnerability of parasites' free-living forms that are exposed to warmer environments vary from species to species. Lack of work on the mechanistic processes poses difficulty in our ability to fully understand and forecast how dynamics within our ecosystems will shift.

Parasitic manipulation

Determining whether an infected host's altered thermal preference is a result of a generalized host response to infection or parasitic manipulations can be extremely challenging. In a study with snail hosts, *Zeacumantus subcarinatus*, and two trematode species, *Maritrema* and *Philophthalmus*, researchers found that those infected with *Maritrema* preferred higher temperatures in comparison to control individuals and those infected with *Philophthalmus*. Since the same host species displayed different thermal preferences upon two different infections, it is unlikely that increased thermal preference is a result of a generalized host response to infections

(Bates, Leiterer, Wiedeback, & Poulin, 2011). For some species of parasites, alteration of hosts' thermal preferences may enhance their development and transmission, potentially increasing the number of completions of life cycles per season. Three-spined stickleback fish *Gasterosteus aculeatus*, when infected with bird tapeworm *Schistocephalus solidus*, demonstrated preference for warmer water relative to their healthy conspecifics. This change in thermal preferences aids *S. solidus* in their development and increases the rate of transmission to their definitive hosts (Macnab & Barber, 2012).

Higher temperatures have been suggested to increase the intensity of parasitic manipulations of host behaviors. Acanthocephalan parasites *Pomphorhynchus tereticollis* exhibited greater efficiency in manipulations of certain behaviors in their gammarid hosts at higher temperatures (Labaude, Cézilly, & Rigaud, 2017). However, this proposed trend has not been widely documented, and more studies are required in order to form a more conclusive argument.

On the contrary, not all parasites will employ manipulations of host thermal preferences, considering these parasitic manipulations are costly to parasites. Studies have shown that altered host thermal preferences may be a byproduct of the infection that happens to benefit parasites (Campbell, Kessler, Mayack, & Naug, 2010). Further experimental work would be beneficial in determining the cause of changes in host behavior.

Parasite dispersal: invasive parasites?

Historically, cooler and shorter summers in the Arctic inhibited the development of many parasites (Dobson et al., 2003). With the Arctic warming at double the rate of the global average, biodiversity should experience shifts when species are able to expand their ranges northward. Yet, the introduction of parasites to a new environment does not automatically ensure successful establishment. In 2001, lungworms *Umingmakstrongylus pallikuukensis* and *Varestrongylus* *eleguneniensis sp.* were found for the first time to have established successfully on Victoria Island. Originally prevalent in the Canada mainland, data suggested that the dispersal of muskox to Victoria Island, while infrequent, had occurred historically, but *V. eleguneniensis sp.* were previously unable to successfully establish in the new environment due to unfavorable climatic conditions (Kutz et al., 2013). *Toxoplasma gondii* have been observed to be more prevalent in northern regions of Europe, largely due to warmer and more moist winters that allow for prolonged survival of oocysts (Meerburg & Kijlstra, 2009). Eastern oyster parasites, *Perkinsus marinus*, have increased their prevalence in northern waters, especially during winter (Cook, Folli, Klinck, Ford, & Miller, 1998).

In addition to creating more favorable conditions for establishment, climate warming facilitates increased abundance of invasive species, leading to more outbreaks. For instance, even slight increases in temperature can result in greater proliferation of cercarial and have little negative effects on transmission competence of these trematode parasites (Poulin, 2006). Under temperature elevation, *U. pallikuukensis* are able to shorten their life cycles from two-year cycles to one-year cycles, overcoming high overwinter rates of mortality and thus increasing their chances of causing disease outbreak (Kutz, Hoberg, Polley, & Jenkins, 2005). The effects of warming on parasite expansion and establishment and their influences on virulence are beyond the scope of this paper but are recognized to be critical in many aspects of biological conservation.

Climate warming and hosts

Host exposure

At higher temperatures, host life cycles and susceptibility to parasites can be modified to varying degrees. For some species of endothermic hosts, even slight increases in temperature can have detrimental consequences (Tewksbury, Huey, & Deutsch, 2008), while other species can withstand a wider range of temperature variations (Grant, 1982). Under temperatures above the TNZ (i.e., thermoneutral zone), endotherms have been reported to utilize a wide array of thermal responses (Boyles, Seebacher, Smit, & McKechnie, 2011; Grant, 1982). Within endothermic animals, homeotherms should function at high levels under specific and shorter ranges of temperatures, while heterotherms function at lower levels across a wider range of temperatures (Boyles et al., 2011). Generally speaking, with increasing temperatures, endotherms decrease many aspects of their metabolism, e.g., food consumption and oxygen uptake, which benefits several elements of their immune systems (Morley & Lewis, 2014). Adaptive responses and phenotypic plasticity help weaken the impact of climate warming on endotherms to a certain extent (Boyles et al., 2011). Past works have shown that elevated air temperatures strengthen the resistance of several host species to viruses, while increasing susceptibility of others to parasites (Kelley, 1980).

On the other hand, ectotherms, which are reliant on environmental temperatures, should be severely impacted by climate warming. With higher temperatures, ectothermic animals will invest more energy in lowering their body temperatures (Fuller et al., 2010). It has been suggested that ectotherms are better at adapting to colder environments but find challenges in acclimating to warmer temperatures (Hoffmann, Chown, & Clusella-Trullas, 2013; Klok & Chown, 2003). Conversely, past works have also shown that some species of ectotherms are able to evolve thermal tolerance for higher temperatures quickly (Logan, Cox, & Calsbeek, 2014; Skelly et al., 2007). Not only do ambient temperatures influence their body heat, immune functions of various species are also temperature-dependent (Ellis, 2001). In three-spined stickleback fish *Gasterosteus aculeatus*, higher temperatures increased mortality as well as immune activity. Sticklebacks residing in warmer waters were less susceptible to heat waves than individuals in cooler waters, but still exhibited increased immune activity, although less pronounced (Dittmar, Janssen, Kuske, Kurtz, & Scharsack, 2014). Interestingly, increased immune activity did not return to baseline level for a period of time after recovery from exposure to higher temperatures. Rainbow trouts *Oncorhynchus mykiss* have shown enhanced complement system under elevated temperatures (Nikoskelainen, Bylund, & Lilius, 2004). Contrarily, lysozyme activity in freshwater carp *Leuciscus cephalus* correlated negatively with temperature, while gonad mass correlated positively with temperature (Poisot, Šimková, Hyršl, & Morand, 2009). This suggests that the need for investment in reproduction is greater than the need for immunocompetence.

Some ectotherms have been shown to utilize behavioral fever as a strategy to manage infections (Adamo, 1998; Burns, Ramos, & Muchlinski, 1996; Kluger, 1977; Landis, Sundin, Rosenqvist, & Roth, 2012; Watson, Mullens, & Petersen, 1993). It is likely that this adaptive response is pathogen and dose dependent, perhaps even influenced by previous exposure to certain pathogens (Burns et al., 1996). Not all ectotherms exhibit behavioral fever upon infections, and those that utilize this strategy only use it for pathogens that are heat sensitive. Higher body temperature can impose costs on hosts as high temperatures can reduce growth and survival rates of the hosts (Adamo, 1998). Behavioral fever has been shown to only be effective in ridding pathogens under specific exposures (Watson et al., 1993). The effects of climate warming on host ability to employ behavioral fever are integral to predicting host susceptibility to infections and survival but have not been well documented. More studies are required for a better understanding of host-parasite interactions under climate change.

Although endotherms and ectotherms show variation in their physiological responses to increasing temperatures, it is undeniable that in some species, heat stress alters host susceptibility to diseases to some extent. Just as seen in parasites, carryover costs can be detrimental for hosts in their adult forms. For example, in insect species, exposure to heat shock damages oocytes as well as ovarian development, leading to a decrease in egg production (Krebs & Loeschcke, 1994; Rinehart, Yocum, & Denlinger, 2000). On the other hand, increasing temperatures have also been shown to be somewhat beneficial to species of hosts in terms of more activated immune functions. More research is important as the effects of elevating temperature on host species vary. Mechanisms of physiological responses to extreme temperatures are beyond the scope of this paper, and a detailed review would benefit the scientific community.

Host dispersal: migration and invasive species

As temperatures continue to rise, some species that are well-adapted to their habitats may be able to expand their ranges as new favorable environments become available. Conversely, climate warming may force species out of their native habitats by generating unsuitable conditions. Host species may utilize migration or shift their ranges to overcome the changing environmental conditions (Fuller et al., 2010). Migration could be an important strategy for hosts to utilize in order to evade areas with increasing abundance of parasites in a given season (Altizer & Oberhauser, 2004; Loehle, 1995). On the other hand, migratory individuals may gradually be displaced by resident conspecifics as climate warming may create year-round favorable conditions for some species (Bradshaw & Holzapfel, 2007; Lusseau et al., 2004). This reduction in migratory behavior may increase parasite transmission and promote higher virulence (De Roode, Yates, & Altizer, 2008). While resident species are likely to suffer from substantial parasite load, migratory species with altered routes or destinations are in danger of encountering novel pathogens (Harvell, Altizer, Cattadori, Harrington, & Weil, 2009). Some terrestrial species have been observed to shift their ranges due to the warming climate, and it is predicted that more animals will follow (Hickling, Roy, Hill, Fox, & Thomas, 2006). Encounters with novel pathogens of another species may lead to spillovers (Brooker, Travis, Clark, & Dytham, 2007; Morgan, Milner-Gulland, Torgerson, & Medley, 2004), which could greatly reduce the number of these migratory animals, and maybe even lead to extinction of some.

Invasive species as a result of host range expansions can be problematic to some native species. After a new species is introduced to a new environment, establishment follows (Jeschke & Strayer, 2005). Successful establishment followed by drastic increase in abundance of invasive species may be the product of decreased hostile interactions with enemies relative to native species, i.e., enemy release hypothesis (Fey & Herren, 2014). Invasive species are likely to be immunologically different from native species, which can influence their success in establishment after introduction to the new habitat (Martin, Hopkins, Mydlarz, & Rohr, 2010). Invasive and non-invasive species are also expected to differ in their levels of performances under a range of temperatures (Angilletta, 2009; Fey & Herren, 2014). Species with lower dispersal rates are inclined to be affected by the arrival of species that have previously been prohibited in their communities due to unsuitable climates (Berggren, Björkman, Bylund, & Ayres, 2009). Warming climate may create favorable habitats for invasive species and exert stress on native species that are not as well adapted to higher temperatures, permitting invasive species to prosper (Sharma, Jackson, Minns, & Shuter, 2007), while simultaneously decreasing the performance of local species. Direct competition with invasive species and chances of newly arrived species preying on native species may result in the decline of the native populations (Jackson & Mandrak, 2002). In some extreme cases, invasive species are able to take over their new habitats, restricting the growth of non-invasive species. For example, southern green stink bugs that have previously lived in sub-tropical regions were found to expand their ranges northward and have outcompeted local species (Musolin, 2007). Amphipod *Gammarus duebeni celticus* have been displaced by an invasive amphipod, *Gammarus pulex* in Ireland and other regions (Kelly, Dick, Montgomery, & MacNeil, 2003). With increasing numbers of invasive species, introduction of non-native parasites is inevitable, and effects of the introduction of novel pathogens should be reviewed for conservation purposes.

Effects on host-parasite dynamics

Physiological responses of hosts to climate warming may influence parasite selection of hosts. For endoparasites, increasing metabolism associated with higher temperatures demands more nutrients from their hosts, allowing parasites to increase body mass at the cost of damaging hosts and decreasing their prevalence (Sakanari & Moser, 1985). In addition, accelerated stages of life cycles of hosts and parasites at varying rates may produce major differences in transmission and infection rates. For instance, temperature elevation of approximately 3˚C increased trematode *Ribeiroia ondatrae* development, allowing for advancement in peak parasite output. Under the same conditions, intermediate snail hosts (*Planorbella trivolvis*) released parasites around 9 months in advance, before any amphibian hosts were able to deposit their eggs, making infection rates lower under elevated temperatures (Paull & Johnson, 2014). Despite the total number of parasite outputs, the net effects on infection rates and pathology did not increase as expected due to the mismatch in host-parasite life cycles. Climate warming can reduce the seasonal overlaps between parasite and host species, disrupting transmission and reducing diseases prevalence (Marcogliese, 2001). Winter ticks *Dermacentor albipictus* have expanded their ranges northward, but potential host barrenground caribou are able to avoid infection due to asynchrony in the timing of host migration and parasite infective stages (Kutz et al., 2009). In addition to the asynchronous host-parasite life cycles, it has been suggested that parasites will expand their ranges faster than their hosts, protecting native and non-native hosts from risks of infections (Lv et al., 2011). The opposite holds true as well, as rapid host range shifts can produce lag between timing of parasite and host expansions, allowing hosts to be parasite free for a period of time after successful expansion and establishment (Phillips et al., 2010). Changes in the timing of parasite-host interactions are hard to predict, predominantly because most studies have focused on the short-term measurements. Continuous studies are required to follow how community structures are changing due to changes in host-parasite interactions.

Implications for biodiversity: why should we be concerned?

Host mobility can serve as a potential range expansion tool for parasites (Kutz et al., 2013). Arrival of non-native hosts and parasites can result in increased biodiversity or, in some cases, extinction of some species (Kutz et al., 2009). With climate warming and parasite range expansions, major declines in some ectothermic species have been observed. For example, warmer climate has been linked to chytridiomycosis outbreaks in amphibian communities, leading to mass die-offs (Harvell et al., 2009). Additionally, there has been immense concern over how vector-borne diseases will affect human health. Although beyond the scope of this paper, the impact of vector-borne pathogens is expected to be significant.

Concluding remarks and further research directions

Climate warming induces significant changes in host-parasite dynamics and biodiversity. These changes are often idiosyncratic, increasing the difficulty in predicting how ecosystems are likely to change. More studies are required for a better understanding of how changes in species interactions perform within and beyond trophic levels to influence our ecosystems. While this paper focuses on a single dimension of climate change and its interaction with biodiversity, it is unlikely that temperature elevation acts alone to produce shifts in host-parasite dynamics. Other elements of climate change, e.g., heavy precipitation, rapid and extreme temperature changes, ocean acidity, etc., are pivotal to changes we have seen and will continue to see in our ecosystems. Understanding the mechanistic processes involved in host-parasite interactions, such as immune function and host manipulation, is necessary in order to develop a deeper insight in regard to how species vary in their responses to climate change and how these ramifications are likely to impact biodiversity. Further, evaluating environmental stressors and their impact on parasite virulence is critical for the conservation of species.

References

Adamo, S. A. (1998). The specificity of behavioral fever in the cricket Acheta domesticus. *The Journal of parasitology*, 529-533.

Altizer, S. M., Oberhauser, K. S., & Geurts, K. A. (2004). Transmission of the protozoan parasite, *Ophryocystis elektroscirrha*, in monarch butterfly populations: implications for prevalence and population-level impacts. *The monarch butterfly: biology and conservation*, 203-218.

Angilletta Jr, M. J., & Angilletta, M. J. (2009). *Thermal adaptation: a theoretical and empirical synthesis*. Oxford University Press.

Barber, I., Berkhout, B. W., & Ismail, Z. (2016). Thermal change and the dynamics of multi-host parasite life cycles in aquatic ecosystems. *Integrative and comparative biology*, *56*(4), 561-572.

Bates, A. E., Leiterer, F., Wiedeback, M. L., & Poulin, R. (2011). Parasitized snails take the heat: a case of host manipulation?. *Oecologia*, *167*(3), 613-621.

Berggren, Å., Björkman, C., Bylund, H., & Ayres, M. P. (2009). The distribution and abundance of animal populations in a climate of uncertainty. *Oikos*, *118*(8), 1121-1126.

Birceanu, O. (2017). Climate change delivers a punch to the gut. *Journal of Experimental Biology*, *220*(3), 331-332.

Boyles, J. G., Seebacher, F., Smit, B., & McKechnie, A. E. (2011). Adaptive thermoregulation in endotherms may alter responses to climate change. *Integrative and Comparative Biology*, *51*(5), 676-690.

Bradshaw, W. E., & Holzapfel, C. M. (2007). Evolution of animal photoperiodism. *Annu. Rev. Ecol. Evol. Syst.*, *38*, 1-25.

Brooker, R. W., Travis, J. M., Clark, E. J., & Dytham, C. (2007). Modelling species' range shifts in a changing climate: the impacts of biotic interactions, dispersal distance and the rate of climate change. *Journal of theoretical biology*, *245*(1), 59-65.

Burns, G., Ramos, A., & Muchlinski, A. (1996). Fever response in North American snakes. *Journal of Herpetology*, 133-139.

Campbell, J., Kessler, B., Mayack, C., & Naug, D. (2010). Behavioural fever in infected honeybees:

parasitic manipulation or coincidental benefit?. *Parasitology*, *137*(10), 1487.

Colinet, H., Boivin, G., & Hance, T. (2007). Manipulation of parasitoid size using the temperature-size rule: fitness consequences. *Oecologia*, *152*(3), 425-433.

Constable, A. J., Melbourne-Thomas, J., Corney, S. P., Arrigo, K. R., Barbraud, C., Barnes, D. K., ... & Davidson, A. T. (2014). Climate change and Southern Ocean ecosystems I: how changes in physical habitats directly affect marine biota. *Global change biology*, *20*(10), 3004-3025.

Cook, T., Folli, M., Klinck, J., Ford, S., & Miller, A. J. (1998). The relationship between increasing sea-surface temperature and the northward spread of *Perkinsus marinus* (Dermo) disease epizootics in oysters. *Estuarine, Coastal and Shelf Science*, *46*(4), 587-597.

De Roode, J. C., Yates, A. J., & Altizer, S. (2008). Virulence-transmission trade-offs and population divergence in virulence in a naturally occurring butterfly parasite. *Proceedings of the National Academy of Sciences*, *105*(21), 7489-7494.

Dittmar, J., Janssen, H., Kuske, A., Kurtz, J., & Scharsack, J. P. (2014). Heat and immunity: an experimental heat wave alters immune functions in three-spined sticklebacks (*Gasterosteus aculeatus*). *Journal of Animal Ecology*, *83*(4), 744-757.

Dobson, A., Kutz, S., Pascual, M., & Winfree, R. (2003). Pathogens and parasites in a changing climate. *Climate change and biodiversity: synergistic impacts. Advances in applied biodiversity science*, *4*, 33-38.

Ellers, J., Van Alphen, J. J., & Sevenster, J. G. (1998). A field study of size–fitness relationships in the parasitoid *Asobara tabida*. *Journal of Animal Ecology*, *67*(2), 318-324.

Ellis, A. E. (2001). Innate host defense mechanisms of fish against viruses and bacteria. *Developmental & Comparative Immunology*, *25*(8-9), 827-839.

Fey, S. B., & Herren, C. M. (2014). Temperature-mediated biotic interactions influence enemy release of nonnative species in warming environments. *Ecology*, *95*(8), 2246-2256.

Ford, S. E., & Smolowitz, R. (2007). Infection dynamics of an oyster parasite in its newly expanded range. *Marine Biology*, *151*(1), 119-133.

Fuller, A., Dawson, T., Helmuth, B., Hetem, R. S., Mitchell, D., & Maloney, S. K. (2010). Physiological mechanisms in coping with climate change. *Physiological and Biochemical Zoology*, *83*(5), 713-720.

Grant, G. S. (1982). Avian incubation: egg temperature, nest humidity, and behavioral thermoregulation in a hot environment. *Ornithological monographs*, (30), iii-75.

Gregory, J., Stouffer, R. J., Molina, M., Chidthaisong, A., Solomon, S., Rage, G., & Lohmann, U. (2007). *Climate change 2007: the physical science basis*.

Harvell, D., Altizer, S., Cattadori, I. M., Harrington, L., & Weil, E. (2009). Climate change and wildlife diseases: when does the host matter the most?. *Ecology*, *90*(4), 912-920.

Hernandez, A. D., Poole, A., & Cattadori, I. M. (2013). Climate changes influence free-living stages of soil-transmitted parasites of E uropean rabbits. *Global change biology*, *19*(4), 1028-1042.

Hickling, R., Roy, D. B., Hill, J. K., Fox, R., & Thomas, C. D. (2006). The distributions of a wide range of taxonomic groups are expanding polewards. *Global change biology*, *12*(3), 450-455.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... & Knowlton, N. (2007). Coral reefs under rapid climate change and ocean acidification. *science*, *318*(5857), 1737-1742.

Hoffmann, A. A., Chown, S. L., & Clusella-Trullas, S. (2013). Upper thermal limits in terrestrial ectotherms: how constrained are they?. *Functional Ecology*, *27*(4), 934-949.

Ibelings, B. W., Gsell, A. S., Mooij, W. M., Van Donk, E., Van Den WYNGAERT, S. I. L. K. E., & De Senerpont Domis, L. N. (2011). Chytrid infections and diatom spring blooms: paradoxical effects of climate warming on fungal epidemics in lakes. *Freshwater Biology*, *56*(4), 754-766.

Jackson, D. A., & Mandrak, N. E. (2002, August). Changing fish biodiversity: predicting the loss of cyprind biodiversity due to global climate change. In *American fisheries society symposium* (pp. 89-98). American Fisheries Society.

Jeschke, J. M., & Strayer, D. L. (2005). Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences*, *102*(20), 7198-7202.

Kelley, K. W. (1980). Stress and immune function: a bibliographic review [animals; changes of the immune system by stressors, disease-environment interactions]. In *Annales de Recherches Veterinaires*.

Kelly, D. W., Dick, J. T. A., Montgomery, W. I., & MacNeil, C. (2003). Differences in composition of macroinvertebrate communities with invasive and native *Gammarus* spp.(Crustacea: Amphipoda). *Freshwater Biology*, *48*(2), 306-315.

Kikuchi, Y., Tada, A., Musolin, D. L., Hari, N., Hosokawa, T., Fujisaki, K., & Fukatsu, T. (2016). Collapse of insect gut symbiosis under simulated climate change. *MBio*, *7*(5).

Kirchman, D. L., Morán, X. A. G., & Ducklow, H. (2009). Microbial growth in the polar oceans—role of temperature and potential impact of climate change. *Nature Reviews Microbiology*, *7*(6), 451-459.

Klok, C. J., & Chown, S. L. (2003). Resistance to temperature extremes in sub-Antarctic weevils: interspecific variation, population differentiation and acclimation. *Biological Journal of the Linnean Society*, *78*(3), 401-414.

Kluger, M. J. (1977). Fever in the frog Hyla Cinerea. *Journal of Thermal Biology*.

Krebs, R. A., & Loeschcke, V. (1994). Effects of exposure to short-term heat stress on fitness components in *Drosophila melanogaster*. *Journal of Evolutionary Biology*, *7*(1), 39-49.

Kutz, S. J., Hoberg, E. P., Polley, L., & Jenkins, E. J. (2005). Global warming is changing the dynamics of Arctic host–parasite systems. *Proceedings of the Royal Society B: Biological Sciences*, *272*(1581), 2571-2576.

Kutz, S. J., Checkley, S., Verocai, G. G., Dumond, M., Hoberg, E. P., Peacock, R., ... & Abrams, A. (2013). Invasion, establishment, and range expansion of two parasitic nematodes in the Canadian Arctic. *Global Change Biology*, *19*(11), 3254-3262.

Kutz, S. J., Jenkins, E. J., Veitch, A. M., Ducrocq, J., Polley, L., Elkin, B., & Lair, S. (2009). The Arctic as a model for anticipating, preventing, and mitigating climate change impacts on host–parasite interactions. *Veterinary parasitology*, *163*(3), 217-228.

Labaude, S., Cézilly, F., & Rigaud, T. (2017). Temperature-related intraspecific variability in the behavioral manipulation of acanthocephalan parasites on their gammarid hosts. *The Biological*

Bulletin, *232*(2), 82-90.

Landis, S. H., Sundin, J., Rosenqvist, G., & Roth, O. (2012). Behavioral adjustments of a pipefish to bacterial *Vibrio* challenge. *Behavioral Ecology and Sociobiology*, *66*(10), 1399-1405.

Loehle, C. (1995). Social barriers to pathogen transmission in wild animal populations. *Ecology*, *76*(2), 326-335.

Logan, M. L., Cox, R. M., & Calsbeek, R. (2014). Natural selection on thermal performance in a novel thermal environment. *Proceedings of the National Academy of Sciences*, *111*(39), 14165-14169.

Lusseau, D., Williams, R., Wilson, B., Grellier, K., Barton, T. R., Hammond, P. S., & Thompson, P. M. (2004). Parallel influence of climate on the behaviour of Pacific killer whales and Atlantic bottlenose dolphins. *Ecology Letters*, *7*(11), 1068-1076.

Lv, S., Zhang, Y. I., Steinmann, P., YANG, G. J., Yang, K. U. N., ZHOU, X. N., & Utzinger, J. (2011). The emergence of angiostrongyliasis in the People’s Republic of China: the interplay between invasive snails, climate change and transmission dynamics. *Freshwater Biology*, *56*(4), 717-734.

Macnab, V., & Barber, I. (2012). Some (worms) like it hot: fish parasites grow faster in warmer water, and alter host thermal preferences. *Global Change Biology*, *18*(5), 1540-1548.

Marcogliese, D. J. (2001). Implications of climate change for parasitism of animals in the aquatic environment. *Canadian Journal of Zoology*, *79*(8), 1331-1352.

Marcogliese, D. J. (2008). The impact of climate change on the parasites and infectious diseases of aquatic animals. *Rev Sci Tech*, *27*(2), 467-484.

Martin, L. B., Hopkins, W. A., Mydlarz, L. D., & Rohr, J. R. (2010). The effects of anthropogenic global changes on immune functions and disease resistance. *Annals of the New York Academy of Sciences*, *1195*(1), 129.

Meerburg, B. G., & Kijlstra, A. (2009). Changing climate—changing pathogens: *Toxoplasma gondii* in North-Western Europe. *Parasitology research*, *105*(1), 17-24.

Meléndez, L., Laiolo, P., Mironov, S., García, M., Magaña, O., & Jovani, R. (2014). Climate-driven variation in the intensity of a host-symbiont animal interaction along a broad elevation gradient. *PLoS*

One, *9*(7), e101942.

Morgan, E. R., Milner-Gulland, E. J., Torgerson, P. R., & Medley, G. F. (2004). Ruminating on complexity: macroparasites of wildlife and livestock. *Trends in ecology & evolution*, *19*(4), 181-188.

Morley, N. J., & Lewis, J. W. (2014). Temperature stress and parasitism of endothermic hosts under climate change. *TRENDS in Parasitology*, *30*(5), 221-227.

Musolin, D. L. (2007). Insects in a warmer world: ecological, physiological and life-history responses of true bugs (Heteroptera) to climate change. *Global Change Biology*, *13*(8), 1565-1585.

Nikoskelainen, S., Bylund, G., & Lilius, E. M. (2004). Effect of environmental temperature on rainbow trout (*Oncorhynchus mykiss)* innate immunity. *Developmental & Comparative Immunology*, *28*(6), 581-592.

O'Connor, C. M., Norris, D. R., Crossin, G. T., & Cooke, S. J. (2014). Biological carryover effects: linking common concepts and mechanisms in ecology and evolution. *Ecosphere*, *5*(3), 1-11.

Pandey, S., & Singh, R. (1999). Host size induced variation in progeny sex ratio of an aphid parasitoid *Lysiphlebia mirzai*. *Entomologia experimentalis et applicata*, *90*(1), 61-67.

Paull, S. H., & Johnson, P. T. (2014). Experimental warming drives a seasonal shift in the timing of host-parasite dynamics with consequences for disease risk. *Ecology letters*, *17*(4), 445-453.

Phillips, B. L., Kelehear, C., Pizzatto, L., Brown, G. P., Barton, D., & Shine, R. (2010). Parasites and pathogens lag behind their host during periods of host range advance. *Ecology*, *91*(3), 872-881.

Poisot, T., Šimková, A., Hyršl, P., & Morand, S. (2009). Interactions between immunocompetence, somatic condition and parasitism in the chub *Leuciscus cephalus* in early spring. *Journal of Fish Biology*, *75*(7), 1667-1682.

Poulin, R. (2006). Global warming and temperature-mediated increases in cercarial emergence in trematode parasites. *Parasitology*, *132*(1), 143.

Rinehart, J. P., Yocum, G. D., & Denlinger, D. L. (2000). Thermotolerance and rapid cold hardening ameliorate the negative effects of brief exposures to high or low temperatures on fecundity in the flesh fly, *Sarcophaga crassipalpis*. *Physiological Entomology*, *25*(4), 330-336.

Sakanari, J., & Moser, M. (1985). Salinity and temperature effects on the eggs, coracidia, and procercoids of *Lacistorhynchus tenuis* (Cestoda: Trypanorhyncha) and induced mortality in a first intermediate host. *The Journal of parasitology*, 583-587.

Sharma, S., Jackson, D. A., Minns, C. K., & Shuter, B. J. (2007). Will northern fish populations be in hot water because of climate change?. *Global Change Biology*, *13*(10), 2052-2064.

Shields, R. J., & Tidd, W. M. (1968). Effect of temperature on the development of larval and transformed females of *Lernaea cyprinacea* L.(Lernaeidae). *Crustaceana. Supplement*, 87-95.

Skelly, D. K., Joseph, L. N., Possingham, H. P., Freidenburg, L. K., Farrugia, T. J., Kinnison, M. T.,& Hendry, A. P. (2007). Evolutionary responses to climate change. *Conservation Biology*.

Stocker, T. F., Qin, D., Plattner, G. K., Tignor, M., Allen, S. K., Boschung, J., ... & Midgley, P. M. (2013). Climate change 2013: The physical science basis. *Contribution of working group I to the fifth assessment report of the intergovernmental panel on climate change*, *1535*.

Tewksbury, J. J., Huey, R. B., & Deutsch, C. A. (2008). Ecology: Putting the heat on tropical animals.*Science*.

Thomas, E. K., Castañeda, I. S., McKay, N. P., Briner, J. P., Salacup, J. M., Nguyen, K. Q., & Schweinsberg, A. D. (2018). A wetter Arctic coincident with hemispheric warming 8,000 years ago. *Geophysical Research Letters*, *45*(19), 10-637.

Van Dijk, J., & Morgan, E. R. (2008). The influence of temperature on the development, hatching andsurvival of *Nematodirus battus* larvae. *Parasitology*, *135*(2), 269.

Van Hemert, C., Flint, P. L., Udevitz, M. S., Koch, J. C., Atwood, T. C., Oakley, K. L., & Pearce, J. M. (2015). Forecasting wildlife response to rapid warming in the Alaskan Arctic. *BioScience*, *65*(7), 718-728.

Watson, D. W., Mullens, B. A., & Petersen, J. J. (1993). Behavioral fever response of *Musca domestica* (Diptera: Muscidae) to infection by *Entomophthora muscae* (Zygomycetes: Entomophthorales). *Journal of Invertebrate Pathology*, *61*(1), 10-16.

Whetton, P. H., Fowler, A. M., Haylock, M. R., & Pittock, A. B. (1993). Implications of climate change due to the enhanced greenhouse effect on floods and droughts in Australia. *Climatic Change*, *25*(3-4), 289-317.