



## Original Research Article

## Climate driven range divergence among host species affects range-wide patterns of parasitism

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## ARTICLE INFO

## Article history:

Received 13 March 2016

Received in revised form 4 October 2016

Accepted 4 October 2016

Available online 16 November 2016

## Keywords:

Boreal

Cervidae

Climate change

Evolution

Parasitism

Synergistic effects

## ABSTRACT

Species interactions like parasitism influence the outcome of climate-driven shifts in species ranges. For some host species, parasitism can only occur in that part of its range that overlaps with a second host species. Thus, predicting future parasitism may depend on how the ranges of the two hosts change in relation to each other. In this study, we tested whether the climate driven species range shift of *Odocoileus virginianus* (white-tailed deer) accounts for predicted changes in parasitism of two other species from the family Cervidae, *Alces alces* (moose) and *Rangifer tarandus* (caribou), in North America. We used MaxEnt models to predict the recent (2000) and future (2050) ranges (probabilities of occurrence) of the cervids and a parasite *Parelaphostrongylus tenuis* (brainworm) taking into account range shifts of the parasite's intermediate gastropod hosts. Our models predicted that range overlap between *A. alces/R. tarandus* and *P. tenuis* will decrease between 2000 and 2050, an outcome that reflects decreased overlap between *A. alces/R. tarandus* and *O. virginianus* and not the parasites, themselves. Geographically, our models predicted increasing potential occurrence of *P. tenuis* where *A. alces/R. tarandus* are likely to decline, but minimal spatial overlap where *A. alces/R. tarandus* are likely to increase. Thus, parasitism may exacerbate climate-mediated southern contraction of *A. alces* and *R. tarandus* ranges but will have limited influence on northward range expansion. Our results suggest that the spatial dynamics of one host species may be the driving force behind future rates of parasitism for another host species.

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## 1. Introduction

As species ranges shift to higher latitudes in response to changing climate, individuals may come into contact with new species that differ in abundance or ecological function compared to those occurring in their historical range. As a result, new interactions may arise that feedback to affect the degree to which range shifts directly tracks changing climate (Van der Putten et al., 2010). It follows that novel interactions may lead to changes in the structure and function of contemporary communities (Hobbs et al., 2006), as well as to the evolutionary processes by which they are governed (Hoffmann and

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<http://dx.doi.org/10.1016/j.gecco.2016.10.001>

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Sgrò, 2011; Chaianunporn and Hovestadt, 2015). However, there is substantial uncertainty related to how and where novel interactions will arise and the extent of adaptive change that will underlie such novelty (Williams and Jackson, 2007; Northfield and Ives, 2013). Therefore, effective forecasting of climate change responses depends upon whether range shifts are associated with the strengthening or weakening of existing interactions, corresponding changes in novel interactions, and how such interactions may vary through space and time. Depending on the characteristics of the species involved, multiple outcomes are possible ranging from interactions facilitating, constraining, or overriding climate's influence on range expansion (Schweiger et al., 2012).

Interactions with parasites may be particularly important in aggravating extinction risk, especially for species that are already in peril (e.g. Pounds et al., 2006). With climate change, parasitism may become more widespread if parasite ranges expand further into the ranges of their hosts (Kutz et al., 2013). Predicting such an outcome is made more challenging when parasite transmission to one host depends on the presence of another host of the same trophic level. For example, parasites may be able to infect but not complete their life cycle in a particular host. Thus, transmission to these “dead-end” hosts can only occur where they co-occur with “reservoir” hosts, species in which the parasite can reproduce. Therefore, in the context of climate-driven shifts of species distributions, the effect of climate change on the reservoir host may have an important role to play in mediating how climate change affects the interaction between a dead-end host and a parasite.

In this study, we evaluate the potential for reservoir host dynamics to drive range changes for *Alces alces* L. 1758 (moose) and *Rangifer tarandus* L. 1758 (caribou) via parasitism from *Parelaphostrongylus tenuis* (Dougherty 1945) (brainworm). Many *A. alces* and *R. tarandus* populations are declining in abundance in accord with global patterns of climate change (Vors and Boyce, 2009; Lenarz et al., 2010). Parasitism-driven mortality, especially from *P. tenuis* is considered another key factor contributing to *A. alces* population decline (Murray et al., 2006; Lankester, 2010). To date, parasites have not been broadly implicated in the declines of natural *R. tarandus* populations, but they are expected to play an increasingly important role (Albon et al., 2002; Vors and Boyce, 2009).

Although *P. tenuis* infect and kill *R. tarandus* and *A. alces*, they are transmitted primarily through *Odocoileus virginianus* Zimmermann 1780 (white-tailed deer); transmission does not occur where *R. tarandus* or *A. alces* do not overlap with *O. virginianus* (Lankester, 2001). Thus, *O. virginianus* expansion into northern ecosystems is hypothesized to be a catalyst of future declines for both *A. alces* (Lankester, 2010) and *R. tarandus* (Vors and Boyce, 2009).

To test the hypothesis, we present a general framework that quantifies the influence of a reservoir host on parasitism of a dead-end host (Fig. 1). If the reservoir host is important, then we would predict that climate change leads to increased (or decreased) range overlap between parasites and dead-end hosts primarily because of changes in range overlap between dead-end hosts and reservoir hosts (Fig. 1, future scenario (i)). Alternatively, if reservoir host dynamics are not as important, then we would predict that climate change leads to increased (or decreased) range overlap between parasites and dead-end hosts, even if range overlap between the dead-end and reservoir hosts does not change or changes very little (Fig. 1, future scenario (ii)). Here we take “range” to mean the locations (e.g. grid cells) a species occurs across space and the probability a species occurs at those locations based on the environment (what is sometimes termed the “niche”; Warren et al., 2008).

Regardless of mechanism, changes in range overlap between parasites and dead-end hosts will influence how dead-end host ranges track climate change. Parasitism may hasten the effects of climate change. If so, we would find that locations of increased habitat suitability for parasites coincide with locations of decreased habitat suitability for dead-end hosts. In other words, the synergy between climate change and parasitism accelerates dead-end host range contraction: locations of declining suitability because of climate change are even more unsuitable once parasite occurrences are included. Alternatively, parasitism may impede the effects of climate change. If so, we would find that locations of increased habitat suitability for parasites coincide with locations of increased habitat suitability for dead-end hosts. In other words the synergy between climate change and parasitism slows dead-end host range expansion: locations of increasing suitability because of climate change are made less suitable once parasite occurrences are included. Of course, parasitism might occur throughout the species range, thereby muting range expansion and exacerbating range contraction.

If the synergistic effects of climate change and parasitism on dead-end host species ranges are constrained by the reservoir host, then being freed from that constraint could lead to a different picture of dead-end host range expansion and contraction. In particular, if parasites could evolve to complete their life cycle in the current dead-end host, then the part of the dead-end host's range susceptible to parasitism would be larger than previously anticipated (see Fig. 1, future scenario (iii)). Host switching and other evolutionary changes in parasitism have been suggested to have occurred during past climatic changes (Brooks and Hoberg, 2007; Hoberg and Brooks, 2008, 2015) though whether host-switching happens in any given system is highly speculative. Nonetheless, creating spatially explicit predictions of where such evolution might occur is a necessary first step toward eventually testing the hypothesis that climate change can affect parasite life-cycles (Kutz et al., 2013, 2014) and feedback to affect hosts at large scales. Hence, in our study, we first determine where in the ranges of *A. alces* and *R. tarandus* parasitism is most likely to occur and then recalculate the same but include parts of the range that do not overlap with *O. virginianus*. We call these areas potential evolutionary hotspots.

## 2. Materials and methods

### 2.1. The parasite

*Parelaphostrongylus tenuis* develops into adults and successfully breeds inside a cervid definitive host (*sensu* Haydon et al., 2002). In North America, *Odocoileus virginianus* (white-tailed deer) is the primary definitive host. Upon

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