Opinion

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Climate change and Arctic parasites

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Climate is changing rapidly in the Arctic. This has important implications for parasites of Arctic ungulates, and hence for the welfare of Arctic peoples who depend on caribou, reindeer, and muskoxen for food, income, and a focus for cultural activities. In this Opinion article we briefly review recent work on the development of predictive models for the impacts of climate change on helminth parasites and other pathogens of Arctic wildlife, in the hope that such models may eventually allow proactive mitigation and conservation strategies. We describe models that have been developed using the metabolic theory of ecology. The main strength of these models is that they can be easily parameterized using basic information about the physical size of the parasite. Initial results suggest they provide important new insights that are likely to generalize to a range of host–parasite systems.

A new need for understanding the relationship between weather and disease transmission

A principle motivation of this article is to encourage more ecologists to come and work in the Arctic [1] because the region is in many ways the definitive environment in which to study the impacts of climate change: Arctic animal communities are relatively simple compared to temperate, Mediterranean, or tropical systems, and the rates of climate change are significantly faster. Although the weather is extreme, it exhibits substantial annual variation, and this allows models of host–parasite systems to be parameterized and tested across a wide range of natural temperature and humidity gradients. The work has important implications for conservation of Arctic ungulates and their parasites, and hence for the welfare of Arctic peoples who depend on caribou, reindeer, and muskoxen for food, income, and a focus for cultural activities [2–4]. We recognize this article focuses significantly on our own research rather than providing a balanced review of this topic, but this is very much an epiphenomenon of the small number of people working on host–parasite problems in the Arctic.

Using weather to predict worm and vector borne disease outbreaks has a long history in domestic animal parasitology [5,6], but these studies were essentially curtailed when cheap drugs with limited side-effects made it less essential to accurately predict the timing of treatment of domestic livestock with helminth infections [7,8]. More recently, a need for a better understanding of how climate modifies transmission dynamics has resurfaced again for three reasons: (i) climate change is already beginning to alter host–parasite systems around the globe; (ii) climate change is progressing much more rapidly than was initially predicted, necessitating a need to implement mitigation strategies sooner rather than later [1]; and (iii) drug resistance has considerably reduced the efficacy of anti-parasitic drugs, resulting in a need to be much more efficient in how and when we target their use against parasites [9,10].

Comprehending the influence of climate change on disease outbreaks generally requires an understanding of how climate variability modifies the various mechanisms that determine the transmission dynamics of parasites. In general, climate change can impact disease transmission in four different ways [11]: (i) by directly affecting the rates of development, mortality, and reproduction in free-living parasites and parasites within ectothermic intermediate hosts; (ii) by affecting the development, mortality, and reproduction of vectors and intermediate hosts; (iii) by inducing behavioral changes in hosts, vectors and/or parasites that modify contact, and thus, transmission rates; and (iv) by changing host susceptibility, for example, through changes in host physiology, host stress, or host immunity. If we are to make accurate predictions of either the seasonal response of parasite dynamics to climate variation, or of changes in the overall distribution, structure, and dynamics of host–parasite systems in response to broad-scale inter-annual climatic trends, then we need to quantify each of these processes for a large variety of systems. This is a Herculean task! Are there any shortcuts? Recent work suggests that we might be able to use

Glossary

Abomasal: living in the fourth stomach (the abomasum) of the ruminant host.
Allometry: the study of the growth rate of the parts of an organism in relation to the whole body.
Degree-day models: temperature-dependent models where development times or mortality rates are a function of the product of daily temperature and number of days for which that temperature operates.
Ectothermic: cold-blooded animals whose body temperature depends on the temperature of their surrounding environment.
Phenology: the study of seasonal variation in the initiation of biological events, such as flowering, emergence from hibernation, mating, births, fruiting, and leaf-fall.
Poikilotherms: organisms whose internal temperature varies considerably.

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metabolic scaling rules to parameterize host–parasite models if we simply have information on host and parasite body size [12–17]. The central part of this review will focus on describing these models and how they can and could be used. Before that, we will briefly consider the types of climate data available for driving climate-based host–parasite models and examine where in the world such models should initially be tested.

Global patterns of climate change

The vast majority of climate scientists are now convinced that climate change is occurring and that it is driven by human activities [18,19] – principally the burning of fossil fuels and the destruction of tropical forests [20,21]. In retrospect, scientists have already done a very solid job of predicting how climate warming will cause changes to the Earth's biomes and the species that inhabit them, with one of the most disconcerting features of these predictions being how much more rapidly they have occurred than was originally predicted [22,23]. Arguably one of the most worrying aspects of climate change is the inefficacy with which necessary policy changes are implemented at the highest political levels; ironically, much of the discussion at these levels hereby often fails to grasp that the inherent uncertainty in climate predictions may not mean that future changes in the climate will be slower than predicted, but rather that past model predictions may have been too conservative.

The geographical patterns of climate change contribute significantly to this confusion. Climate change is most pronounced in the polar regions where very few people live, and is occurring at its slowest rates in the tropical regions where billions of people coexist with numerous pathogens [24]. Moreover, the tropical and temperate zones are also those regions where land-use change and economic development are proceeding most rapidly [25]. These activities and other changes, such as the evolution of drug resistance, confound any simple attempt to detect a signature of climate change in the dynamics of host–parasite interactions (see, for example, the discussion on malaria in Kenya [26]). By contrast, in polar regions climate change is proceeding rapidly and there have been few confounding land-use change problems [27]. While this will quickly change as the Arctic opens up for resource extraction, at the present time the 'cleanest signature' of climate change and its impacts can be seen in high Arctic communities of parasites and hosts. Studies here will provide a diversity of important insights into what will eventually happen in the temperate zones and then in the Tropics [28,29].

Climate data are gathered at hundreds of thousands of locations throughout the world, and in the atmosphere above it, multiple times per day. Climate data define the concept of 'big data'! Unfortunately, this contrasts with the rate and spatial scale at which data on neglected tropical diseases and infectious disease of wildlife are currently being collected [30]; in these cases, the majority of studies collect data with a weekly or monthly frequency, often for only 2–3 years (the average duration of a PhD) or sometimes, at a specific location, for the duration of the career of a dedicated academic team leader. This creates a significant disparity between the quality and quantity of climate and epidemiological data, making the forecasting of disease outbreaks both complicated and controversial [30]. This limitation re-emphasizes the above-described need for host–parasite models that can be parameterized independently – that is, even in systems where data are scarce or completely absent – using allometrically scaled physiological models (see Glossary).

Several recent empirical studies have permitted quantification of the role that temperature plays in driving the transmission dynamics of parasitic helminthes of muskoxen and caribou in the Canadian Arctic [31–34]. Moreover, the Arctic also holds a sufficient diversity of pathogens to allow comparing the influence of seasonal climate variability on the dynamics of nematodes with direct life cycles, with those that include an intermediate host, and with pathogens that are vector-transmitted [29]. Botflies and other ectoparasites, such as winter ticks, also play a major role in the health of Arctic and sub-Arctic mammals, providing us with opportunities to also understand how climate change might impact upon insect parasites and parasitoids. In short, almost all modes of disease transmission that are of concern in more temperate zones are also present in the Arctic, and we argue that these systems provide unique opportunities to shed light on the manner in which climate can impact host–parasite systems.

We will focus here on understanding the impacts of temperature changes on host–parasite systems. However, we also acknowledge explicitly that understanding the roles that alternative abiotic factors (e.g., humidity, day length) play in driving seasonal transmission patterns will be central to quantifying how host–parasite systems will respond to climate change. One confounding effect that we do not discuss here explicitly is that, while climate change will modify temperature and snowfall relationships, it will have no impact on day length. This means that day length-driven cues, such as the onset of host migrations or the initiation of reproduction, may become desynchronized from processes that are temperature-driven [35], potentially creating further significant changes in host–parasite interactions [36,37]. Some of these mismatches will increase the impact of parasites on their hosts, while others may be more detrimental to the parasite and lead to reductions in host worm burdens. At present, there are very few data to quantify these responses, and therefore no generalities can be described. Similarly, climate change will often allow both hosts (including intermediate and definitive hosts) and parasite species to expand their ranges, but potentially at different rates [37]. Such range expansions would merit a review in their own right, and thus we only briefly note below how the physiological models described here could be used to predict parasite range expansions, and emphasize that the introduction of novel pathogens by host species expanding their ranges has a huge potential to detrimentally impact on Arctic wildlife.

Finally, we emphasize throughout that many of the host species are vital resources for the aboriginal peoples who live in the Arctic. Much of their nutritional needs are met by terrestrial and marine mammals [3] whose distribution and abundance will be impacted by climate-driven changes in their parasites and pathogens [27,38]. Arctic peoples are already suffering huge changes in their lives due to climate change, and we believe that the lessons learned from them will be highly relevant to many other people as the major impacts of climate change move from the poles into temperate and tropical regions.

Physiologically based models of climate change impacts

Mathematical models will play a key role in predicting the impacts of climate change on the dynamical interactions of hosts and parasites, but to date such models only exist for a few well-studied systems [39–43]. If we want to develop a predictive theory of climate and host–parasite interactions we need a quantitative physiologically based theory of how host–parasite population dynamics respond to climate variability [14,16,44,45]. Molnár, Kutz, and Dobson [16,46] have been developing such an approach for several parasitic nematode species in Arctic ungulates. Their initial application to data collected in the Arctic suggests that it is possible to develop physiologically based population models that provide high predictive accuracy for how host–parasite systems respond to climate variability. While the specifics of the host–parasite interactions will vary across systems, the underlying physiological principles that determine the rates of development, mortality, reproduction, and other model parameters can be seen as largely invariant [47,48], and can therefore be readily extrapolated from polar regions to systems in the temperate and tropical zones.

One fundamental reason for the current scarcity of predictive models is a lack of data describing how the parameters that drive host–parasite dynamics might change under future conditions. For example, in helminth parasites such parameters may include the development and mortality rates of larvae that are free-living in the environment or within ectotherm intermediate hosts, the uptake rate of infective larvae by intermediate or definite hosts, or – in trematodes – the rates of cercarial production within intermediate hosts. Each of these parameters is likely to exhibit a non-linear response to varying environmental conditions, such as temperature and humidity; this will in turn create complex and difficult-to-predict changes in the dynamics of host–parasite systems under climate change. In principle, the impacts of temperature and humidity on these parasite life-history components can be measured in carefully designed laboratory or field studies, and such data could then be used to assess the likely impacts of future climates (e.g., [41,42]). However, the sheer multitude of parasite species prevents the development of experimental studies across broad scales and multiple species. At first sight this makes the development of species-specific climate change impact models for all existing and emerging parasites of humans, wildlife, and livestock logistically impossible. The natural question therefore becomes whether there exist any generalities that allow predicting how the parameters describing parasite life-histories would change under future conditions.

One method to derive such generalities may be through the metabolic theory of ecology, which posits that metabolism in all species scales allometrically with body size and exponentially with temperature, or specifically, $I \propto M^{3/4}e^{-E/kT}$, where I represents metabolic rate, M is body mass, E is the average activation energy of respiration, T is temperature in degrees Kelvin, and k is Boltzmann's constant [49]. Because metabolism and energy use can be considered to be one of the fundamental mechanisms underlying all ecological processes, the theory further suggests that the same scaling relationships transfer to processes and patterns across all levels of biological organization [48,49], and in particular to the parasite life-history parameters of interest here: development, mortality, reproduction, and parasite uptake. Moreover, the theory suggests that the activation energy E will center around 0.55–0.65 eV in most species [50–52], or will vary systematically around this value with covariates such as latitude and phylogenetic association [52,53], and this would make temperature effects on parasites inherently predictable even if species-specific data are lacking.

Mathematical models for climate-driven infection dynamics of nematodes

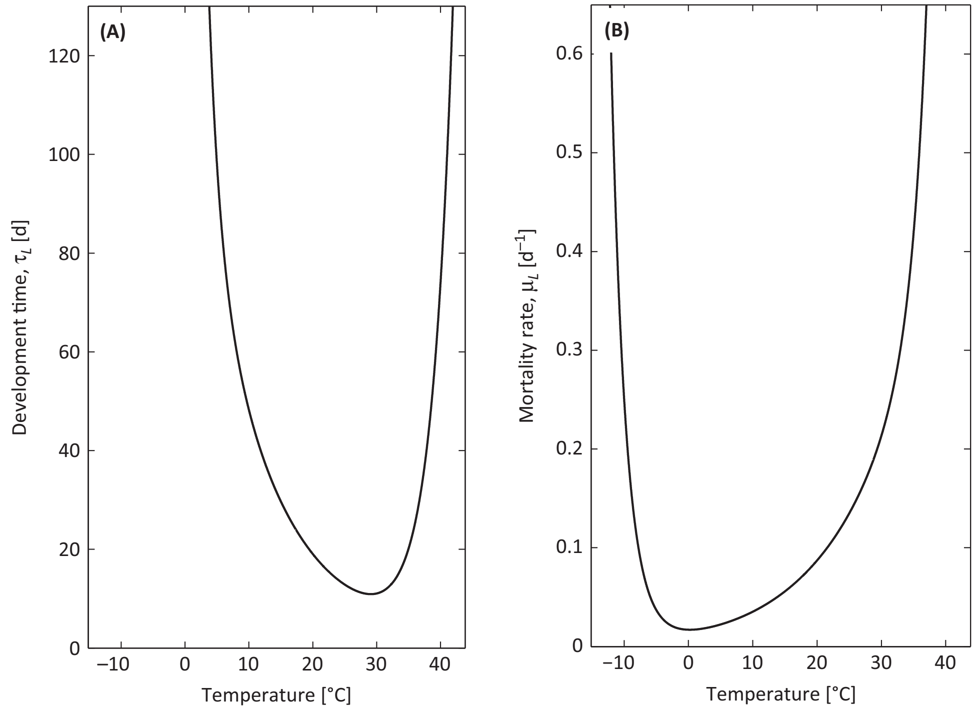
Molnár *et al.* [16] show how the metabolic theory of ecology can be used to predict climate change impacts on parasites. Specifically, they suggest using the Sharpe–Schoolfield model [47,54] in lieu of the Arrhenius relationship that is embodied in the equation $I \propto M^{3/4}e^{-E/kT}$ to account for lower and upper temperature thresholds in parasite development, mortality, and other life-history components [16]. For example, the development times of free-living parasite larvae or of larvae living in ectothermic intermediate hosts, $\tau_L(T)$, as well as the mortality rates of these parasites, $\mu_L(T)$, can be represented as a function of temperature by

$$\tau_L(T) = \tau_0 e^{-\frac{E_\tau}{k}\left(\frac{1}{T}-\frac{1}{T_0}\right)} \cdot \left(1 + e^{\frac{E_\tau^L}{k}\left(\frac{1}{T}-\frac{1}{T_\tau^L}\right)} + e^{\frac{E_\tau^H}{k}\left(-\frac{1}{T}+\frac{1}{T_\tau^H}\right)}\right)^{-1} \qquad [1a]$$

$$\mu_L(T) = \mu_0 e^{-\frac{E_\mu}{k}\left(\frac{1}{T}-\frac{1}{T_0}\right)} \cdot \left(1 + e^{\frac{E_\mu^L}{k}\left(\frac{1}{T}-\frac{1}{T_\mu^L}\right)} + e^{\frac{E_\mu^H}{k}\left(-\frac{1}{T}+\frac{1}{T_\mu^H}\right)}\right) \qquad [1b]$$

where τ_0 and μ_0 represent the development time and mortality rate at a reference temperature T_0, E_τ and E_μ represent the respective activation energies of development and mortality, and E^L and E^H represent the respective inactivation energies at the lower and upper temperature thresholds, T^L and T^H (Figure 1).

From this basis, Molnár *et al.* [16] show how incorporating these metabolic relationships into population models of the host–parasite dynamics allows predicting changes to these dynamics under yet-to-be-observed temperatures, at least as a first approximation. Moreover, through calculating the basic reproductive number R_0, now as a function of temperature T, this approach allows estimating the fundamental thermal niche of a parasite under present and future conditions, and thus likely range changes. For example, a range contraction is likely to occur in areas where current temperatures permit persistence (i.e., $R_0(T) \geq 1$), but predicted temperatures would decrease $R_0(T)$ beneath the persistence threshold (i.e., $R_0(T) < 1$). The



TRENDS in Parasitology

Figure 1. Sharpe-Schoolfield model (Equation 1) for the temperature-dependence of **(A)** development times and **(B)** mortality rates of free-living parasite larvae and larvae living within ectothermic hosts. The models are parameterized for *Ostertagia gruehneri*, an abomasal nematode parasite of caribou. Parameter values are as in Molnár *et al.* [16]: $\tau_0 = 29.6$ d, $E_\tau = 0.65$ eV, $E_\tau^L = E_\tau^H = 3.25$ eV, $T_0 = 15\,^\circ$C, $T_\tau^L = 2.5\,^\circ$C, $T_\tau^H = 32.5\,^\circ$C for development times (Equation 1a), and $\mu_0 = 0.056$ d^{-1}, $E_\mu = 0.65$ eV, $E_\mu^L = E_\mu^L = 3.25$ eV, $T_0 = 15\,^\circ$C, $T_\mu^L = -2.5\,^\circ$C, $T_\mu^H = 37.5\,^\circ$C for mortality rates (Equation 1b); $k = 8.62 \times 10^{-5}$ eV K^{-1}.

converse (i.e., temperature changes that raise $R_0(T)$ from <1 to >1) indicates that the parasite could expand its range into this area based on its physiological constraints (Figure 2). However, whether or not such range expansions will actually occur will not only depend on the ability of the parasite to cope with predicted temperatures but also on a variety of other factors such as the presence of suitable hosts [46,55]. For nematode parasites of caribou and musk-oxen, this model provides an excellent fit to the observed experimental data, and this allowed Molnár *et al.* [16] to examine what will happen to seasonal patterns of transmission potential as temperatures in the Arctic begin to warm (Figure 3). Crucially, we expect that the approach will continue to hold for parasites around the globe owing to the overarching power of the metabolic theory of ecology to describe the temperature-dependence of physiological parameters in a wide variety of species [49,52]. This focus on understanding host–parasite dynamics through temperature impacts on physiological parameters is particularly promising because the laws of thermal dynamics will continue to hold, no matter how much the global climate changes.

Phenological changes in the seasonal dynamics of host–parasite systems can also be understood and anticipated with the proposed approach. To achieve this, Molnár *et al.* [16] suggest calculating R_0 separately for each day of the year where parasite larvae may be shed by hosts to begin the part of their life cycle that is free-living in the environment. Using this 'birth date'-dependent approach to fitness they show that, for Arctic nematodes with a direct life cycle, climate warming may shift the season that allows parasite larvae to develop to infectivity towards earlier in the spring and later in the fall (Figure 3). As climate change progresses, stronger warming may fragment a previously continuous spring-to-fall transmission period into two separate transmission periods in spring and fall, a prediction that was consistent with field observations for *Ostertagia gruehneri*, an abomasal parasite of caribou [36]. The magnitude and duration of each of these patterns can again be predicted using metabolic theory. A key extension of this model was provided by Rohr *et al.* [14] who allowed for temperature acclimatization of both hosts and parasites in variable environments. Their model essentially achieved this by letting individuals acclimatize after a temperature shift, with the time to acclimatization being determined by the metabolic theory of ecology, and by letting the low- and high-temperature thresholds T^L and T^H in Equation 1 vary with the current acclimatization status of hosts and parasites. This approach is useful for understanding the impacts of changes in climatic variability and, in particular, for understanding the impacts of the predicted increases in the frequency of extreme weather events such as heat waves [1].

Overall, the metabolic approach can potentially serve as a framework for understanding and predicting climate change impacts on a broad diversity of host–parasite systems throughout the world [14,45]. First, it allows estimation of temperature effects on any parasite life-history component, and thus model parameterization even in systems where data are scarce or absent. The approach can therefore be particularly useful to inform public health planning in cases where quick decisions are needed

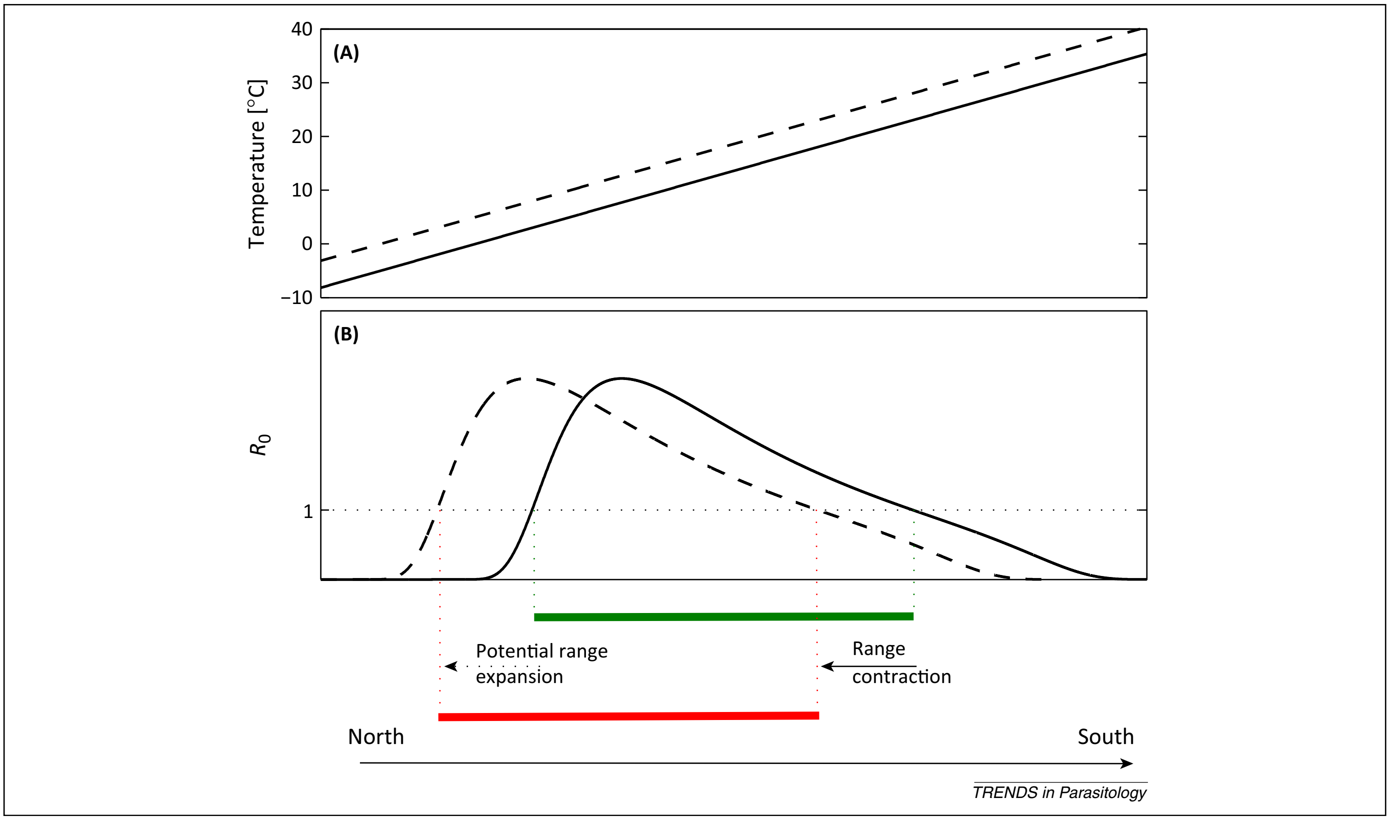


Figure 2. Conceptual illustration of how to use the metabolic host–parasite model for predicting parasite range shifts under climate warming. The panels show a hypothetical north-to-south latitude gradient along the *x* axis, with panel **(A)** depicting temperatures at each location, and panel **(B)** depicting the resultant basic reproductive number (R_0) of a parasite at the corresponding locations. In both panels, unbroken lines refer to temperatures pre-climate-warming, and broken lines to an environment that is 5 °C warmer at each location. The green unbroken line shows the fundamental thermal niche of the parasite pre-warming (i.e., locations where $R_0 \geq 1$). Following warming, the R_0 curve shifts northwards, with parasite fitness increasing at northern locations, but decreasing at southern locations; the red unbroken line shows the fundamental thermal niche of the parasite under these warmed conditions. The unbroken arrow marks the area where a range contraction is likely to occur (as R_0 fell from >1 to <1). The broken arrow shows the area that was outside the tolerance range of the parasite before climate warming but could permit a parasite range expansion given the physiological constraints of the parasite (as R_0 rose from <1 to >1); whether or not this range expansion would occur depends, however, also on other factors such as the presence of suitable hosts.

(for example, in newly emerging diseases). Second, by considering the entire host–parasite dynamics, the approach allows simultaneous consideration of nonlinear temperature-dependencies on different life-history components, thus allowing us to evaluate the net effects of both positive and negative impacts of climate change. As such, the approach advances traditional approaches, such as degree-day models, which only allow considering climate change impacts on a single life-history component [56,57]. Third, because the approach only focuses on model parameterization, but makes no assumptions about the structure of the host–parasite system, it can be applied to any system globally provided that the life cycle of the parasite is understood and represented in the model. Fourth, because the metabolic parameterization approach meshes with the existing theory of modeling host–parasite systems, it can be used to estimate any characteristic of host–parasite systems according to tried and tested methods – but now as a function of temperature – including R_0, the threshold host density allowing parasite persistence H_T [58], the stability of stationary states, or the parasite burden and prevalence in a host population. Fifth, the approach provides additional flexibility for considering the effects of behavioral thermoregulation, either by the parasite or by ectotherm hosts. Microhabitat selection can be incorporated by replacing the ambient temperature T in Equation 1 by a function $\Phi(T)$ that represents the actual temperature experienced by the parasite as a function of ambient temperature. Behavioral thermoregulation by an ectotherm intermediate host could then result in a 'shelter effect' that buffers parasitic helminths with an indirect life cycle against the most severe impacts of climate warming (e.g., extremes in temperatures), thus challenging the notion that parasites with an indirect life cycle would be more vulnerable to changing conditions than parasites with a direct life cycle [46]. Sixth, because many climate change impacts on hosts can also be understood and predicted by considering their energy budgets [59], the metabolic approach for parasites provides a natural way to link the host and parasite levels through the common currency of energy. This could allow a comprehensive predictive approach that also considers the roles of changes in host body condition, host immunity, or host range in determining the interaction between hosts and their parasites under climate change [14,15,60].

To fully exploit the power of the metabolic theory of ecology for host–parasite systems it will be key to validate the theory for parasites with extensive data, as has been done for free-living species [49,52,61,62]. In particular, it will be important to determine to what degree the

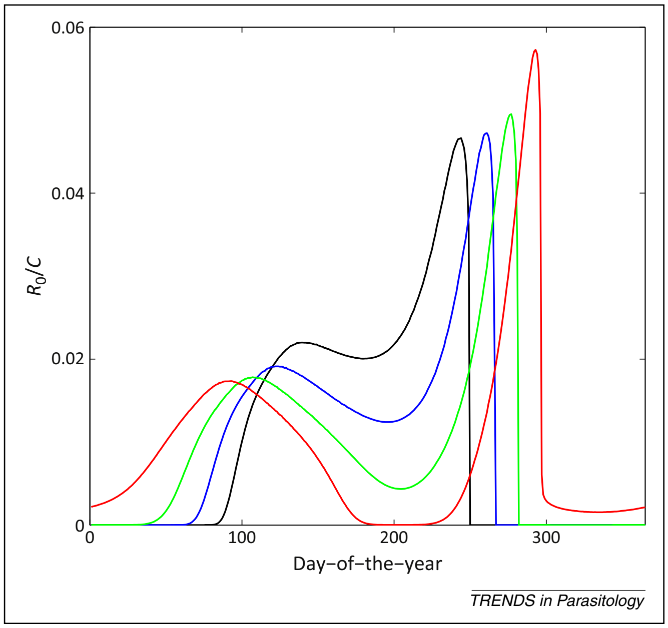


Figure 3. Model predictions for climate change impacts on the day-of-the-year-dependent fitness of *Ostertagia gruehneri*, an abomasal parasite of caribou. Fitness is represented by R_0/C, which corresponds to the temperature-dependent component of the basic reproductive number R_0, calculated as a function of parasite 'birth date'. A warmer climate is expected to shift the season that allows parasite larvae to develop to infectivity and subsequently reproduce towards earlier in the spring and later in the fall. Strong warming may hereby fragment the previously continuous spring-to-fall transmission period into two separate transmission periods in spring and fall owing to the inability of the parasite to survive extreme heat. Four successively warmer climate scenarios are shown by the black, blue, green, and red lines. The figure is from Molnár *et al.* [16], with spring initially starting at around day 100, and fall commencing at around day 250.

activation energies in different parasite life-history components conform to the expected 0.55–0.65 eV value, or whether deviations from this expectation can be predicted with confidence from covariates such as latitude or phylogenetic association [52,53,63]. Initial results are encouraging, with the expectation of $E = 0.65$ eV explaining development and mortality patterns in the free-living stages of several nematode species with a direct life cycle extremely well [16].

The second component of the metabolic equation $I \propto M^{3/4}e^{-E/kT}$ describes the dependence of the metabolic rate I on body mass M, and is particularly useful for determining the baseline values of metabolism, development, mortality, reproduction, and other life-history components *a priori* (e.g., τ_0 and μ_0 in Equation 1). Initial tests of this relationship for parasites revealed some discrepancies with the patterns observed in free-living species [64], but Hechinger *et al.* [17] later demonstrated that parasite abundance and biomass production do conform to the predictions of the metabolic theory of ecology, once the relatively high trophic level of parasites is accounted for. Nevertheless, as with the temperature-dependence of metabolism, extensive tests of the predicted relationships for mass-dependence are necessary to allow parameterizing host–parasite models based on metabolic principles alone. How other environmental covariates that are known to affect parasites, and are likely to be affected by climate change, such as humidity, influence the relationships predicted by the metabolic theory of ecology remains unclear. Potential applications of the metabolic theory of ecology for disease control and public health planning are potentially huge, and certainly justify concerted efforts to extensively test and further develop the theory for parasitic species. Guidance for the development of metabolic host–parasite models could hereby also be obtained from free-living species, where the application of metabolic models not only provided predictions for climate change impacts on plants, invertebrates, amphibians, and reptiles [65,66] but also provided novel methods for understanding temperature impacts on dynamical interactions such as in herbivore-plant systems [67], predator–prey systems [68], carbon cycling [69], and food webs [70]. One advantage that parasites hold over many free-living species is that many of the relationships proposed by the metabolic theory of ecology (e.g., for development, mortality, reproduction, and infectivity) can be tested in laboratory experiments (e.g. [71]). Arctic ecosystems – owing to their low species diversity, relatively simple host–parasite systems, a strong climate warming signal, strong seasonality, and limited confounding anthropogenic factors – could then provide a relatively simple setting to test these relationships in the field and assess the validity of climate change impact predictions in real time.

Concluding remarks and future perspectives

The next decade is likely to see a multitude of papers on climate change and the dynamics of host–parasite life cycles; the majority of these papers will be for human pathogens such as malaria, parasites of domestic livestock, and the neglected tropical diseases that have their biggest impact in the Tropics. Only very rarely will data be available for the huge diversity of parasites that live in, or on, wildlife species [72]. If we are to understand the impacts of parasites on wildlife we will need a framework that extrapolates across different host–parasite systems, but can be parameterized using relationships that are quantified in well studied and data-rich systems. The approaches described above provide a framework for developing this new class of models. The next challenge is to apply these methods to different classes of parasite (cestodes, trematodes, and perhaps protozoa) and to develop models where the dynamics and physiological responses of both the parasite and the host are parameterized as functions of body size and environmental temperatures. It should then be possible to produce parasite and vector maps for changes in pathogen fitness with latitude to match those produced by Deutsch *et al.* [66] for various free-living poikilotherms. We do not think this is an impossible task; in fact, it may be the only option available to us. We also see considerable advantages in first applying these methods in Arctic and northern temperate zones before attempting to apply them to Mediterranean and tropical systems. The change in the shape of the annual transmission rate from a short unimodal peak to a longer bimodal transmission function suggests that even simple systems will exhibit a complex response to climate change. The species-rich tropical systems are likely to have similar patterns underlying their response to climate change, but the huge diversity of confounding interspecific interactions in these regions will make it much harder to disentangle signal from noise. Although we feel that the physiologically based models provide an insightful null model for examining the impact of climate change on parasites, we ultimately feel that best advice is to be prepared, but be very prepared to be surprised.

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