Global warming is predicted to change ecosystem functioning and structure in Arctic ecosystems by strengthening top-down species interactions, i.e. predation pressure on small herbivores and interference between predators. Yet, previous research is biased towards the summer season. Due to greater abiotic constraints, Arctic ecosystem characteristics might be more pronounced in winter. Here we test the hypothesis that top-down species interactions prevail over bottom-up effects in Scandinavian mountain tundra (Northern Sweden) where effects of climate warming have been observed and top-down interactions are expected to strengthen. But we test this ‘a priori’ hypothesis in winter and throughout the 3–4 yr rodent cycle, which imposes additional pulsed resource constraints. We used snowtracking data recorded in 12 winters (2004–2015) to analyse the spatial patterns of a tundra predator guild (arctic fox Vulpes lagopus, red fox Vulpes vulpes, wolverine Gulo gulo) and small prey (ptarmigan, Lagopus spp). The a priori top-down hypothesis was then tested through structural equation modelling, for each phase of the rodent cycle. There was weak support for this hypothesis, with top-down effects only discerned on arctic fox (weakly, by wolverine) and ptarmigan (by arctic fox) at intermediate and high rodent availability respectively. Overall, bottom-up constraints appeared more influential on the winter community structure. Cold specialist predators (arctic fox and wolverine) showed variable landscape associations, while the boreal predator (red fox) appeared strongly dependent on productive habitats and ptarmigan abundance. Thus, we suggest that the unpredictability of food resources determines the winter ecology of the cold specialist predators, while the boreal predator relies on resource-rich habitats. The constraints imposed by winters and temporary resource lows should therefore counteract productivity-driven ecosystem change and have a stabilising effect on community structure. Hence, the interplay between summer and winter conditions should determine the rate of Arctic ecosystem change in the context of global warming.

Keywords: bottom-up versus top-down effect, seasonality, Arctic ecosystems
Introduction

Global warming is one of the main anthropogenic drivers of biodiversity loss, and of changes in ecosystem structure and functioning (Montoya and Raffaelli 2010). These effects are most pronounced in Arctic and sub-Arctic regions, where climate and resources should impose relatively strong constraints on the structure and functioning of tundra ecosystems (CAFF 2013). Processes such as species interactions change along latitudinal gradients, suggesting that climate change might cause new patterns in the abundance and distribution of species. Hypotheses on biodiversity patterns in northern latitudes suggest that the relative contribution of top-down and bottom-up control changes at high latitudes and altitudes; specifically that herbivore biomass is controlled bottom-up in unproductive tundra, but top-down in productive tundra and boreal forest (Oksanen and Oksanen 2000, Aunapuu et al. 2008). In line with this theory, herbivory intensity decreases at lower latitudes while predation pressure increases, suggesting that top-down effects would increase with warmer temperatures in tundra ecosystems (Legagneux et al. 2014). Northward expansion of boreal predators is also likely to strengthen such top-down effects (Post et al. 2009). Interactions between trophic levels would be affected, but also interference within the predator guild, as illustrated by the mesopredator release phenomenon, where top predators can control medium-sized predators through competition or intraguild killing and in turn benefit small herbivores (Soulé et al. 1988, Elmhagen and Rushton 2007, Elmhagen et al. 2010, Pasanen-Mortensen et al. 2013).

In addition to harsh climate related constraints in northern latitudes, the intensity of constraints also varies in time. Firstly, the importance of seasonality should not be overlooked. Winter is the longest season and its severity may play a crucial role in the dynamics of tundra ecosystems. Despite this, summer observations provide the basis for most of our knowledge on the structure and functions of tundra ecosystems, potentially giving a misleading picture of ecosystem functioning (Ims and Fuglei 2005). In winter, the harsher conditions may shift the system towards a state characterised by stronger bottom-up effects compared to summer. Secondly, pulsed resources characterise tundra ecosystems in the form of multi-annual fluctuations of small rodents which affect all levels of the food web. The dynamics of most predators track the rodent cycle, due to a tightly linked reproductive success (Krebs 2011, CAFF 2013). Hence, pulsed resources impose multiannual variation in resource constraints, which could alter the relative importance of top-down and bottom-up drivers within the tundra ecosystem. Predation can also force medium-sized prey into the cycle, as the predation pressure on alternative prey increases when rodents are scarce (Ims and Fuglei 2005). This has for example been observed in summer in the low phase of the rodent cycle when predation pressure strengthens on nesting birds (Béty et al. 2002). Similarly, top-down effects on alternative prey might increase in winter when rodents are less accessible. High-quality snow provides a subnivean space which offers protection (against many predators and cold) and resources (for food and reproduction) for lemmings Lemmus lemmus (Ims et al. 2011). Thus, these resource pulses are ultimately linked to the prevailing climate conditions, as snow quality in winter is a prerequisite for rodent cycles (CAFF 2013).

The mountain tundra in Fennoscandia is a southern extension of the Arctic tundra distinctive from typical alpine sub-biome (Virtanen et al. 2016). In the last century, the altitudinal treeline has advanced by an average of 70–90 m with an increased shrub cover (Kullman and Öberg 2009, Callaghan et al. 2013). The Arctic characteristics of the tundra vegetation has become less pronounced (Vuorinen et al. 2017). Mammals and birds have advanced north in the boreal vegetation zone and for example the red fox Vulpes vulpes has also expanded in the mountain tundra, partly favoured by a bottom-up cascade due to global warming (Killengreen et al. 2007, Elmhagen et al. 2015, 2017). The expansion of competitive mesopredators such as the red fox is one of the changes which could alter tundra ecosystem structures. The red fox is a generalist species with a significant impact on lower trophic levels in boreal ecosystems, and on the smaller arctic fox Vulpes lagopus in tundra ecosystems (Hersteinsson and Macdonald 1992, Lindström and Hörnfeldt 1994, Elmhagen et al. 2017). Increased interference competition from the red fox is one of the main factors threatening the persistence of the arctic fox in Fennoscandia (Angebjörn et al. 2013). However, the potential top-down effect of red fox on arctic fox and its herbivore prey could vary in space and time depending on changes in bottom-up constraints (Elmhagen et al. 2017). For example, Killengreen et al. (2012) observed strong interference competition between arctic fox and red fox in winter at sites where food subsidies favoured the red fox, whereas Ehrich et al. (2016) found that the association between the species varied, likely due to local fluctuations in food resources. In addition, although large carnivores are generally rare in tundra ecosystems (CAFF 2013), top-down effects on red fox could potentially limit its abundance. The red fox expansion has been related to mesopredator release in sub-Arctic areas, where wolf Canis lupus can act as an apex predator and suppress red fox populations (Ehrich et al. 2016). Lynx Lynx lynx is known to limit red fox abundance in boreal forest (Elmhagen et al. 2010), but its distribution generally does not comprise Arctic and sub-Arctic tundra (Anon 2015, Breitenmoser et al. 2015). Finally, wolverine are known to kill red fox (Mattisson et al. 2016), suggesting wolverine potentially could exert top-down control on red fox and counteract its expansion in the mountain tundra.

Our study focuses on the structuring rules of a Fennoscandian mountain tundra community composed of arctic fox, red fox, wolverine, medium-sized alternative prey (willow ptarmigan Lagopus lagopus, rock ptarmigan Lagopus muta) and small rodents. According to theory, climate warming should strengthen top-down effects (Fig. 1) and in our sub-Arctic study area, top-down effects have been observed, such as arctic fox decline due to red fox expansion. Hence we test the ‘a priori’ hypothesis that top-down interactions (interference and predation) prevail over bottom-up effects.
However, this a priori hypothesis is based on research biased towards summer conditions, and our study was carried out in winter when theory suggests that Arctic ecosystem characteristics could be more pronounced due to stronger resource constraints. Predators are also exposed to stronger resource constraints at low rodent abundance. Hence, we also test if the structural rules are independent of pulsed food resources, by testing the top-down hypothesis in each rodent phase. In case top-down effects are not omnipresent, we predict that their intensity should increase at high rodent abundance, as the density of many predators should increase in response to this.

**Material and methods**

**Overall approach**

We used data from a 12-year snowtracking survey to study species and habitat associations in a Scandinavian mountain tundra community in different phases of the rodent cycle. Because these phases represent different ecological conditions for the species involved, tundra ecosystem functioning and species demography is often described in relation to rodent phase (Ims and Fuglei 2005, Henden et al. 2009, Legagneux et al. 2012, Meijer et al. 2013). Accordingly, and because our dataset covered more than three rodent cycles, we used rodent phase as a treatment to study its impact on community structure. We used a three-step approach. Firstly, we analysed temporal variation in rodent abundance to establish the phase of the rodent cycle each winter. We also tested the response of the community to the rodent cycle, taking snow conditions into account, to ascertain that the snowtrack data reflected the assumed variation in species abundances rather than snow conditions. The latter might be the case if tracks were more visible during certain snow conditions, with a negative effect on data quality. Secondly, to assess which landscape features represent ecologically important bioclimatic gradients and bottom-up processes, we tested the spatial landscape associations of the study species in each phase of the rodent cycle. Finally, for each phase of the rodent cycle, we tested the a priori hypothesis suggesting that the species of interest could affect each other through top-down processes, taking into account the bottom-up effect of landscape features which potentially could modify the strength of top-down effects.
Mustela erminea, least weasel Mustela nivalis, and pine marten Martes martes near forest edges. Some birds of prey are present in winter such as gyrfalcon Falcon rusticolus, golden eagle Aquila chrysaetos and raven Corvus corax. The main herbivores present in winter are ptarmigan (willow ptarmigan and rock ptarmigan), mountain hare Lepus timidus, Norwegian lemming, voles (Myodes rufocanus, Myodes glareolus, Microtus agrestis) and reindeer Rangifer tarandus. However, reindeer presence is limited since most reindeer spend winter in the boreal forest.

Site selection and data samples

The abundance of species was monitored through snowtracking surveys every year from 2004 to 2015. The surveys were mostly performed in March and April, following the Wildlife Triangle Scheme method (Lindén et al. 1996, Hellström et al. 2016). Surveys were carried out along 20 triangle-shaped transects which were 12 km in length (4 km per side). The triangles were exclusively present in the treeless tundra and distributed throughout the nature reserve (Fig. 2a). Their locations were permanent throughout the study period, although some triangles could not be surveyed in all years due to difficult weather conditions. In total, 217 triangle surveys were performed, on average 18 triangles per year. The exact locations of the triangles were set randomly but their spread was limited by steep terrain and accessibility, and locations too close to known arctic fox dens were avoided. The surveys were performed from a snowmobile within a day after a snowfall or wind had erased old tracks, and only in good snow and weather conditions (no new wind, no new snowfall) to guarantee the detection of all recent footprints (Lindén et al.)

Figure 2. (a) Map of the study area representing the transects used for the study (20 triangles in red). The green areas represent the forested valleys while the white areas represent the treeless mountain tundra. The black square indicates the area zoomed in (b), a subset displaying two triangles. The transect covered by snowmobile is shown as a red line, the snowtracks found along the transects are represented as white circles and the yellow buffer (500m total width) shows how the triangles have been split into corners. The CIR ortho-photo is displayed as background (©Lantmäteriet, photo taken the 3 Sept 2015, 0.5m spatial resolution).
1996). For each snowtrack crossing the transect, the species (or genus if the species could not be determined) was identified and a GPS point recorded. Arctic fox snowtracks were distinguished from red fox snowtracks by trained and calibrated fieldworkers, who based their identification on the overall shape of the trail and its pace. A snowtrack index representing the total number of tracks was calculated for each year, rendering the mean number of recorded snowtracks per triangle per year. To compute an abundance index for each species, the 12 km triangle transects were split into three 4 km long corner transects (Fig. 2b). The abundance index was calculated as the number of snowtracks per 10 km for each triangle corner, each year. The triangles were split into corners to decrease the within-transect variation in landscape features such as altitude and productivity (see below), while still keeping the transects long enough to have a decent probability of recording snowtracks during each survey. In the years 2007 and 2014, GPS locations were missing. The abundance index was therefore estimated at the scale of the triangle and the values assigned for each corner were the same for each triangle.

**Landscape features**

Information on landscape variables was obtained with ArcMap (ESRI 10.4). The main landscape features selected to represent bottom-up effects were primary productivity, altitude and other topographic variables. Although we lacked data about snow precipitation, the topography of the landscape was assumed to affect snow depth and snow cover, where e.g. north-facing slopes would accumulate more snow for longer periods than south-facing slopes, due to lower insulation (Dahlström 1995). The topography of the landscape was assessed for each triangle corner using a set of variables derived from the Digital Elevation Model (DEM, https://www.geodata.se/): aspect, slope, planear and tangential curvatures.

To assess primary productivity, the Normalised Difference Vegetation Index equation was used (Tucker 1979):

\[
rel \text{- NDVI}_{ortho} = \frac{near \text{ infrared} - red}{near \text{ infrared} + red}
\]

This equation was applied to Coloured Infrared ortho-photos. The outcome was therefore considered as a relative index (rel-NDVI<sub>ortho</sub>, Erlandsson et al. under review). Shadows were excluded and abnormally high rel-NDVI<sub>ortho</sub> values in water bodies (due to light reflecting in the water) were corrected to −1, i.e. the lowest productivity value. To ensure that details would not be lost, water elements were not removed from the analysis. The corrections were done using supervised classification in R ver. 3.1.1 (R core team, package ‘rpart’).

Along each corner, a total buffer width of 500 m was produced on which we extracted zonal statistics for each landscape feature: mean rel-NDVI<sub>ortho</sub>, mean altitude, the proportion of northerly, southerly, easterly and westerly aspects, maximum slope, proportions of planear concaveness and convexness and proportions of tangential concaveness and convexness.

**Rodent trapping data**

Information about the rodent cycle was obtained from an environmental monitoring programme based on systematic trapping in Vindelfjällen in summer (Swedish Univ. of Agricultural Sciences, <http://www.slu.se/institutioner/vilt-fisk-miljo/miljoanalys/>). We included data on all rodent species, except Myopus schisticolor which is found only in forest habitats. The data were compiled per year to form a rodent abundance index (number of rodents trapped per 100 trapping nights) and used to identify the phase of the rodent cycle each winter (Table 1). Lemming snowtracks were also counted during winter snowtrack surveys, but preliminary analyses indicated that lemming snowtracks were not reliable for studying lemming distribution, most likely because lemmings primarily live under the snow in winter. Hence, lemming snowtracks might actually show where the subnivean space is unsuitable for lemmings.

**Weather data**

Weather data were obtained from the Swedish Meteorological and Hydrological Inst. from the weather station closest to the study area, in Hemavan, on average 54.15 ± 11.5 km from the triangles (65°49N, 15°05E, <http://opendata-download-metobs.smhi.se/>). For each winter, mean snow depth and winter length (number of days with snow) were calculated.

**Statistical analysis**

Statistical analysis was carried out in R. Spearman’s correlation tests were used to test the community effect of the rodent cycle in winter and the relationship between the number of tracks counted and snow conditions. To test the effect of the phase of the rodent cycle on species abundances, generalised linear models (GLM, family quasi-poisson) were used with the phase of the cycle as a fixed factor, while site (triangle) and year were used as random factors. Residuals of the models were examined to ensure goodness-of-fit.

| Description of the phase for winter time | Name of the phase for winter time |
|----------------------------------------|----------------------------------|
| Winter between two years with decreased rodent density sampled in summer | Low |
| Winter before a summer with the rodent density increase | Pre-peak |
| Winter after a summer with increasing rodent density | Post-peak |
Non-metric multidimensional scaling ordination (NMDS, package 'vegan') was performed to study the spatial distribution of the species in relation to landscape features.

Structural equation modelling (SEM) was used to test the hypothesis that top-down species interactions prevailed over bottom-up effects, hence being more important in determining the community structure. SEM is based on a ‘model-oriented philosophy’ which tests whether there is a match between a hypothetical model (path-diagram) based on available a priori knowledge and observed data (Grace 2006). The same path-diagram was used for each phase of the rodent cycle (Fig. 1), but the strength of the causal relationships was expected to vary with rodent availability with top-down effect being stronger following high rodent abundance, when predator density was expected to be the highest. The number of parameters used in a SEM is limited by the sample size (Grace 2006). To avoid overfitting the model, we included only a selection of landscape parameters. Based on the NMDS analysis of landscape features (above) and theory (Oksanen and Oksanen 2000, Dalén et al. 2004, Copeland et al. 2010, Inman et al. 2012, Christie et al. 2014, Carricondo-Sanchez et al. 2016), we hypothesised that the bottom-up features potentially affecting all species were mean altitude, mean primary productivity (represented by rel-NDVI<sub>erdus</sub>) and the aspect represented by the proportion of westness. In line with existing knowledge, altitude and aspect were also assumed to affect plant productivity (Gerell et al. 1996).

Concerning potential interactions between predators and prey, a dominant top-down effect from predation on ptarmigan was assumed (Legagneux et al. 2012, 2014). Concerning interference relationships between predators, red fox was expected to suppress arctic fox by interference competition and/or intraguild killing (Elmhagen et al. 2017). As a potential top predator, wolverine was predicted to potentially suppress both fox species by intraguild killing (Ehrich et al. 2016, Mattisson et al. 2016).

Three SEM were produced, one for each phase of the rodent cycle. Parameters which were not significant were excluded from the final models. SEM was performed using the piece-wise approach with Bayesian statistics, following Grace et al. (2012) (package ‘MCMCglmm’), where spatial auto-correlation was controlled using site (triangle) as random factor. This model produced standardised path coefficients and explained variance (R<sup>2</sup>) for each parameter. To implement the Bayesian models, we set a weak prior distribution, with 500 000 MCMC iterations and a burn factor of 0.5, with a thin rate of 100. For assessing the convergence of our models, we used the Gelmann-Rubin criterion, with convergence met when the criterion was < 1.1 (Gelman and Rubin 1992). Effective sample size and auto-correlation were assessed for goodness-of-fit.

### Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.rk64m4c> (Stoessel et al. 2018).

## Results

Firstly, the quality of the dataset was tested by verifying that the snowtrack index reflected variation in species abundances rather than snow conditions. This was supported at the community level by a significant positive correlation between the rodent abundance index in summer and the snowtrack index from the following winter (Fig. 3, rho = 0.68, p = 0.019). The community snowtrack index was not correlated to winter length or snow depth (respectively rho = 0.035, p = 0.92; rho = 0.15, p = 0.65), suggesting that the quality of the index was independent of snow conditions.

At the species level, wolverine, red fox and ptarmigan abundance were significantly affected by the rodent cycle (Fig. 4; red fox χ² = 74.14, df = 2, p < 0.001; wolverine χ² = 19.17, df = 2, p < 0.001; ptarmigan χ² = 8.24, df = 2, p = 0.016). Wolverine showed a significant increase in abundance in low winters compared to post-peak winters (Tukey post-hoc test, p < 0.001). Red fox had a higher abundance in post-peak winters compared to other phases of the rodent cycle (Tukey post-hoc test, p < 0.001). Arctic fox abundance seemed to follow a similar pattern as red fox, but the between-phase differences were not significant (Fig. 4). Ptarmigan abundance was significantly higher in post-peak winters than in pre-peak winters (Tukey post-hoc test, p = 0.012).

In the second step we assessed which landscape features were associated with the species and thus should be included as bottom-up factors in the model testing the top-down hypothesis. The analysis of spatial distributions of the species (NMDS) had a stress value of 0.14, which implies that the 2D-representation renders an appropriate interpretation of dissimilarities recorded in the landscape (Clarke and Warwick 2001). For simplicity, only the landscape features best represented within the set of transects were retained in the figures (Fig. 5). The main horizontal axis represented an altitudinal gradient, negatively related to primary productivity (rel-NDVI<sub>erdus</sub>). The vertical axis characterised the variation in aspect of the mountains, from northness-eastness to southness-westness. Throughout all rodent phases, ptarmigan and red fox abundances were strongly associated with south-westness and primary productivity (Fig. 5). Arctic fox abundance was associated with altitude in all rodent phases, although the intensity varied, while the association with aspect switched from south-westness in post-peak and low winters to north-eastness in pre-peak winters (Fig. 5). The wolverine abundance index was consistently associated to south-westness, but with varying intensity, being strong only in pre-peak winters (Fig. 5b) and potentially with a weak influence of primary productivity in post-peak winters (Fig. 5c).

In the third step, we tested whether the data supported a priori theory on top-down relationships by modelling species interactions (SEM), taking into account the effect of selected landscape features from the previous step. Only two of the hypothesised top-down effects were supported by the data. Both of these were found at intermediate and high rodent availability. There was a negative top-down effect of wolverine...
on arctic fox in pre-peak winters, and a negative top-down effect of arctic fox on ptarmigan in post-peak winters (Fig. 6). Contrary to the top-down hypothesis, some species relationships were positive. Red fox and arctic fox were positively associated in the low rodent phase, and red fox and ptarmigan were positively associated in pre-peak and post-peak winters (Fig. 6). Regarding the landscape features representing potential bottom-up effects, primary productivity decreased at higher altitude as predicted. Red fox abundance decreased at high altitudes in post-peak winters, while arctic fox abundance increased at high altitudes in those winters. Westness had a positive effect on ptarmigan in all rodent phases, on red fox in low and post-peak winters, and on wolverine in pre-peak winters (Fig. 6). The final estimates of the three SEM are reported in Supplementary material Appendix 1 Table A1.

Discussion

The aim of this study was to test if top-down drivers, previously studied primarily in summer, have significant structuring effects on the mountain tundra community...
also in winter, and whether the top-down intensity changes with the rodent cycle. In line with a priori knowledge suggesting that predator interactions are more intense in more productive tundra ecosystems (Oksanen and Oksanen 2000, Aunapuu et al. 2008, Legagneux et al. 2014), i.e. where prey resource constraints are lower, top-down effects were found in phases with relatively high food abundance (pre-peak and post-peak winters). However, top-down effects were weak and fewer than expected. For instance, there is substantial knowledge supporting a negative effect of red fox on arctic fox in summer (Elmhagen et al. 2017), but this top-down effect was not reflected in winter abundance distributions. Instead, bottom-up relationships appear to dominate the tundra community in winter. This pattern is particularly clear for the red fox, for which the tundra represents a marginal habitat on the edge of its distribution. The northern predators (wolverine and arctic fox) appear to use a different strategy to handle winter conditions. We hence suggest that winter constraints might be an important force maintaining ecosystem structure and function in tundra ecosystems.

Community effect of rodents in winter

The rodent cycle had a community effect apparent in winter, which suggests that the survey method was sufficiently robust to reflect the dynamics of the community rather than snow conditions. Ptarmigan and red fox abundance indices were significantly affected by the phase of the rodent cycle. A likely reason for the lack of a significant effect on arctic fox might be its low abundance, hence a low detectability. A contributing factor might be that conservation actions have been carried out in favour of this species in the nature reserve, including feeding at arctic fox dens (Angerbjörn et al. 2013). This has led to an increase in arctic fox population size since 2011, which could confound and reduce the effect of the rodent cycle. The feeding stations have a small entrance suitable for arctic foxes, while the larger red fox and wolverine cannot access the food. The wolverine abundance index also showed a significant increase during low years. Due to delayed implantation, the reproductive output of wolverine is affected by the food supply in early winter (Rauset et al. 2015). Hence, the increased number of wolverine tracks in low years might be due to an increased number of dispersing subadults following an increased denning success the year before, i.e. in post-peak winters. This suggests that wolverines are favoured by high food availability in the early winter after a rodent peak, although additional research is required to determine whether the effect is direct or indirect.

Spatial pattern analysis and species interactions modelling

Altitude, primary productivity and aspect appeared essential for understanding species habitat associations in the mountain tundra in winter. High altitude would represent mostly harsh weather and difficult terrain (Dahlström 1995) while primary productivity would represent food availability (MacDonald 2003). Concerning aspect, south-westness represents relatively little snowpack accumulation with shorter duration compared to north-eaestness, as solar irradiance is more intense on south-facing slopes than north-facing slopes.
and since westerly winds usually prevail in Northern Europe (Salomonsson 1995), which means that snow would predominantly drift onto the east-facing slopes.

In the associative models (NMDs), red fox and ptarmigan abundance indices were consistently associated with south-westness and primary productivity, suggesting a bottom-up effect which was confirmed when we evaluated the a priori model (SEM). Our findings suggest that red fox was limited by environmental conditions in winter, independently of the phase of rodent cycle. This result points in the same direction as other studies showing that the distribution of red fox is limited by snow depth, altitude and food resources in winter (Dalén et al. 2004, Carricondo-Sanchez et al. 2016). Although we did not find a significant top-down effect of red fox on ptarmigan, we cannot rule out the possibility that red fox has some effect on prey abundance in the mountain tundra. According to mesopredator release theory, red fox would be expected to suppress small herbivores such as ptarmigan (Soulé et al. 1988). Yet, to fully test this assumption, one would need to contrast our study area to a similar area (or a different time period) where red fox is absent.

In contrast to red fox, the landscape associations of wolverine and arctic fox appeared to vary between the phases of the rodent cycle. We suggest this indicates an ecological strategy founded in flexibility. These two species are well-adapted to cold environments and have to be opportunistic to survive the tundra winter (Prestrud 1991, Inman et al.)

Figure 6. Final structural equation model for (a) low winters (2006, 2009, 2013); (b) pre-peak winters (2004, 2007, 2010, 2014); (c) post-peak winters (2005, 2008, 2011, 2012, 2015). Path coefficients were standardised and R² indicated the variance explained by the model. Significant positive path coefficients are shown in green arrows while significant negative path coefficients are represented in red arrows. Non-significant path coefficients retained in the final model are shown in thin gray arrows.
Overall, the arctic fox abundance index appeared related to altitude. In summer, this seems to be due to exclusion from red fox at lower altitudes (Dalerum et al. 2002, Elmhagen et al. 2002). However, red fox did not appear to directly suppress arctic fox in this study. Yet, an indirect effect of red fox on arctic fox through altitude could be suggested in post-peak winters, where the effect of altitude was positive on arctic fox while negative on red fox. On the other hand, a positive association between arctic fox and red fox was found in the low rodent phase. It is therefore plausible that food scarcity and challenging winter conditions constrained both fox species and forced them to use the same resources. This is supported by Dalén et al. (2004) who observed both species within the same altitudinal range in winter, but not in summer. During harsh winter conditions, carrion and artificial food supplies are resources that both fox species would exploit and possibly share, although there is a risk that red fox monopolises such resources (Killengreen et al. 2012). Environmental constraints on both species could therefore be greater than competition, although this is likely to be the case only when red fox abundance is low (Elmhagen et al. 2017).

Our models largely failed to explain the abundance distribution of wolverine, showing only a few and weak relationships. Wolverine’s high ability to cope with unpredictable food resources, as a facultative scavenger with a food-caching behaviour, might explain the lack of pattern (Inman et al. 2012). Theory predicts that a top predator, such as wolverine, may suppress smaller predators by intraguild killing (Palomares and Caro 1999). In this study, wolverine did not appear to affect red fox in any of the models, indicating that wolverine does not exert a top-down control on red fox in the Scandinavian mountain tundra. In contrast, wolverine had a negative effect on arctic fox in the winters before peaks, although this explained very little of the variation in arctic fox abundance. As cold specialists and opportunists, wolverine and arctic fox share some characteristics which make them likely to compete for food resources. Yet, while predation on arctic fox juveniles occurs, killing of adult arctic foxes by wolverine appears rare (Tannerfeldt and Angerbjörn 1996, Mattisson et al. 2016). Also, the analyses of the spatial patterns contrast with the hypothesis-testing SEM model and suggest that, in pre-peak winters, slope aspect might be determining the distribution of wolverine and arctic fox. The second top-down effect observed in our models was of arctic fox on ptarmigan in post-peak winters which suggests that the arctic fox may suppress ptarmigan through an alternative prey mechanism. However, this relationship appeared when an altitudinal segregation between arctic fox and red fox was found, and when red fox was positively associated with ptarmigan. This indicates that red fox may be monopolising the ptarmigan resource in productive low altitude areas, excluding arctic fox at higher altitude in those years. We suggest that ptarmigan may be more sensitive to fox predation in typical arctic fox habitat, due to lower ptarmigan densities combined with lower availability of alternative food resources.

Conclusions

While global warming may induce a dominance of top-down processes on tundra ecosystem functioning, bottom-up effects might still overrule competition and predation pressures, especially during periods of strong constraints. In the case of our study, the results did not support the a priori hypothesis that top-down interactions prevail over bottom-up effects in winter. It shows that seasonality and pulsed resources can influence this dominance ratio and therefore be key to the maintenance of ecosystem functioning and structure in sub-Arctic tundra. In harsh winter conditions, and when food supply is low, environmental constraints appear to have a stronger influence on the community structure than species interactions. The observed lack of negative associations between red fox and arctic fox supports this idea; as well as the fact that the northern predators (arctic fox and wolverine) used the landscape differently over the years, suggesting their ecology to be driven more by the unpredictability of food resources than the presence of competitors. Interestingly, red fox distribution was opposite to this pattern, being mainly dependent on westness and ptarmigan presence. The different strategies in cold specialists and ‘boreal invaders’ might even reinforce the lack of top-down effects, but only as long as there are periods or habitats characterised by strong resource constraints. Conversely, in a biome increasingly affected by global warming, weakened bottom-up control would imply that boreal species such as red fox are no longer constrained from expanding in northern ecosystems. The interaction between summer and winter conditions could have important consequences for the rate of ecosystem change in response to climate change, where slower changes in winter climate could buffer against productivity-driven changes in summer. Thus, this study highlights the importance of seasonal constraints in northern ecosystems and that winter severity still appears to be an important force counteracting the effects of global warming in the Fennoscandian mountain tundra. It also shows the need to investigate ecosystem structure and functioning through the scope of seasonality, where main ecological theories should include winter and a more dynamic perspective in order to better grasp the future effects of global warming on biodiversity.

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Supplementary material (Appendix ECOG-03984 at <www.ecography.org/appendix/ecog-03984>). Appendix 1.