Impacts of predator-mediated interactions along a climatic gradient on the population dynamics of an alpine bird

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Abstract

According to classic theory, species interactions are less important than climatic variation for species' population dynamics and distributions in climatically harsh regions compared with more climatically benign regions. In boreal ecosystems, the cyclic dynamics of rodents strongly affect many other species, including ground-nesting birds. According to the 'alternative prey hypothesis' (APH), high rodent densities positively affect the abundance of ground-nesting birds due to predator-mediated interactions. We analysed a spatiotemporal dataset of willow ptarmigan (*Lagopus lagopus*) and rodents to examine how the role of predator-mediated interactions changes along a climatic harshness gradient in comparison with climatic variation. Ptarmigan and rodent data were collected during a national program of line-transect sampling across Norway during 2007–2017. We build a hierarchical Bayesian model to estimate the sensitivity of ptarmigan populations to interannual variation in climate and rodent occurrence. Ptarmigan abundance was positively linked with rodent occurrence, consistent with the APH. Moreover, we found that both rodent dynamics and temporal climatic variation had stronger effects on ptarmigan in colder regions. Our study highlights how species interactions play an important role for the population dynamics of species at higher latitudes and suggest that they become even more important in the most climatically harsh regions.

Keywords: Boreal ecosystems; Climate change; Indirect interactions; Population cycles; Predator-prey interactions

Introduction

Climatic variability and species interactions both influence spatial and temporal patterns in species' population abundances [1-3]. An old hypothesis, originally proposed by Charles Darwin, posits that climate is the main determinant of species' range limits in harsh abiotic regions whereas species interactions are a more important determinant under benign abiotic conditions [4]. Range limits are determined by local population growth rates; hence, this hypothesis also implies that population growth rates are more sensitive to climate variability in climatically harsh regions but more sensitive to species interactions in more climatically benign regions. Previous studies have examined changes in demographic and population processes along elevational and latitudinal climatic gradients [5-8], but few studies have been able to tease apart the sensitivity of population growth to climate and species interactions over large spatial and temporal scales.

In the cold environments of alpine and boreal areas, vertebrate species co-exist in relatively simple food-webs but biotic interactions still exert strong impacts on species' population dynamics [9]. One particular characteristic of northern alpine and boreal ecosystems is the rodent population dynamics, which are characterized by large inter-annual cyclic fluctuations in abundance, with peak years coming at regular intervals [10, 11]. Although still contested, predator-prey interactions are generally regarded as the most parsimonious explanation underlying the cyclic dynamics of rodents in these ecosystems [12, 13]. Deep snow during the boreal winters also affords the rodents protection from predators while the rodents continue to breed, increasing the instability of the rodent dynamics [14].

The population dynamics of many species of alpine and boreal communities, including the avian community, often covary with the rodent cycle phase [14, 15]. One hypothesised reason for this covariation is that ground-nesting birds (such as ptarmigan and grouse, Tetraonidae) and rodents share a similar set of generalist predators, including the red fox (*Vulpes Vulpes*) and corvids [16, 17]. Based on this observed correlation, Hagen [18] proposed the 'alternative-prey hypothesis' (APH), stating that ground-nesting birds are less vulnerable to predation in peak rodent years because generalist predators switch to feeding on rodents. By contrast, birds suffer greater predation in rodent decline/crash years when there are fewer prey options available to hunting predators. Other indirect interactions based on shared predators, such as apparent competition, typically lead to negative associations among alternative prey [19, 20]. However, here, predator-mediated interactions between rodents and ground-nesting birds are hypothesized to lead to a positive association, such that ground-nesting birds are more abundant in peak rodent years. Indirect effects

of rodent population dynamics have been reported in a range of ecosystems, even beyond the boreal, and for a range of alternative prey species [14, 21-23].

Previous studies have found at least partial support for the main predictions of the APH [14, 24]; however, the APH also makes secondary predictions about how the importance of these predator-mediated interactions should change along ecological gradients. In particular, Angelstam [15] predicted that the interactions should be stronger in regions with fewer prey resources because the predators become functionally more specialist, causing tighter linkages between predators and prey. By contrast, in regions where predators have access to a more diverse array of prey species, fluctuations in rodent populations should have weaker effect on the dynamics of predator populations. Indeed, the amplitude of the rodent population cycle is usually lower at lower latitudes, probably due to a stabilising effect of more generalist predators [25-27]. Based on these arguments, ground-nesting birds might be less affected by the rodent cycle in less climatically harsh areas, where there is a more diverse set of prey resources and weaker linkage between rodents and predators.

Montane birds in Scandinavia are reported to be declining in abundance over the last decades [28], but currently the main causes for this decline is not well understood. Willow ptarmigan (*Lagopus lagopus*) is a resident montane species for which long-term declines are a concern [29]. Previous studies on willow ptarmigan population dynamics have shown that they typically fluctuate in synchrony with the small rodent dynamics [14, 30]. In addition, recruitment rates seems to be affected by weather conditions [30]. Thus, the ptarmigan is a good model species for testing alternative hypotheses about the relative importance of climate forcing and species interactions on species' population dynamics in boreal habitats. In this study, we compared the sensitivity of willow ptarmigan population dynamics to both variability in climate and rodents using a multi-year (2007–2017) dataset covering a large geographic gradient across Norway. While the time-series is not especially long, we taken advantage of it being replicated across 725 line-transects. We assumed no direct effect of rodents on ptarmigan, but expected their population dynamics to be linked due to prey-switching of predators as predicted by the APH. Therefore, we used the statistical relationship between rodent abundance and ptarmigan population dynamics as a signal of predator-mediated interactions (Fig. 1). We examined how both inter-annual climatic variability and predator-mediated interactions with rodents change along a climatic harshness gradient, and tested the predictions that emerge based on the classic hypothesis about the relative importance of climate vs species interactions, and the alternative prey hypothesis. We made the following predictions (Fig. 1):

1) Under the classic hypothesis, we predicted that predator-mediated interactions, and hence rodent population dynamics, would more strongly affect ptarmigan in warmer regions. By

contrast, under the APH, we predicted that predator-mediated interactions, and hence rodent population dynamics, would more strongly affect ptarmigan in colder regions, where there are fewer prey sources for predators and greater linkage between predators and prey populations.

2) Under both hypotheses, we predicted that population growth would be more sensitive to inter-annual climatic variability in colder regions. Individuals in climatically harsh environments are more likely to be closer to edge of the species' physiological (climate) and ecological (food availability) niche space, which may render them more sensitive to climatic change.

3) Finally, we predicted that the standardized effects sizes of rodents on ptarmigan would be generally greater than those of any climatic variables since predation is a major determinant of reproductive success and the willow ptarmigan is well-adapted for life in cold environments.

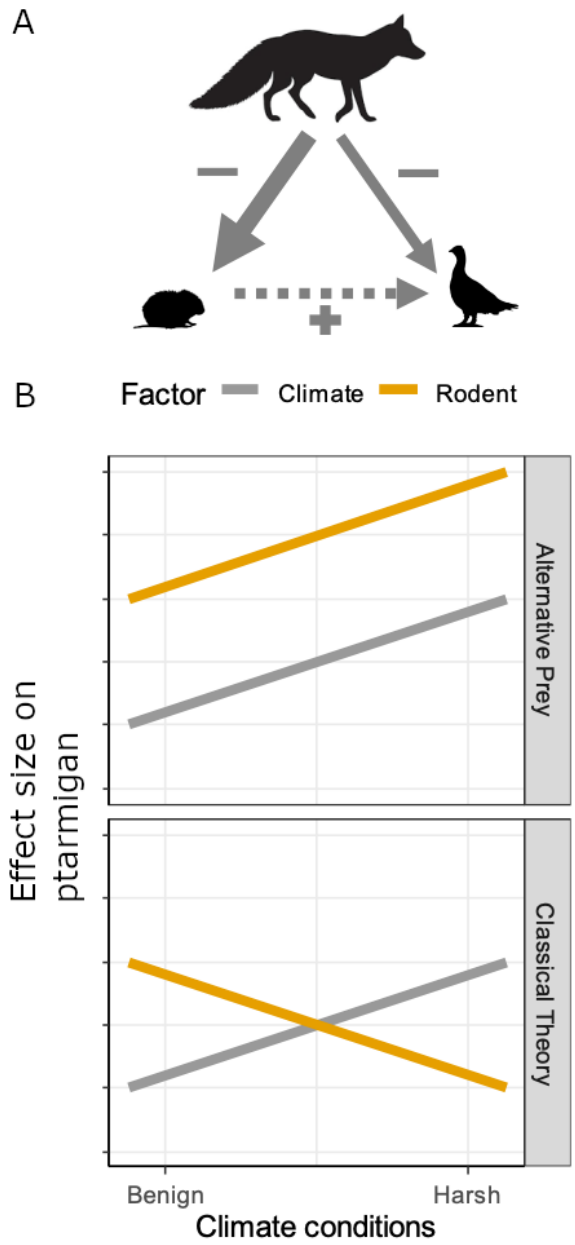

Fig. 1 (A) The hypothesized relationships between ptarmigan, rodents and generalist predators. Rodents are the preferred prey of generalist predators such as the red fox, which also prey on ground-nesting birds, such as the willow ptarmigan. In peak rodent years, ptarmigan are mostly ignored by predators; by contrast, in crash rodent years, ptarmigan are more frequently predated. Together, these processes lead to a positive effect of rodent abundance on ptarmigan abundance. (B) Predicted effects of interannual climatic variability (grey lines) and rodent abundances (orange lines) on ptarmigan population dynamics according to classic theory (bottom) and the alternative boreal theory derived from the 'Alternative Prey Hypothesis' (top).

Methods

Population abundance data

We used a large-scale line-transect survey dataset covering almost the full latitudinal extent of Norway for an 11-year period (2007–2017). The surveys come from a structured citizen science program, based on coordinated collection by local and regional initiatives. At a study-site level, surveyors were instructed to follow common field procedures, and local surveys were mainly established using common protocols for design decisions. The study protocol was designed to allow for analysis of the data using distance-sampling methods [31]. At a national or regional scale, however, the program does not allow for a random selection of study sites, because site selection is contingent on landowners establishing surveys on their land. Surveys were mainly conducted by volunteers. During the surveys, a team of two persons followed pre-defined transect lines, using trained pointing dogs to search both sides of the transect line, usually during August. For each detection of ptarmigan (a group or an individual bird), surveyors recorded the perpendicular distances of the ptarmigan from the transect, the number of birds, the GPS coordinates and time of day. In addition, length (and geographical position) of the transect line is recorded, as well as some other auxiliary data [32]. Since 2013, all data management, and development of field procedures and coordination of study design has been coordinated by the Hønsefuglportalen project (http://honsefugl.nina.no). Transects are spatially clustered into survey regions (median of 17 line-transects per survey region), reflecting data that are reported to the same survey coordination node. We used all data collected since 2007, when the monitoring was substantially expanded, until 2017. The total effort varied across the period, and not all study sites were surveyed each year. We subsetted our analysis to 725 relatively well-sampled line-transects that were regularly visited (a median of 10 years) between 2007 and 2017, each with a mean length of 4.3 km. We excluded some extreme observations seen at distances greater than 200 m, as well as detections by the surveyor, and not by the dog, at distances > 10 m away from the transect line because those observations were likely due to the surveyor flushing birds when moving towards the pointing dog and would not been observed unless the surveyor left the transect line.

Covariate data

Rodent data: During the line surveys, surveyors recorded whether they observed rodents or not along the transect as binary variable (yes/no). The surveyors were not asked to distinguish among rodent species, but the main species in the study area that show cyclic dynamics are lemming (*Lemmus lemmus*), tundra vole (*Microtus oeconomus*), field vole (*Microtus agrestis*), bank vole

(*Myodes glareolus*) and red-backed vole (*Myodes rufocanus*). Rodent occurrence is denoted by *R* in subsequent statistical models.

Climatic data: We obtained high-resolution climatic data from the Norwegian Meteorological institute (MET Norway: www.met.no), Data are based on an interpolation from local weather stations, with a spatial resolution of 1x1 km and are available on a daily basis. For each line-transect, we applied a buffer of 200 m and intersected the transect data with the climate data. With these data, we characterised the spatio-temporal variation in climatic conditions during spring (prior to and at the start of the breeding period) and winter (marking the end of the breeding period). Specifically, we calculated:

1) Spring onset - first year day with a rolling 7-day mean snow depth of zero. We use the term 'spring' loosely since snow cover did not completely disappear until summer in some regions.
2) Spring temperature - average daily mean temperature during March, April and May
3) Winter onset - first year day with a rolling 7-day mean snow depth above zero
4) Winter temperatures – average daily mean temperature during December, January and February

For each climatic variable, we calculated (1) the average climatic conditions for each transect between 2007 and 2017, which defined the spatial climatic gradient (denoted as *CS*) and (2) the difference between the climatic value of each year at each transect and this spatial variable of each transect, which defined the temporal variation (i.e., anomalies, denoted as *CT*). Hence, we considered the effects of different characterisations of the climatic harshness gradient.

Habitat data: We extracted habitat data from the Satveg dataset [33], available at a 30 x 30 m resolution, containing 25 habitat classes. For each line-transect, we applied a 200 m buffer and extracted the habitat information to calculate the number of cells with open and forest habitat.

Statistical analysis

Rodent dynamics

We first investigated how rodent dynamics changed along the climatic gradient. In Bayesian mixed-effects models with binomial errors, we tested the effects of the spatial climatic variables and temporal climatic anomalies variables on the probability of rodent occurrence. Line-transect and survey regions were included as random intercept to account for the spatial clustering of the line-

transects. Each of the four types of climatic variables (winter temperature, winter onset, spring temperature, spring onset) were tested in separate models.

Ptarmigan dynamics

We modelled ptarmigan dynamics using a hierarchical state-space Bayesian model that included two linked models: a model for the observation process along each transect line (i.e. the observation model) and a model that described the ecological dynamics including the effect of climate and rodents on ptarmigan density as the latent variable (i.e. *the state model*).

(1) Observation model: Estimation of effective strip width of the ptarmigan line-transects

We fitted a distance-sampling detection model to estimate the effective strip width of each transect [31]. The effective strip width, together with the transect length, can be used to calculate the effective area sampled, and hence to calculated the density of ptarmigan [31]. The central assumption of distance-sampling theory is that the detection probability of individuals decrease with increasing distance from the line-transect (and observer on it). We modelled the perpendicular distances of observation events (one or more birds in a group) from the line-transect as a half-normal distribution. On the transect line, we assumed perfect detection – a common assumption in distance-sampling [31]. We modelled sigma - the parameter of this half-normal distribution that reflects the rate of distance-decay of detections - to be dependent on group size (i.e. the number of birds in each observation) as well as random effects of transect and survey region. We also considered effects of forest cover or precipitation amount during the survey but found no effects (their 95% credible intervals overlapped zero), thus these factors were dropped from the model. The final model for sigma was:

$$log(sigma_{i,t}) = b_0 + b_{GS}GroupSize_{i,t} + L_i + SR_i$$

Once sigma was estimated, the effective strip width of each transect (*i*) in each year (*t*) was calculated by:

$$ESW_{i,t} = \sqrt{\frac{(\pi * sigma_{i,t}{}^2)}{2}}$$

(2) State model: Testing the effect of climate and rodent on ptarmigan populations

We built a model to use this estimated effective strip width (ESW) and data on transect length (TL) to relate the total number of individuals detected along each transect (N) to the latent variable, ptarmigan density, D, (abundance per km^2) for each year *t* and each transect *i*:

$$N_{i,t} = D_{i,t} \times TL_{i,t} \times ESW_{i,t} \times 2$$

Ptarmigan density ($D_{i,t}$) was modelled in two different ways. In a first model ("random-effects model"), we modelled the ptarmigan dynamics using a series of random effects that reflected the spatial and temporal structure of the data. These random terms were year, transect, survey region and survey region-year. We used this model to make predictions of the realized ptarmigan dynamics, without explicitly specifying the underlying ecological covariates.

In a second set of models ("mixed-effects model"), we tested the additive effects of the two main ecological variables of interest: rodent occurrence and climate (the following climatic variables were tested in separate models: winter temperature, winter onset, spring temperature, spring onset) as well as the interaction between rodent occurrence and the spatial climatic variable. We modelled spatial (*i*) and temporal (*t*) variation in ptarmigan density as:

$$\ln D_{i,t} = b_0 + b_A \ln D_{i,t-1} + L_i + SR_i + b_{CS}\, CS_i + b_{CT}\, CT_{i,t} + b_R\, R_{i,t} + b_{RL}\, R_{i,t-1} + b_{int_CT}\, CS_i\, CT_{i,t} + b_{int_R}\, CS_i\, R_{i,t}$$

where $D_{i,t-1}$ accounts for temporal autocorrelation in ptarmigan density among consecutive years. L and SR were normally-distributed random effects with mean zero and estimated variance to account for the spatial grouping of data into line-transects (L) and survey region (SR). CS and CT were covariates for the spatial gradient in climate and temporal anomalies for the climatic variable, respectively. Two coefficients for rodents (R) tested the effects of rodent occurrence immediately preceding the ptarmigan survey (during the same year, *t*) and a lagged effect of rodent occurrence (during the previous year, *t-1*).

The most important parameters of our model were the interaction terms, testing the core hypotheses of interest. The interaction terms were: (1) between CS and CT to test whether the effect of annual climatic anomalies changed along the gradient or (2) between CS and R (of the same year) to test whether the effect of rodents changed along the climatic gradient.

Table 1. Table of model parameters on ptarmigan density and their meanings.

Terms of model	Statistical meaning
$\boldsymbol{b_0}$	Overall intercept
$\boldsymbol{b_A}$	Autocorrelation in density
$\boldsymbol{L}$	Random line-transect effect
$\boldsymbol{SR}$	Random survey region effect
$\boldsymbol{b_{CS}}$	Spatial climatic variable
$\boldsymbol{b_{CT}}$	Temporal climatic variation
$\boldsymbol{b_R}$	Rodent occurrence (same year)
$\boldsymbol{b_{RL}}$	Lagged effect of rodent occurrence (previous year)
$\boldsymbol{b_{int_CT}}$	Interaction term between temporal and spatial climate
$\boldsymbol{b_{int_R}}$	Interaction term between rodents and spatial climate

We included a submodel for rodent occurrence within our hierarchical model. This submodel was based on a series of random terms (for survey region [SR], year [Y] and their interaction) to flexibly predict the interannual variability, as well as the spatial pattern in this variability based on the raw data on rodent observations. Modelling rodent occurrence allowed us to account for missing data in the rodent dataset. Additionally, we predict rodent occurrence at the level of the survey region rather than transect, which mean meant smoothing over reporting and ecological variation at the transect level. This decision could be justified by the spatially autocorrelation in rodent populations and the fact that highly-mobile predators are not likely affected by fine-scale variation. Hence, the rodent submodel was:

$$logit(R_{i,t}) = b_0 + Y_t + SR_i + Y_t\, SR_i$$

Models were fitted using JAGS within R version 3.6.1. We used three MCMC chains, ran for 200,000 iterations, discarding the first 50,000 as burn-in. We used uninformative priors or weakly informative priors. We assessed model convergence using MCMC chain traceplots and the Gelman-Rubin R-hat statistic (all <1.1). Covariates were centered prior to analysis. Covariate effects were inferred when the 95% credible intervals did not overlap zero. Code for the fitted model is available in the SOM.

Results

Data description

The 725 line-transects were distributed along a long latitudinal gradient across Norway (Fig. 2A). Along each transect, a mean of 2.6 groups were observed (range = 1–18), with a mean of 4 (1–35) individuals seen per group. As expected by distance-sampling theory, the frequency of observations declined with increasing distance from the line-transect (Fig. 2B). The average effective strip width was 107 m (range = 72–139 m). Sigma of the half-normal distribution was positively affected by group size and the estimated effective strip width was, on average, 95 m for the smallest group size of 1 and, on average, 126 m for the largest group size of 35. Therefore, we included group size in the observation model for further analysis (Fig. 2B).

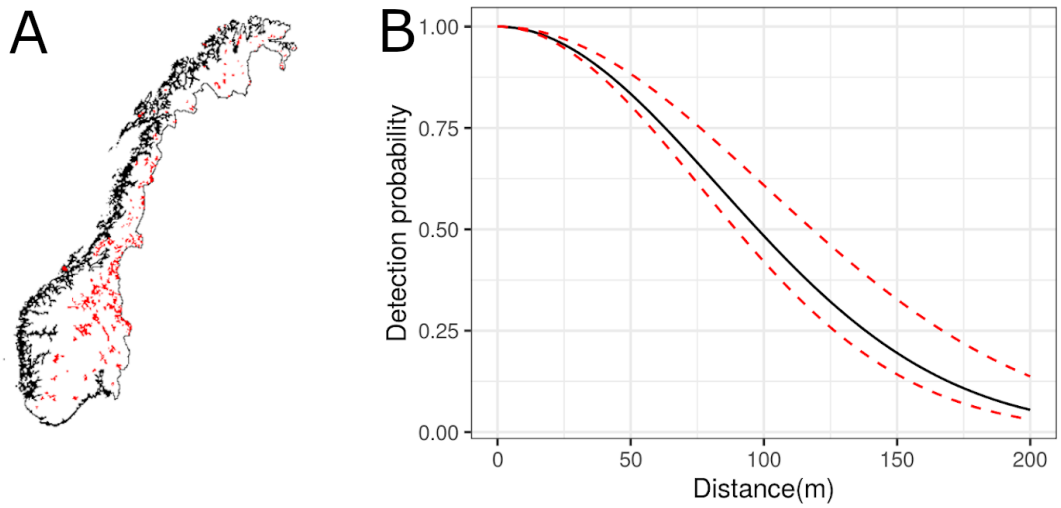

Fig. 2 (A) Location of the line-transects across Norway are shown by red lines. (B) Distance-dependent decay of ptarmigan detectability along the line-transects. The black line is the prediction for the median ptarmigan group size; the lower and upper dashed red lines are the predictions for the minimum and maximum ptarmigan group size.

Climatic, rodent and ptarmigan population variation

Both climate and rodents showed large and generally spatially synchronized fluctuations (Fig. 3). Our 11-year dataset spanned c. 2.5 rodent cycles (Fig. 3). The probability of rodent occurrence increased along the climatic harshness gradient, driven by greater occurrence in peak years within colder regions (Table S1). For instance, in the first peak rodent year, during 2010/2011, mean rodent

presence across transects was 40% in the region of the warmest quantile (as assessed by winter temperature) but 66% in the coldest. In the second peak rodent year, during 2014/2015, rodent presence was 17% in the warmest and 39% in the coldest.

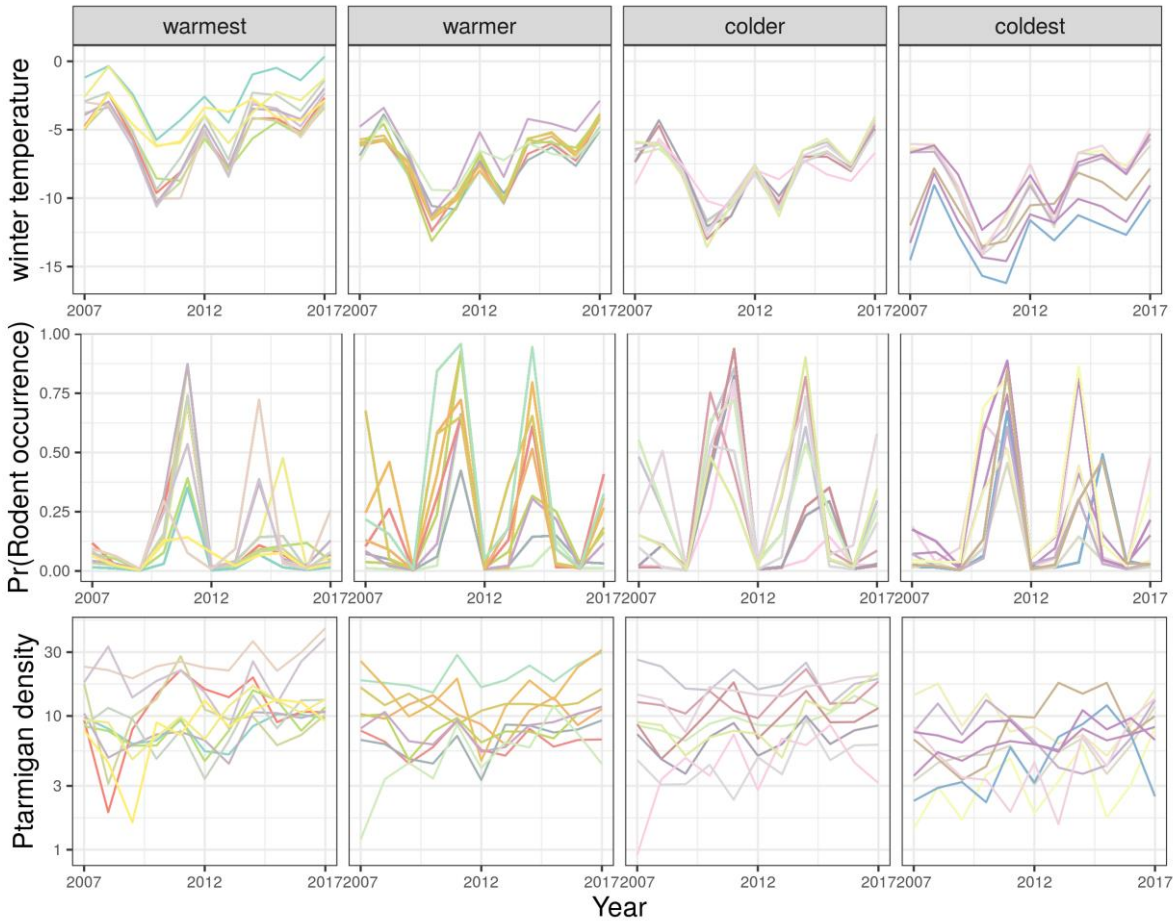

Fig. 3 Time-series of winter temperature (°C), probabilities of rodent occurrence and willow ptarmigan density (abundance per km^2) as predicted by the random-effects models. In the analysis, the spatial climatic gradient was treated as a continuous variable but for presentation purposes, we divided here the spatial climatic gradient into 4 quantiles with equal numbers of transects within each. Lines shown are means for each of the 37 survey regions (for simplification of presentation, averaged over the 725 transects). Fig. S1 shows the time-series for the other climatic variables.

Mean effects of climatic and rodent fluctuations on ptarmigan populations

Ptarmigan density was higher in less climatically harsh regions; specifically, in regions with later winter onset and warmer winter temperatures (spatial effects of climate shown in Fig. 4). Similarly,

temporally, ptarmigan density increased in years with later winter onset, as well as warmer spring and winter temperatures (temporal effects of climate shown in Fig. 4). Effect sizes for winter temperature and winter onset were generally larger than those for spring temperature and spring onset. Ptarmigan density was positively associated with rodent occurrence of the same year, but negatively associated with rodent occurrence in the previous year (Fig. 4).

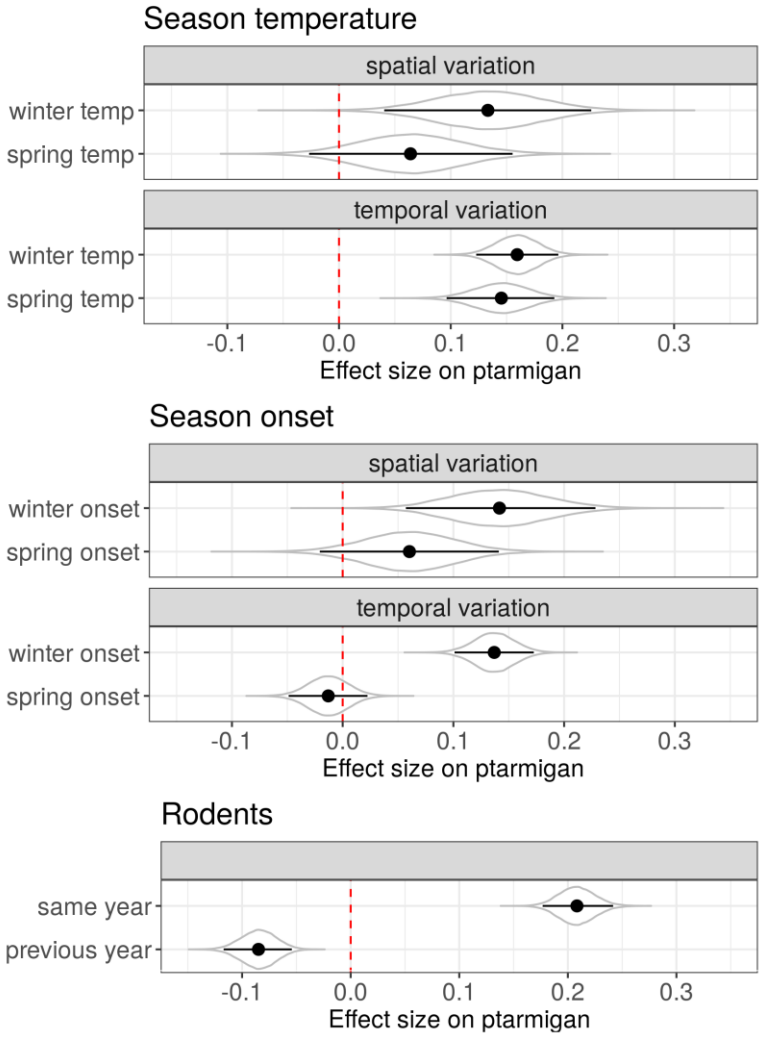

Fig. 4 Effects of seasonal temperatures, seasonal onsets and rodent occurrence on changes in ptarmigan population density. Covariates were standardized to units of standard deviation to facilitate comparison of effect sizes. Violins represent the full posterior distributions. Point and ranges represent mean effects and 95% credible intervals of the distributions. The dashed vertical red line is the line of no effect. The sign of the effects of spring onset were flipped so that larger values represent lower climatic harshness (i.e., earlier springs), consistent with the other climatic variables.

Changes in the effects of climatic and rodent fluctuations along the climatic harshness gradient

The statistical effects of rodent occurrence probability on ptarmigan densities were more positive in more climatically harsh areas compared with more climatically benign areas (Fig. 5). In fact, the predicted effects of rodent occurrence were close to zero in regions with the warmest winters and springs, and earliest springs, but were strongly positive in the regions with the coldest winters and coldest and latest springs. In the case of winter onset, similar positive effects of rodent were found along the whole spatial climatic gradient and there was no significant interaction (Fig. S2).

The effects of temporal climatic variability also tended to increase along the climatic harshness gradient, but only when the gradient was described in terms of season onset (Fig. S2). In regions with earlier winters and later spring, there were positive effects of temporal climate variation, but not in regions with later winters and earlier springs (Fig. 5). For spring and winter temperature, temporal variability was similarly important for ptarmigan across the whole climatic gradient.

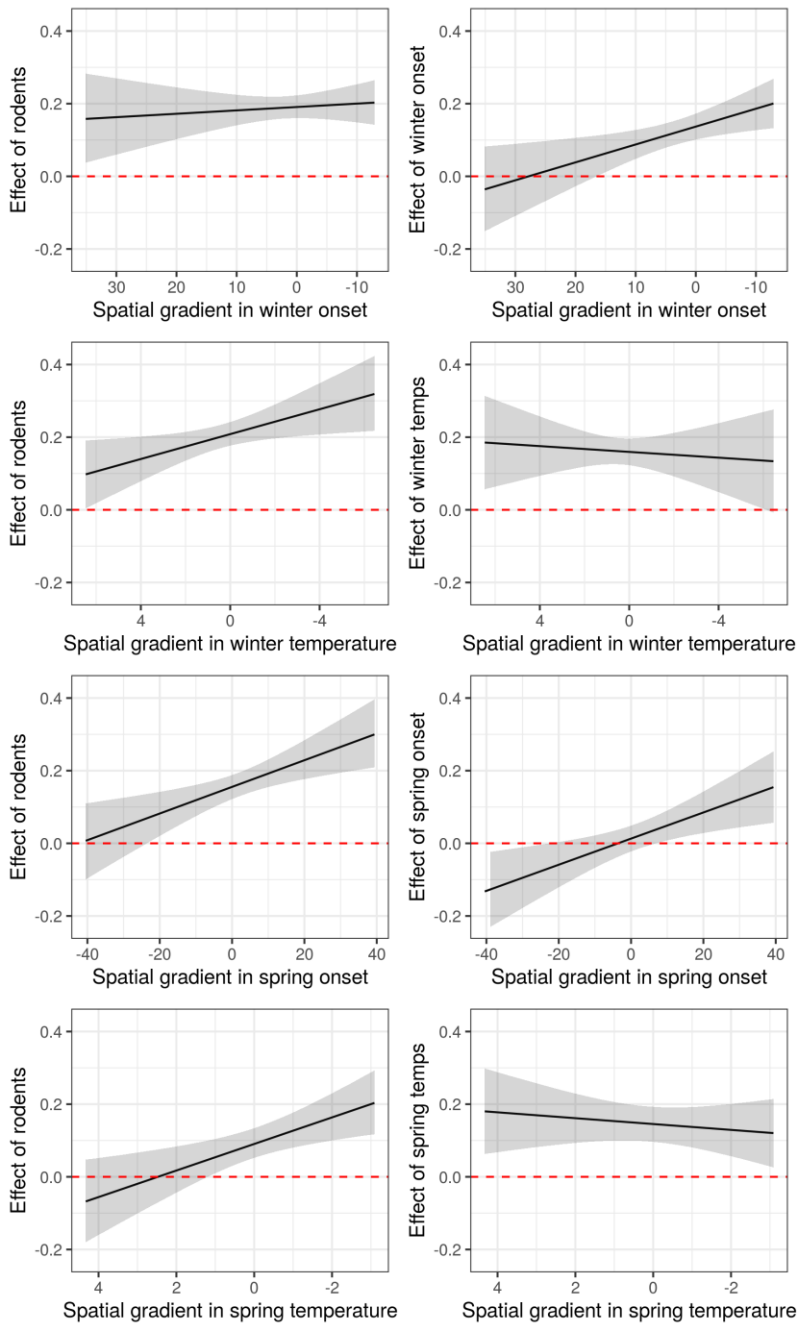

Fig. 5 Changes in the effect sizes of temporal variability in climate and rodent occurrence and along each climatic spatial gradient on ptarmigan density. X-axes are transformed so that left to right is an increasing climatic harshness gradient (i.e., the values towards the right represent colder temperatures, earlier winters and later spring). Shown are the mean standardized effect size and 95% credible interval. X-axes variables are also scaled so that 0 represent the median value. Temperature values are in °C. Onset values are year day values.

Discussion

Understanding how fluctuations in climatic conditions and species interactions affect species' population dynamics is central to current research in population ecology. We outlined two different hypotheses about how the strength of species interactions might vary along a climatic gradient, and tested our predictions using a large-scale dataset on the willow ptarmigan. Our results suggest that the impact of predator-mediated interactions on willow ptarmigan increase along the climate gradient, indicated by more strongly positive signals of rodent occurrence in colder areas. Hence, our results were consistent with predictions stemming from the alternative prey' hypothesis (APH) rather than the classical view of how species interactions change with increasing climatic harshness.

Our results support our main prediction based on the 'alternative prey' hypothesis (APH): a stronger link between rodent fluctuations and ptarmigan dynamics in colder regions. According to the APH, shared predators are expected to prey-switch towards rodents, and away from ptarmigan, when rodents are more abundant [15, 18, 24]. We found that ptarmigan were more abundant during years with more rodents, which would be consistent with lower predation pressure. Hence, our results are consistent with the APH, previously tested over smaller-scales [24, 26, 34, 35]. While the APH primarily considers the immediate functional response of predators, the contrasting negative lagged effects of rodents is consistent with a numerical response of predators due to greater prey density, leading to negative effects of rodents on ptarmigan in the subsequent year. The weaker effect of rodents, and hence predator-mediated interactions, on ptarmigan density in warmer regions might have been caused by greater prey diversity available to shared predators, weakening the trophic links among the dynamics of predators and prey species [15]. Changes in species richness and community composition, and increasingly generalistic predators, has already been evoked to explain the decreased amplitude of rodent cycles in more southerly parts of Fennoscandia [9].

Previous research has shown how the role of species interactions can increase or decrease in strength along an ecological gradient due to different processes [6, 36-39]. Probably the most common reason for changing strengths of interactions over a geographic range is changes in community assemblages and the availability of interacting partners [4, 40, 41]. Our results appear to be at odds with the classic prediction of stronger species interactions at the warmer end of a species range [4], but this prediction arises from the assumption that the occurrence and abundance of interacting partners is greater in warmer regions. Although this is likely to be true in many scenarios, in our case rodents showed greater peaks in occurrence in colder regions. Indeed, other studies have shown an increase in the amplitude of rodent dynamics from southern to northern Fennoscandia [9]. Hence, our results are consistent with species interactions being important in areas where potential interacting partners are more common.

Another factor likely to affect the changing importance of species interactions is whether they are between specialist or generalist species. When interactions involve specialists, they can be important over the whole distributional range of an organism [42]. Although none of the interactions between ptarmigan, rodents and predators are intrinsically specialist, they may be regarded as functionally specialist in cold regions due to the relatively low number of species in the food web. Since interaction networks at high latitudes tend to be often more specialised [43], other type of indirect interactions may also become more important in more northerly regions.

We also found that interannual climatic variability had a greater effect on ptarmigan populations in colder regions. In colder regions, effect sizes of climatic variability were largely similar to those of rodent occurrences, suggesting similar importances. Climatic effects may be direct and related to species' physiology, or more likely indirect and related to climate-caused changes in the availability of resources or suitable habitat. Since extreme conditions may expose an organism to the edge of its niche space, climatic variation at the colder edge of a species' range should be more likely to affect its population growth; however, this has rarely been tested [44]. One exception is a recent meta-analysis [45] that found that temperature generally had positive effects of population abundance but found no evidence that this effect varied over latitude. However, this meta-analysis was based on a heterogeneous dataset of different species and habitats, which might make such effects harder to detect. We provide more convincing evidence that temporal climatic fluctuations become more important for species towards the colder edge of their range, even for a well-adapted montane species such as the willow ptarmigan.

High-altitude or -latitude organisms are among those most strongly exposed to climate change [46]. Our findings help understand the main pathways through which climate change may affect the population dynamics of ptarmigan, including the direct effects of warming versus indirect effects mediated through predators [47, 48]. Ptarmigan benefit from warmer and earlier springs, hence, climate change, at least in the short-term, may have some positive effects [49]. However, changes in predation pressures mediated via rodents are likely to be more important. One predicted consequence of climate change is a dampening of the rodent cycles [14]. Dampening cycles could mean no or less frequent years of high rodent abundance, which offer ptarmigan temporal refuges from predation. Hence, a warming climate may lead to a more constant rate of predation pressure on ptarmigan, lowering population growth rates. However, dampening of the cycles might also reduce the long-term abundance of predators, lowering predation pressure on the ptarmigan [12].

Our analysis has several limitations. First, the rodent data was only collected as a binary presence/absence variable along each line-transect and hence may not fully reflect changes in the

relative abundances of rodents among years. Nonetheless, the patterns in the proportion of rodents seen across transects showed the expected large-scale synchronised cycles consistent with other data [50]. Second, although we can reasonably infer the interaction between ptarmigan and rodents to be caused by shared predators, data on predators would also help better understand the links between predator abundance and prey preference, and alternative prey availability, and compare the functional and numerical responses [24]. Last, our analysis only focused on changes in the strength of one specific type of species interaction. Willow ptarmigan may be involved in various other types of species interactions (e.g., competition with other herbivorous species), which differ in their strength along the climate harshness gradient. Hence, cumulatively, species interactions could still be more important at the warmer edge, both elevationally and latitudinally, of its distribution.

Our analyses suggest that predator-mediate interactions become even more important in the colder regions of boreal ecosystems, contrary to the classic view that species interactions are more important at the warmer-edge of species' distributions. The role of predator-mediated interactions along a climatic gradient are more generally likely to depend on the diet breadth of predators and availability of different prey types. The rodent cycles – regarded as the heartbeat of the boreal - cause changes in prey availability that lead to predator-mediated interactions for alternative prey species. Long-term dampening of the rodent cycles, predicted to arise due to climate change, is likely to have widespread repercussions for the dynamics of many other species in the boreal, especially ground-nesting birds such as the willow ptarmigan.

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Data availability

The ptarmigan dataset (for different geographic regions) is freely available at the following links:

https://www.gbif.org/dataset/b49a2978-0e30-4748-a99f-9301d17ae119

https://www.gbif.org/dataset/6a948a1c-7e23-4d99-b1c1-ec578d0d3159

https://www.gbif.org/dataset/c47f13c1-7427-45a0-9f12-237aad351040

Competing interests

The authors have no competing interested to declare.

Author contributions

DB developed the research questions, with contributions from EBN. DB conducted the statistical analyses. DB wrote the first draft of the manuscript, with input from EBN. EBN and HCP designed the line-transect sampling protocols and helped to develop and maintain the Hønsefuglportalen system. All authors helped refine the hypotheses and develop the manuscript.

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