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Original Research Article

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

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## 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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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).

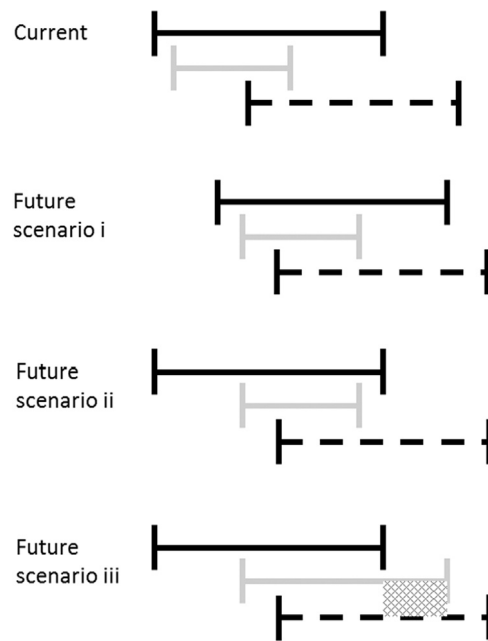
Regardless of mechanism, changes in range overlap between parasites and dead-end hosts will influence how dead-end host ranges track climate change. Parasitism may hasten the effects of climate change. If so, we would find that locations of increased habitat suitability for parasites coincide with locations 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



**Fig. 1.** We contrast two ways in which a reservoir host (solid black) transmits a parasite (grey) to a dead-end host (dashed black). In one possible future scenario (i), range overlap of the parasite and dead-end host increases primarily because range overlap of the reservoir and dead-end host increases. In a second possible future scenario (ii), parasitism increases because the parasite range moves further into the range of the dead-end host irrespective of the reservoir host's range shift (or lack thereof). A third scenario (future scenario (iii)) illustrates the outcome of host-switching, whereby the parasite evolves to complete its life cycle in the dead-end host and, thus, expand its range (cross-hatching).

excretion from *O. virginianus*, the parasite develops further inside a gastropod host (Anderson, 1963). It is then transmitted to grazing cervids where it develops into adults. However, *A. alces* and *R. tarandus* are considered dead-end hosts because *P. tenuis* never successfully reproduces inside them. In contrast, because the parasite can reproduce in *O. virginianus*, that cervid is called a reservoir host.

Due to this complexity, a full life-cycle accounting of parasitism must include the intermediate hosts. While more than 20 gastropod species are described as intermediate hosts of the larval stage of *P. tenuis*, we focus on those considered as the main reservoirs of infection: the meadow slug *Deroceras laeve* (Müller 1774) and snails *Discus cronkhitei* (Newcomb 1865) and *Zonitoides arboreus* (Say 1817).

## 2.2. Modelling species ranges

Following Pickles et al. (2013), we created separate species distribution models for the parasite (i.e. based on all recorded occurrences, regardless of host), its gastropod hosts, and its cervid hosts. We used the program MaxEnt (Phillips and Dudík, 2008) to model probabilities of occurrence across each species' range. We chose MaxEnt because it outperforms other presence-only modelling techniques (Elith et al., 2006), and recent evidence demonstrates that range limits derived from MaxEnt models correspond well with constraints on population growth and persistence (Lee-Yaw et al., 2016; Searcy and Shaffer, 2016). We obtained presence data for each species using a literature search of the Global Mammal Parasite Database ([www.mammalparasites.org](http://www.mammalparasites.org); Nunn and Alitzer, 2005), Manisnet ([www.manisnet.org](http://www.manisnet.org)), the Global Biodiversity Information Facility (GBIF; [www.gbif.org](http://www.gbif.org)), and a Google Scholar search. For the parasite data, in particular, records come from observations inside mammalian hosts or their faeces. We assume these occurrence records come from within the parasite's range.

Where latitude and longitude information was lacking, we georeferenced locality based on the description of the collection site using Google Earth 5.0 and Biogeomancer (Guralnick et al., 2006). We transferred all occurrence data onto a 10 km × 10 km grid cell map of the United States and Canada, using ArcGIS 10.0 (ESRI, 2010), which matches the resolution of the environmental data (see below). Hence, georeferenced data could be imprecise up to a circle with a radius of 5.6 km. We used the 10 km × 10 km grid cell resolution for all species distribution projections. We used Albers equal area projection for all mapping and projected all coordinates accordingly. We only ever had one occurrence record per grid cell (see Fig. S1 & Fig. S2 for occurrence records used in the modelling).

Presence records obtained from GBIF or similar sources can be biased given collection patterns favouring sites closer to human settlements (Phillips et al., 2006). We addressed the potential for disparity in sampling intensity among different regions using two methods: a bias grid that down-weighs the importance of presence records from areas with more intense

sampling (i.e., areas with a high density of presence records, [Elith et al., 2010](#)) and spatial thinning that removes records if they are within a certain distance of another record ([Boria et al., 2014](#); [Aiello-Lammens et al., 2015](#)). Importantly, there is little evidence that any one method is inherently better at removing bias than another ([Fourcade et al., 2014](#)).

For the bias grid, we weighed each grid cell by the number of sampling localities within a neighbourhood, which we defined as a Gaussian kernel with a standard deviation of 200 km. The value of each grid cell was a sum of the inverse of distance of the samples in the neighbourhood. The weighted grid became the bias file that was entered into the MaxEnt analysis. To reduce the influence of highly sampled outlier cells, we reclassified the grid into 20 classes ([Pickles et al., 2013](#)). By applying a bias grid, we assumed that any spatial clumping of our presence data was not based on patterns of occurrence or habitat selection for either species. We feel that this is an accurate judgement given the form of opportunistic sampling (i.e. museum collections, etc.) that occurred to map these localities.

To thin cervid data sets, we used the package `spThin` ([Aiello-Lammens et al., 2015](#)) in R. We specified a nearest neighbour distance of 100 km and ran the `spThin` algorithm five times. Each time, the algorithm removes, one-by-one, the locality with the most number of nearest neighbours. Ties will result in different final grids. The thinned grid used in further analysis is the final grid with the most occurrence records ([Aiello-Lammens et al., 2015](#)).

We did not find any major differences between the modelled cervid distributions using a bias grid or thinned data (Fig. S3). Hence, we use the distributions modelled with the bias grid for all further analyses.

To predict species occurrences, we used the set of 19 bioclimatic variables from WorldClim, which provides climatic data averaged over the years 1950–2000 ([Hijmans et al., 2005](#)). We removed highly correlated environmental variables by conducting pairwise Pearson correlation tests on the entire set, noting which pairs were correlated at  $r > 0.85$ , and keeping the most biologically relevant of the correlated pair (*sensu* [Milanovich et al., 2010](#)). In addition to the bioclimatic data, we used soil drainage, compound topographical index (a measure of wetness), and pH from the Food and Agriculture Organisation's Harmonized World Soil Database (HWSD) ([www.fao.org/nr/land/soils/harmonized-world-soil-database/en](http://www.fao.org/nr/land/soils/harmonized-world-soil-database/en)) because they have been shown to influence *P. tenuis* transmission ([Lankester, 2001](#); [Pickles et al., 2013](#)). We also used land cover classes from the European Space Agency ([http://due.esrin.esa.int/page\\_globcover.php](http://due.esrin.esa.int/page_globcover.php)) and deciduous and coniferous forest layers ([DeFries et al., 2000](#)) because *O. virginianus* are known to be strongly associated with deciduous forest. We list all the environmental data we used in our models in Table S1 of the Supporting Information.

We built MaxEnt models for cervid, gastropod, and parasite species using background records sampled from within the species' range and a 500 km buffer; using such restricted backgrounds (i.e. excluding areas that have not been surveyed for the target species) can improve the performance of the initial model ([Elith et al., 2011](#)). We downloaded mammal species range data from NatureServe ([Patterson et al., 2007](#)). For the parasite and gastropods, we created species range maps by drawing a minimum convex polygon around all occurrence points. Although these maps had fairly large extents, there is still the possibility of projecting into an environmental space more extreme than what was used to train the models (i.e. the selection of training points consistently misses some environmental values). MaxEnt addresses this problem through clamping, where variables beyond the training range are treated as though they were at the limit of the training range. Comparing probabilities of occurrence maps with and without clamping demonstrates that clamping had minimal influence on our projections (Fig. S4).

For each species, we built models using several regularization multipliers (1–7), which can affect model fit around presence records ([Radosavljevic and Anderson, 2014](#)). We selected the model (i.e. regularization multiplier) to use for inference and analysis as the one with the highest adjusted Area Under the Curve (AUC) statistic ([Hijmans, 2012](#)). We calculated adjusted AUC using presence testing data and background data that are within a similar distance from the presence training data. This creates a conservative estimate of model performance, and helps prevent inflated AUCs merely due to the fact that test and training presence data are closer to each other in space than background data and training data ([Hijmans, 2012](#)). These adjusted AUC values are also more appropriate as a means to compare fit across species that have differing spatial bias in presence locations. In the adjusted AUC calculation, we applied a threshold value of 0.33, and selected three background samples for every testing data record from a random set of 10 000 background samples (see [Hijmans, 2012](#)). We performed a 10-fold cross-validation procedure (where we randomly split the data into training and test sets 10 different times) to create the MaxEnt models and calculate adjusted AUC statistics, which we present in Table S2.

To further assess model performance, we compared our AUC values against those generated from a null model. Following [Raes and Ter Steege \(2007\)](#), we selected points at random from within the species range, modelled them with our environmental variables, and calculated an AUC value. We repeated the procedure 10 times and averaged the AUC among the models; we found that our observed AUC values exceeded the null average (Table S2).

We modelled occurrence probabilities for 1950–2000 (hereafter called 2000) and 2050. For the latter, we used a climate grid averaged from three different general circulation models (GCMs): the Canadian Centre for Climate Modelling and Analysis model CGCM2, the Commonwealth Scientific and Industrial Research Organization model CSIRO mk 2, and the Hadley Centre for Climate Prediction and Research's model HadCM3. For each GCM we used the upper carbon emission scenario to provide the most realistic, current projection of global carbon emissions (see [Raupach et al., 2007](#); [Beaumont et al., 2008](#)). While the climate models have recently been updated, the change has not been so substantial as to alter projections of species distributions ([Wright et al., 2016](#)). We downloaded climate grids in WorldClim format for each GCM from the Climate Change, Agriculture and Food Security (CCAFS) website ([www.ccafs-climate.org](http://www.ccafs-climate.org)). In each future projection, we included the environmental variables mentioned above, as well as soil and tree cover data as static variables to improve predictive accuracy ([Stanton et al., 2011](#)).

For the resulting species distribution models for all species, we considered any grid cell with a predicted occurrence probability below the fixed cumulative value of 10 logistic threshold supplied by MaxEnt as being unoccupied (Milanovich et al., 2010). The cumulative output of MaxEnt is best interpreted as predicted omission rate (where omission rate is the proportion of presence records that would be classified as being located in unsuitable habitat based on a binary map). Thus, using a fixed cumulative value of 10 to use as a threshold for our maps should correspond to a predicted omission rate of 10%.

### 2.3. Modelling parasite occurrences

To account for the full parasite transmission cycle in current and future climates, we generated separate probability of occurrence maps for the parasite's free-living larval stage, intermediate hosts, and final hosts. Because multiple species could act as intermediate hosts (i.e. the gastropods *Deroceras laeve*, *Discus cronkhitei*, and *Zonitoides arboreus*), we defined intermediate host occurrence probability as the maximum of the three species' occurrence probabilities in each grid cell (Pickles et al., 2013). Because *P. tenuis* needs *O. virginianus* to complete its life cycle, we equated the final host's probability of occurrence to that of *O. virginianus*.

At this point, we had occurrence probabilities from each stage in the transmission cycle for each grid cell. We defined the overall risk of transmission in each grid cell as the minimum of all the occurrence probabilities (Pickles et al., 2013). Hence, the parasite could only occur in cells that were also climatically suitable for their intermediate and reservoir host. (If any host is absent, its occurrence probability is zero and this becomes the occurrence probability of the parasite). We defined this output as the *restricted* parasite occurrence map. However, one goal of our study is to quantify the contribution of the reservoir host to changes in range overlap between the parasite and the dead-end host. Hence, we calculated the parasite's *unrestricted* occurrence map, i.e. what it would be if it could complete its life cycle in any of the cervid hosts. We calculated the unrestricted map by equating the final host's probability of occurrence to the maximum of *O. virginianus*, *A. alces*, or *R. tarandus* in each grid cell. We created parasite occurrence maps (restricted and unrestricted) for 2000 and 2050, the difference of which we used to calculate temporal change in range overlap (see below).

### 2.4. Analysing range overlap

We calculated range-wide risk of transmission by quantifying overlap between the dead-end host and the parasite occurrence probability maps in 2000 and 2050. We quantified overlap with Schoener's *D* (Schoener, 1968; Warren et al., 2008) using the *dismo* package (Hijmans et al., 2015) in R 3.3.0 (R Development Core Team, 2016). Schoener's *D* ranges from 0 (no overlap among range models) to 1 (models identical). We quantified the temporal shift in overlap ( $\Delta D$ ) by subtracting the Schoener's *D* value in each grid cell in the 2000 map from the 2050 map, expressing the difference as a percent of the 2000 map. We ran the range overlap analysis using both the unrestricted and restricted parasite ranges. We compared the change in range overlap values between the two range types.

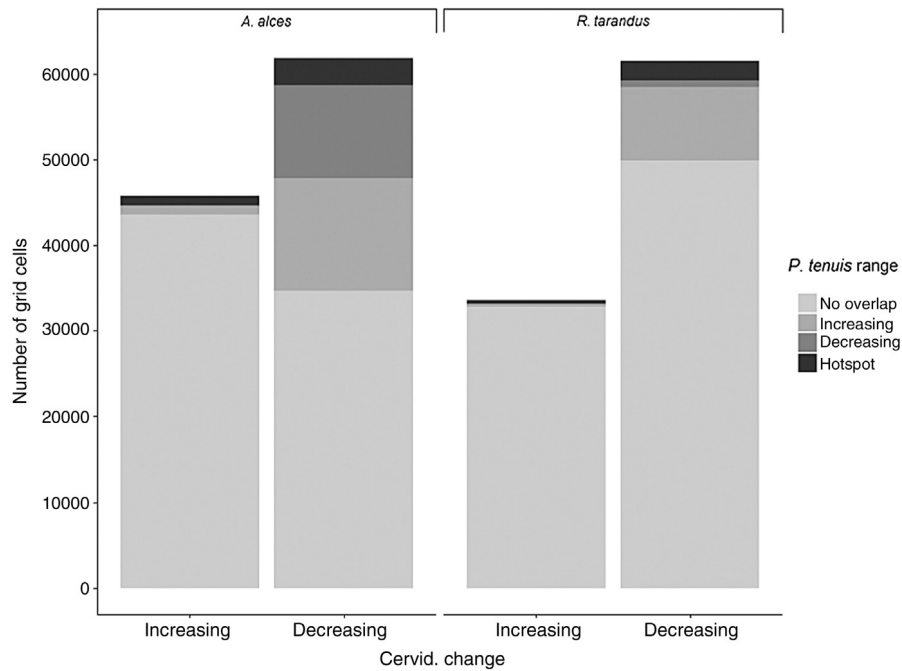
We assessed the importance of the reservoir host by applying the following rationale. We quantified temporal change in range overlap between the dead-end host and parasite in a hypothetical context as if the parasite did not depend on the reservoir host for transmission (unrestricted range overlap). We compared this value to the temporal change in range overlap assuming that the parasite's range is restricted to locations also occupied by the reservoir host (restricted range overlap). If host–host range dynamics drive changes in parasitism, then we predict a difference in the unrestricted and restricted values. For example, if range overlap between the dead-end and reservoir host increases with climate change, then we would expect temporal change in restricted range overlap to be greater than temporal change in unrestricted range overlap. If host–parasite range dynamics drive changes in parasitism, then we predict little difference in unrestricted and restricted values, i.e. parasitism intensifies or diminishes even if the range overlap between the two hosts remains relatively static.

We assessed whether the shifting *A. alces* and *R. tarandus* species ranges were more or less likely to encounter parasitism by a three stage process. First, we subtracted each grid cell's occurrence probability in 2000 from 2050. Second, we stratified the outcome into grid cells with an increase in the probability of occurrence between 2000 and 2050 and grid cells with a decrease in the probability of occurrence between 2000 and 2050. Third, for each of these categories, we calculated the proportion of the cells in which our models predicted an increased parasite occurrence between 2000 and 2050. As above, we conducted the analysis considering the restricted and unrestricted parasite ranges. We suggest that cells within the unrestricted range but outside the restricted range could be where parasites could evolve to complete their life cycle within the dead-end hosts assuming that (1) infected *A. alces* and *R. tarandus* disperse to areas not occupied *O. virginianus*, and (2) those environments select for novel traits. We call these locations potential evolutionary hotspots.

## 3. Results

### 3.1. Temporal change in range overlap

We found that potential climate-driven changes to parasitism of dead-end hosts are influenced primarily by changes in range overlap between the dead-end hosts (*A. alces* and *R. tarandus*) and the reservoir host (*O. virginianus*), rather



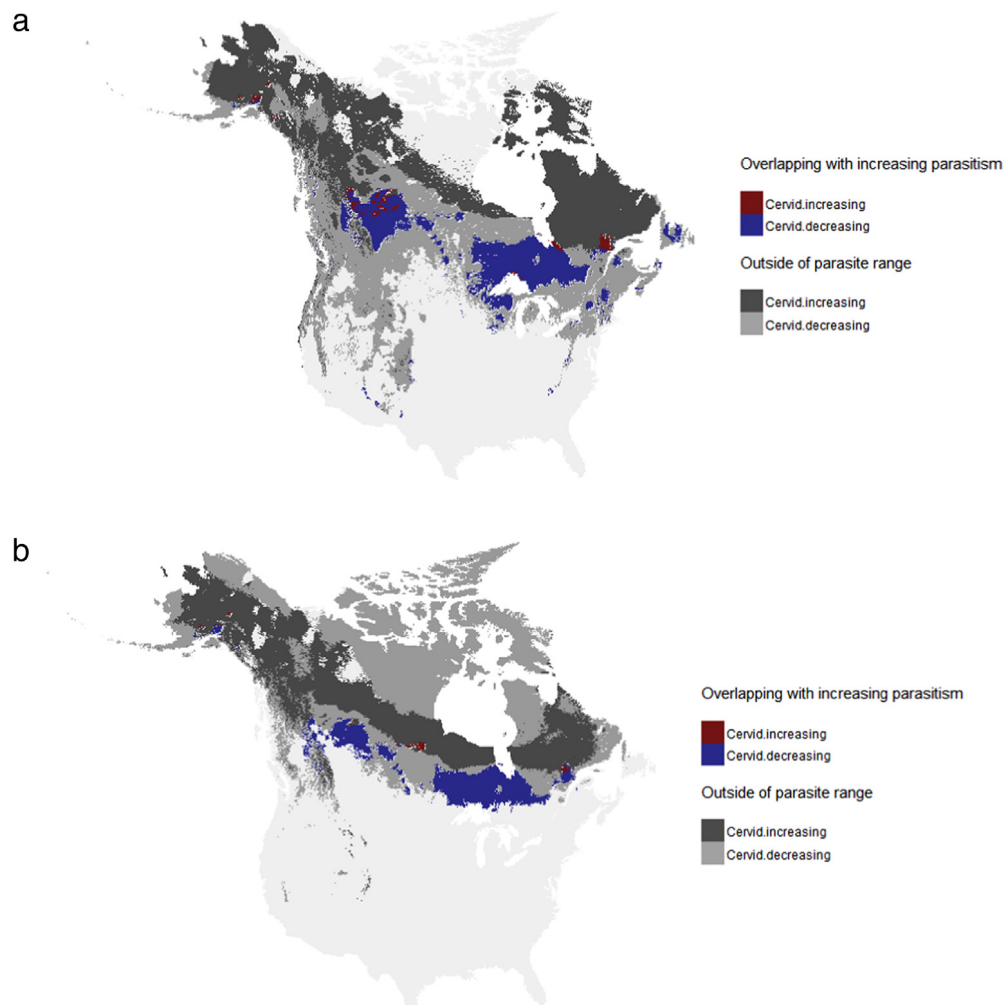
**Fig. 2.** The proportion of the range of *Alces alces* and *Rangifer tarandus* (defined by the number of grid cells) that do not overlap with *Parelaphostrongylus tenuis*, overlap with cells of increasing probability of *P. tenuis* occurrence, and overlap with cells of decreasing probability of *P. tenuis* occurrence. Hotspots are cells within the cervid range that overlap with increasing probability of *P. tenuis* occurrence but do not overlap with *Odocoileus virginianus*.

than between the dead-end hosts and their parasite (*P. tenuis*). Our models predicted a decrease in range overlap from year 2000 to 2050 between *A. alces* and *O. virginianus* ( $\Delta D = -0.043$  [−12.89%]) and *R. tarandus* and *O. virginianus* ( $\Delta D = -0.035$  [−46.15%]). Likewise, our models predicted a decrease in range overlap between *O. virginianus* and *P. tenuis* ( $\Delta D = -0.062$  [−10.20%]), *A. alces* and *P. tenuis* ( $\Delta D = -0.011$  [−5.78%]) and *R. tarandus* and *P. tenuis* ( $\Delta D = -0.014$  [−38.67%]). However, if we relaxed the assumption that *P. tenuis* needs *O. virginianus* to be transmitted, then our models predicted an increase in range overlap for *A. alces* and the parasite ( $\Delta D = 0.028$  [12.53%]). Our models still predicted a decrease in range overlap between *R. tarandus* and *P. tenuis* ( $\Delta D = -0.0097$  [21.75%]), though less than if we restricted the parasite's range to where it co-occurs with *O. virginianus*. Thus, the reduced range overlap between the dead-end hosts and parasite reflects the reduced range overlap between the dead-end hosts and *O. virginianus*.

Our models predicted that the majority of the dead-end hosts' ranges would not spatially overlap with the range of *P. tenuis* (13.86% overlap with *A. alces*; 10.37% overlap with *R. tarandus* [Fig. 2]). However, where they did overlap, we predicted that more of the cervids' contracting (cells of decreasing probability of occurrence) than expanding range (cells of increasing probability of occurrence) would coincide with *P. tenuis* expansion (cells of increasing probability of occurrence). For *A. alces*, our models predicted that 22.65% of its contracting range would overlap with cells of increasing probability of occurrence of *P. tenuis* (Fig. 2). Meanwhile, our models predicted that 2.29% of its expanding range would overlap with cells of increasing probability of occurrence of *P. tenuis* (Fig. 2). For *R. tarandus*, our models predicted that 14.41% of its contracting range would overlap with cells of increasing probability of occurrence of *P. tenuis* (Fig. 2). Meanwhile, our models predicted that 0.82% of its expanding range would overlap with cells of increasing probability of occurrence of *P. tenuis* (Fig. 2). Geographically, our models suggest that overall, parasitism for both cervid species will occur primarily along their southern range boundaries in Canada's Hudson Plains and Boreal forest, and, for *A. alces*, additionally in its most southern locations in the US: the Appalachians, mountainous areas of the US southwest, and the Pacific coast (Fig. 3).

### 3.2. Identifying possible evolutionary hotspots

If evolution takes place such that *P. tenuis* is able to complete its life cycle in what are currently dead-end hosts then our models predict the phenomenon to be most pronounced in central Quebec (Fig. 4). Furthermore, the negative effects of evolution (i.e. increased parasitism) would affect *A. alces* both where it is expected to increase (2.62% of its expanding range that does not overlap with *O. virginianus* [Fig. 2]) and decrease (5.21% of its contracting range that does not overlap with *O. virginianus*). Likewise, parasitism arising through evolution would affect *R. tarandus* where it is expected to increase (1.59% of its expanding range that does not overlap with *O. virginianus*) and decrease (3.80% of its contracting range that does not overlap with *O. virginianus*).



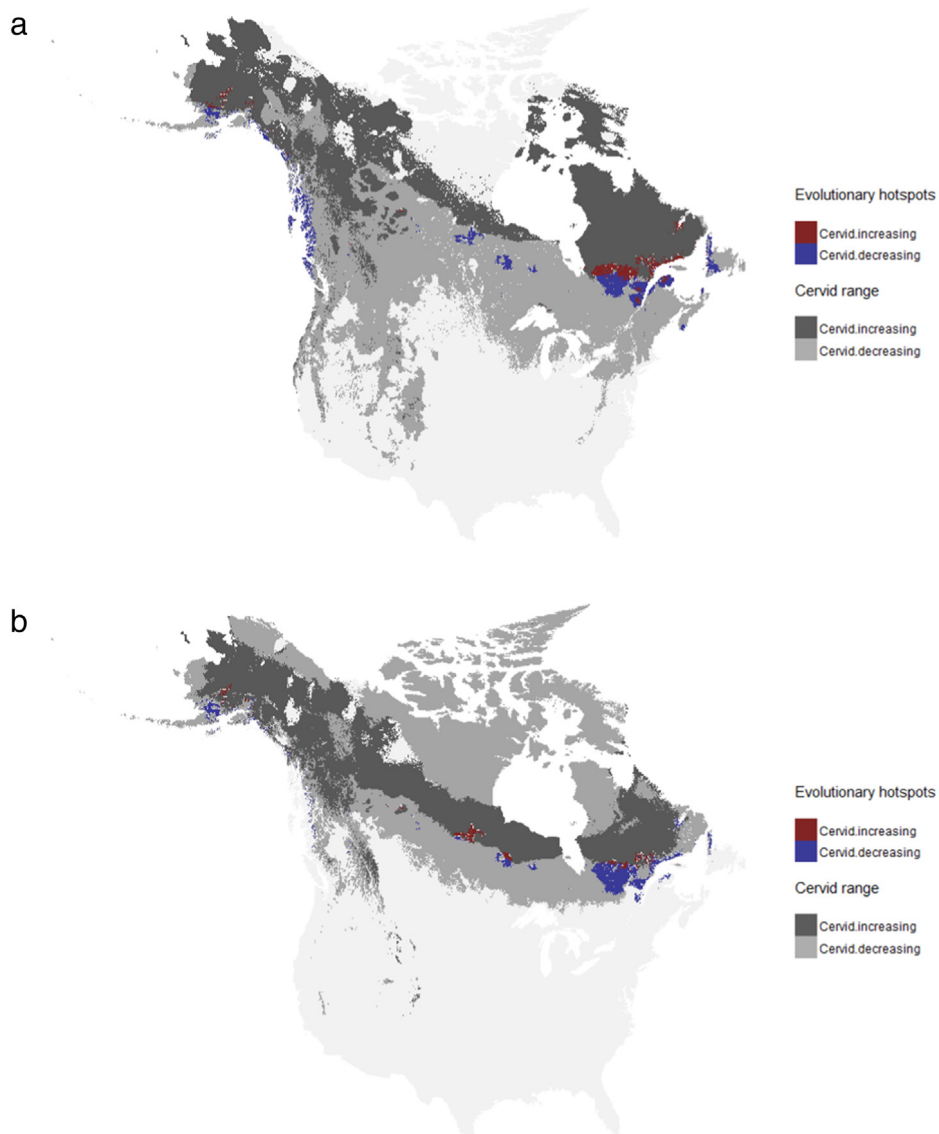
**Fig. 3.** Range expansion, contraction, and parasitism for *A. alces* (a) and *R. tarandus* (b). Range expansion refers to those grid cells where our species distribution models predicted an increase in the probability of cervid occurrence between 2000 and 2050. Range contraction refers to those grid cells where our species distribution models predicted a decrease in the probability of cervid occurrence between 2000 and 2050. Parasitism refers to those grid cells where models predicted an increase in the probability of occurrence for the parasite *P. tenuis* between 2000 and 2050 and co-occurrence with *O. virginianus*.

## 4. Discussion

### 4.1. Future parasitism to one host may depend on another host

One of the greatest challenges in forecasting the effects of climate change on species ranges concerns predicting future species interactions (Van der Putten et al., 2010). This challenge is made more difficult when complex ecological communities comprise multiple species interactions spanning several trophic levels (Gilman et al., 2010), as is the case when one host mediates the interaction between another host and a common parasite. Predicting the eventual outcome of parasitism depends on how all actors (including intermediate hosts (Pickles et al., 2013)) respond to climate change. We proposed two ways in which independent climate change driven range shifts may combine to characterize parasitism from the perspective of a dead-end host: (1) range overlap between the host and parasite may change after accounting for the range shift of the main reservoir of the parasite or (2) range overlap between the host and parasite may remain invariant after accounting for the range shift of the reservoir host.

In our *A. alces* and *R. tarandus* study system, where transmission of *P. tenuis* requires *O. virginianus* to complete its life cycle, we found support for the first scenario. We found that if we ignored *O. virginianus*, our models predicted range convergence between the dead-end hosts and *P. tenuis*, whereas after restricting the *P. tenuis* range to where it co-occurs with *O. virginianus*, our models revealed divergence or very little convergence between the ranges of the dead-end hosts and *P. tenuis*. This pattern mimics the predicted range divergence between dead-end hosts and *O. virginianus*. Thus, the pattern



**Fig. 4.** Potential evolutionary hotspots across the ranges of *A. alces* (a) and *R. tarandus* (b). Range expansion refers to those grid cells where our species distribution models predicted an increase in the probability of cervid occurrence between 2000 and 2050. Range contraction refers to those grid cells where our species distribution models predicted a decrease in the probability of cervid occurrence between 2000 and 2050. Evolutionary hotspots are those grid cells where models predicted an increase in the probability of occurrence for the parasite *P. tenuis* between 2000 and 2050 but fall outside the grid cells occupied by *O. virginianus*.

of *O. virginianus* range shift relative to that of dead-end hosts accounts for much of the modelled variability in parasitism through time.

Our forecasts of range divergence between *P. tenuis* and *A. alces*/*R. tarandus* implies that parasitism might increase where those hosts are most at risk from climate change, specifically along their southern range edges. Thus, the likely deleterious effects of *P. tenuis* will aggravate patterns of range contraction already occurring for both *A. alces* and *R. tarandus* (Vors and Boyce, 2009; Lenarz et al., 2010).

We also predicted extensive parasitism in northwestern Alberta and the Rockies (see also Pickles et al., 2013), a region currently beyond the western limits of *P. tenuis*' distribution. The finding underscores the fact that our models highlight future suitable habitat but not whether dispersal will lead to actual occupancy. Importantly, however, our models suggest the presence of a potential dispersal corridor: we predicted patches of suitable habitat connecting the enzootic region of southern Manitoba to northwestern Alberta through the otherwise unsuitable prairies. We suggest that the region should be monitored closely for *P. tenuis* infection in local *O. virginianus* populations.

Our knowledge of *A. alces* ecology allows us to paint a picture of how climate change and parasitism might act synergistically to affect range dynamics. For *A. alces*, warming temperatures may lead to heat stress and reduced body



condition, which can contribute to immunosuppression and thereby aggravate susceptibility to parasite infection (Murray et al., 2006). In turn, this may affect *A. alces* productivity or survival even via sublethal effects, and thereby contribute to population decline. It follows that parasite-driven fitness declines may reduce *A. alces* populations below their carrying capacity, thereby shifting the factors that drive population growth from those that are primarily density-dependent to those that are density-independent. Such changes may render *A. alces* populations increasingly susceptible to future environmental changes and demographic stochasticity (Ebert et al., 2000; Murray et al., 2006).

#### 4.2. The influence of climate change on the evolution of parasitism

We suggest that one potential outcome of host–host range divergence is increased selection for parasites to complete their life cycles in what are currently dead-end hosts. Theory predicts that hotspots in host–parasite evolution will arise in areas where environments are changing rapidly, such as those undergoing climate change (Hoberg and Brooks, 2008, 2015; Northfield and Ives, 2013). Through time, a mosaic of evolutionary hotspots and coldspots will arise that reflects localized environmental conditions affecting evolutionary interactions (Thompson, 1999). Whether such evolution takes place is highly speculative: we cannot identify the particular genetic changes that would permit transmission to *A. alces* or *R. tarandus*—nor do we suggest that such a transmission necessarily follows climate change. That being said, our results establish a spatially-explicit framework for assessing potential changes in the functional genomics of cervids and their parasites across the North American landscape, especially in the context of potential evolutionary responses. In particular, our models predicted that portions of the *A. alces* and *R. tarandus* species ranges would be climatically suitable for the parasites, but not for *O. virginianus*. Thus, we might expect the parasites to be carried out of the *O. virginianus*'s range by dispersing *A. alces* and *R. tarandus* (*sensu* Kutz et al., 2014) but persist only if they are able to develop into adults and produce eggs in those hosts. Overall, the new habitat would expand the parasite's range, which otherwise is predicted to contract because of declining overlap with *O. virginianus*.

It is possible that new transmission pathways could develop even without genetic changes (Gienapp et al., 2008). Climate-driven increases in range overlap may provide the novel conditions that promote the expression of pre-existing traits, such as those that allow persistence in multiple hosts (Janz, 2011). While we emphasize that a change in parasite life-cycles is speculative, our goal here has been to demonstrate that host-switching may also be a mechanism by which interactions feedback to affect the way species ranges track rapid climate change. For example, when we ignored host-switching, our models predicted that the northward expansion of boreal *A. alces* and *R. tarandus* populations would be largely unaffected by parasitism from *P. tenuis*. However, when we included potential for evolution, then we predicted that the northward expansion of the cervids could be under constraint from parasitism. Thus, we advocate that evolution or, at least, change in phenotypic expression, must be included in community frameworks that assess the effect of climate change on species interactions (e.g. Gilman et al., 2010).

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#### Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2016.10.001>.

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