

RESEARCH ARTICLE

Predator co-occurrence in alpine and Arctic tundra in relation to fluctuating prey

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Abstract

1. Large carnivores influence ecosystem dynamics in multiple ways, for example, by suppressing meso-carnivores and providing carrions for smaller scavengers. Loss of large carnivores is suggested to cause meso-carnivore increase and expansion. Moreover, competition between meso-carnivores may be modified by the presence of larger carnivores. In tundra ecosystems, the smallest meso-carnivore, the Arctic fox, has experienced regional declines, whereas its larger and competitively superior congener, the red fox, has increased, potentially due to changes in the abundance of apex predators.
2. We explored if variation in the occurrence of wolverine and golden eagle impacted the occurrence and co-occurrence of the Arctic fox and red fox in relation to varying abundances of small rodents within the Scandinavian tundra.
3. We applied multi-species occupancy models to an extensive wildlife camera dataset from 2011–2020 covering 98 sites. Daily detection/non-detection of each species per camera trap site and study period (late winter; March–May) was stacked across years, and species occupancy was related to small rodent abundance while accounting for time of the year and status of simulated carcass.
4. The Arctic fox was more likely to co-occur with the red fox when the wolverine was present and less likely to co-occur with the red fox when golden eagles were present and the wolverine was absent. Red foxes increased in occupancy when co-occurring with the larger predators. The Arctic fox responded more strongly to small rodent abundance than the red fox and co-occurred more often with the other species at carcasses when rodent abundance was low.
5. Our findings suggest that the interspecific interactions within this tundra predator guild appear to be surprisingly intricate, driven by facets of fear of predation, interspecific mediation and facilitation, and food resource dynamics. These dynamics of intraguild interactions may dictate where and when conservation actions targeted towards the Arctic fox should be implemented.

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KEYWORDS

carnivores, competition, co-occurrence, intraguild interaction, occupancy, predation, resource availability, tundra

1 | INTRODUCTION

Terrestrial carnivore communities are among the most susceptible to change in the Anthropocene (Estes et al., 2011). From a global perspective, many large carnivore populations have declined over the past century (Ripple et al., 2014), although recently some have started to recover following protection and conservation-orientated action plans (Chapron et al., 2014; Miller et al., 2013). Large predators have several important ecosystem functions, one of which is the top-down structuring of the carnivore guild by suppressing meso-carnivores, either by killing them or instilling fear (Ritchie & Johnson, 2009). A decline in large predator populations may, thus, allow meso-carnivores to increase in abundance and extend their range (Hellmann et al., 2008; Ritchie & Johnson, 2009), which could impose cascading negative effects on smaller carnivores through changes in both intra-guild predation and interspecific competition (Elmhagen et al., 2010; Polis et al., 1989; Prugh et al., 2009).

An important driver of interspecific interactions is resource availability, which constrains species' distributions, particularly in marginal ecosystems such as the alpine and Arctic tundra. Many tundra ecosystems are characterized by relatively low primary productivity and cyclicity in primary consumer populations within simple tri-trophic food webs (Ims & Fuglei, 2005; Killengreen et al., 2007; Legagneux et al., 2012). The ecological context characteristics of Arctic-alpine tundra are, however, rapidly changing due to climate warming (IPCC, 2018; Post et al., 2009). Increasing frequency of rain-on-snow and icing events in winter (Peeters et al., 2019) disrupt cyclicity and reduce the abundance of small rodents (Kausrud et al., 2008) and cause increased reindeer mortality (Hansen et al., 2019; Sokolov et al., 2016). While the former phenomenon poses a challenge for carnivores that are specialized in rodent prey (Ims et al., 2017), the latter poses an opportunity for generalist carnivores, in particular scavengers (Killengreen et al., 2011). Consequently, while rodent specialists have been declining in alpine, sub-Arctic and low-Arctic tundra ecosystems (Elmhagen et al., 2017; Ims & Fuglei, 2005), boreal scavengers have experienced range expansions, likely facilitated by increased access to carcasses in winter (Elmhagen et al., 2015; Henden et al., 2014; Killengreen et al., 2012).

The Arctic fox *Vulpes lagopus* has been considered critically endangered for the past 90 years in Fennoscandia (Henriksen & Hilmo, 2015), struggling to recover from an extinction-critical event in the early 20th century from overharvest. Conservation efforts (supplemental feeding, red fox culling and release of captive-bred foxes) were initiated in 2000 to increase the population (Angerbjörn et al., 2013; Hemphill et al., 2020; Ims et al., 2017; Landa et al., 2017), and the population has since started to recover (Ulvund et al., 2021; Wallén et al., 2021).

Expansion of the red fox *Vulpes vulpes* has been identified as the most important limitation to Arctic fox recovery (Elmhagen et al., 2017). Interference competition between the fox species favours the larger red fox, and several cases of intraguild predation on Arctic foxes have been documented (Pamperin et al., 2006; Tannerfeldt et al., 2002). The presence of larger predators could influence interactions between the two fox species, thus impacting Arctic fox conservation efforts. In the Fennoscandian tundra, the wolverine *Gulo gulo* and golden eagle *Aquila chrysaetos* are the most commonly occurring large predators, although at varying densities (Chapron et al., 2014). The wolverine is considered a facultative scavenger and predator that uses carrion to a large extent, notably in winter (Mattisson, Persson, et al., 2011), but may kill both Arctic and red fox (Frafjord et al., 1989). Wolverine populations have recovered from low densities, but are strongly regulated through political management in Norway, whereas the wolverine population in Sweden is fully protected (Gervasi et al., 2015). After being protected for half a century, the abundance of golden eagle has also increased in both countries, becoming common in alpine and Arctic tundra (Dahl et al., 2015; Linnell & Tveraa, 2015). Although the golden eagle within tundra habitats mainly prey on grouse *Tetraonidae* spp. and mountain hare *Lepus timidus*, they can kill and consume both red and Arctic fox (Nyström et al., 2006; Sulkava et al., 1999). Since the Arctic fox is small and restricted to habitats without vegetation cover, they may be more vulnerable to predation from eagles than red foxes. Little is however known about the functional role of these apex carnivores in tundra ecosystems, and their impact on meso-carnivores is not fully explored. Understanding the complex relationships between species in the broader context of the food webs is imperative for successful ecosystem-wide management.

Here, we investigate the patterns of species co-occurrence within the tundra carnivore guild in alpine and Arctic Norway. We used a spatially and temporally extensive dataset derived from camera traps placed on simulated carcasses, focusing on how species co-occurrence may be conditionally dependent on local guild structure and fluctuating resource availability (density of small rodents). We were particularly interested in assessing whether the presence of the two larger predators (wolverine and golden eagle) impacted the occurrence of the meso-carnivores (red fox and Arctic fox), and the impact of the occurrence of the red fox on the occurrence of the Arctic fox. We expect the Arctic fox to respond most strongly to changes in small rodent density, being the smallest and potentially most vulnerable member of the guild, and also a specialist on small rodents (Elmhagen et al., 2000). We predict a relatively higher dominance of the larger carnivores and lower occurrence of meso-carnivores at carcasses when rodents are abundant, as the foxes could then afford to avoid the risky encounters with the larger carnivores at the simulated carcasses. Conversely, due to an increased

willingness to risk predation, or to accept competition, we predict to find a higher level of co-occurrence between the species on simulated carcasses when rodent abundance is low.

2 | MATERIALS AND METHODS

2.1 | Study areas

We conducted camera trap studies from 2011 to 2020 during late winter (March–May) within four alpine tundra areas (Snøhetta, Kjøli, Lierne and Børgefjell (63–66°N)) and in one low-Arctic tundra area (eastern Finnmark, 70–71°N) in Norway (Figure 1). The alpine tundra areas, predominantly within the lower to mid-alpine vegetation zones with a continental climate, are dominated by willow shrubs *Salix* spp., juniper *Juniperus communis* and dwarf birch *Betula nana* (Moen, 1998). The low-Arctic tundra area covers coastal lowlands and tundra highlands (Ims et al., 2017), dominated by dwarf-shrub heath (Killengreen et al., 2007).

Most of the alpine and Arctic tundra in Fennoscandia represents historical breeding grounds for Arctic fox, though the current population is highly fragmented into small and fairly isolated subpopulations (Herfindal et al., 2010). The Snøhetta population (Figure 1) was functionally extinct at the start of the 21st century but has recovered due to the release of captive-bred foxes (Landa et al., 2017). In Kjøli and Lierne, the population is recovering through natural immigration, supplemental feeding and culling of red foxes (Angerbjörn et al., 2013; Hemphill et al., 2020). In Børgefjell, the Norwegian part of the population has remained stable without conservation actions. The northernmost population in eastern Finnmark (Varanger peninsula) has decreased over the past decades (Ims et al., 2017), but has from 2018 started to recover through the release of captive-bred foxes and supplemental feeding. Culling of red foxes has been conducted here since 2005 in the eastern part of the study area. In 2021, the total population size within the alpine tundra study areas has been estimated to 178–188 individuals, with 22–26 individuals in the Arctic tundra study area (minimum estimates based on genetic identification; Ulvund et al., 2021).

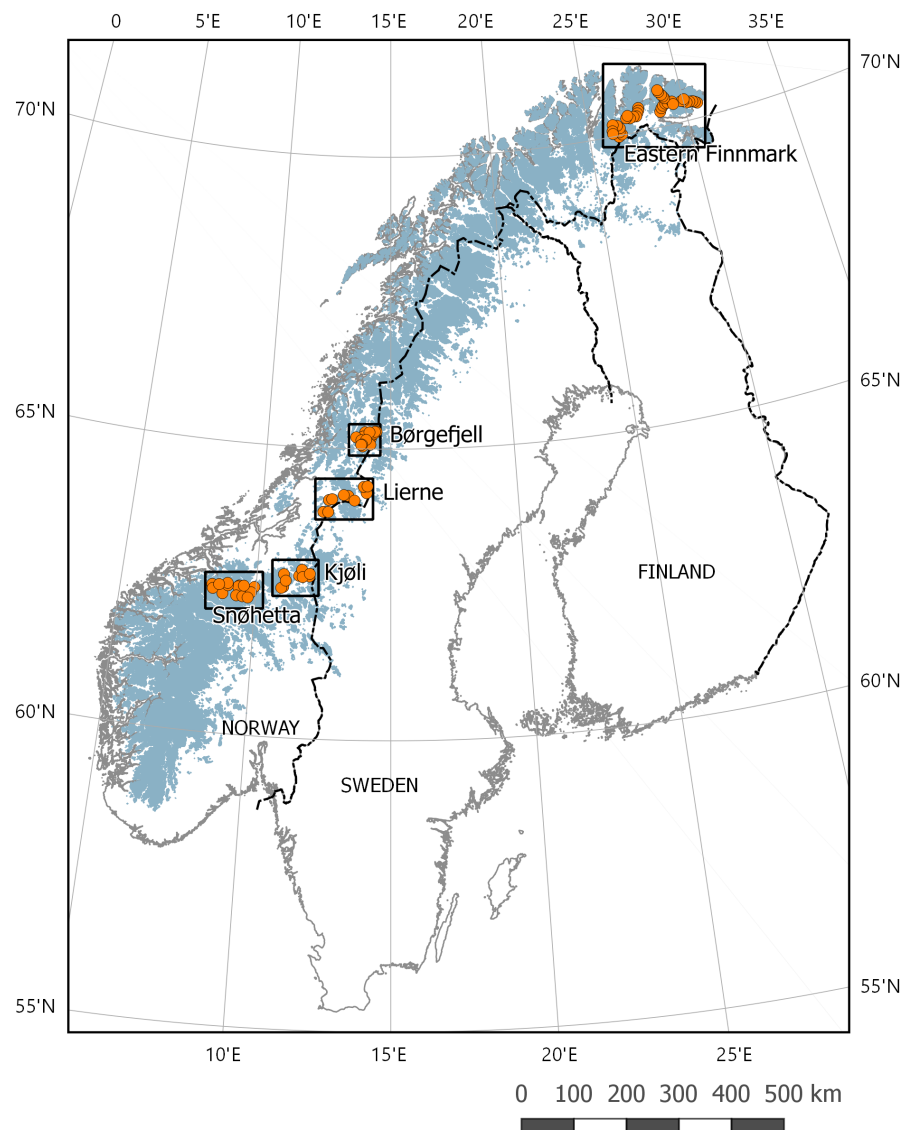


FIGURE 1 Location of the five study areas in Norway. Blue areas represent areas above the forest line. Orange points represent camera trap locations. The four southernmost areas belong to the alpine tundra region, while the northernmost area belongs to the Arctic region.

The current densities of red foxes are unknown, although likely lower in the alpine than in the Arctic regions (Ims et al., 2017). The abundance of wolverine and golden eagle is fairly similar between the two regions (Bischof et al., 2019; Dahl et al., 2015). Common prey species for the carnivore guild include Norwegian lemming *Lemmus lemmus*, vole *Microtus* spp. and *Myodes* spp., mountain hare, ptarmigan *Lagopus* spp. and reindeer *Rangifer tarandus*. Population dynamics of both the Arctic fox and red fox are influenced by the abundance of small rodents (lemmings and voles), and both use carrion, in particular reindeer carrion in the Arctic tundra, to a large extent in winter (Angerbjörn et al., 2013; Henden et al., 2009; Killengreen et al., 2011). Lemmings and voles exhibit inter-specifically synchronous 3–5-year population cycles in alpine and Arctic tundra in Fennoscandia (Ehrich et al., 2020; Henden et al., 2009). However, the small rodent cycles are often spatially asynchronous between the two regions, as the Arctic cycle length tends to be on average longer (4–5-year) than the alpine cycles (3–4-year) (Henden et al., 2009).

The availability of carrion in tundra regions is closely linked to the abundance of reindeer (Henden et al., 2014). In the alpine tundra region, wild reindeer occur in Snøhetta (approximately 2500), whereas semi-domesticated reindeer migrate into Kjølø, Lierne and Børgefjell in summer (approximately 20,000) (Norwegian Agriculture Agency, 2019; Solberg et al., 2017). In the low-Arctic tundra study area, there are approximately 40,000 semi-domesticated reindeer present in summer, with a varying number in winter due to partial migration (Henden et al., 2014; Norwegian Agriculture Agency, 2019).

Since the alpine and Arctic areas are different in terms of availability and temporal dynamics of resources (small rodents and reindeer), the abundance of species within the carnivore guild, as well as varying intensity of conservation actions directed towards the recovery of the Arctic fox, we chose to treat them as two separate regions in our analysis.

2.2 | Camera trapping

We used a total of 98 camera trap sites (Reconyx HyperFire PC800; Reconyx, Inc.), with 18 at Snøhetta (2011–2013), 7 at Kjølø (2011–2019), 10 at Lierne (2011–2020), 18 at Børgefjell (2011–2020) and 44 in eastern Finnmark (2011–2020), with some variation between years in the number of sites used. Camera traps were placed semi-randomly (adjusted for topography) above the tree line within each mountain area, with an average of 10 kilometres between cameras, and on the same locations in subsequent years. Necessary permits for the placement of baited camera traps were acquired from landowners and local management authorities for the study period (2014/602-432.3, 2010/9302-432.2, 2008/875/6/K45, 2014/2107-432.3). The study followed guidelines provided by the Norwegian Data Protection Authority regarding remote sensing and the Norwegian Food Safety Authority regarding the use of locally procured and certified baits, in addition to current Norwegian legislation.

Data were collected during March, April and May, when both the red and Arctic fox increase their activity due to mating and foraging

prior to denning (Landa et al., 1998; Lindström, 1989), thus increasing the probability of detection. We used the camera trapping protocol developed by Hamel et al. (2013). Each camera trap site was baited with scraps and trimmings from locally slaughtered reindeer, frozen into blocks weighing 15–20 kg, simulating a carcass. The bait, batteries and memory cards were replaced once after approximately 3 weeks. Camera traps were mounted approximately 1 m above the snow, tilted slightly towards the bait at a distance of 5–6 m. The cameras were set to a time lapse of 5 min (10 min in eastern Finnmark 2011–2014), and photos from all the camera traps were manually processed according to a predefined template, ensuring the uniform recording of metadata.

2.3 | Explanatory variables

As the population dynamics of fox species are influenced by the cyclicity of small rodent abundances, we included *relative rodent abundance* as our main predictor for estimating occupancy, using rodent indices (number of trapped rodents per 100 trap days) obtained from the Terrestrial Monitoring Program in Norway (TOV) for the alpine region (index range 0–33.9; Framstad & Eide, 2021) and the Climatological Observatory for Arctic Tundra (COAT) for the low-Arctic region (index range 0–15; Ims et al., 2017). To control for geographic variation in the probability of occupancy within regions, we included the product of *longitude* and *latitude* for each site as a covariate for the marginal occupancy, that is, species-specific occupancy unconditional on the presence or absence of other species. We included *carcass availability*, coded as either present (1) or absent (0), as a detection covariate for all species, as empirical observations indicated a decrease in species detections when the bait was absent or unavailable (i.e. consumed or buried in snow). Similarly, we included *day of the year* as a detection covariate for all species to account for temporal variation in detection throughout each study period.

2.4 | Statistical analysis

A total of 6,472,453 images were included in the dataset. From these, we removed 727,753 images that were of too poor quality due to ice/snow on the camera lens or technical failure. Camera traps were active at a median of 45 days in the alpine region (range 1–78) and 33 days in the Arctic region (range 2–58; short activity periods were due to technical failures) per year. To balance the data, the detection period replicates were limited to the 75% quantile of active camera trap days, that is, the first 54 days in the alpine region and the first 37 days in the Arctic region, which would ensure the capture of elusive species (c.f. Hamel et al., 2013; Kays et al., 2020). This resulted in 3,403,116 images included in the analysis for the alpine region, and 2,031,706 images for the Arctic region. As our data consisted of binary detection/non-detection (0/1) events for each species, we used a multi-species occupancy model (Rota et al., 2016) to investigate the co-occurrence of >2 species, using the function 'occuMulti'

in package 'UNMARKED' in R version 4.0.3 (Fiske & Chandler, 2011; R Core Team, 2021). This type of model, extended on the occupancy modelling framework proposed by MacKenzie et al. (2003), was designed to analyse spatial co-occurrence of multiple species at a large geographical scale using detection/non-detection data while accounting for imperfect detection (c.f. Rota et al., 2016).

The main aim of our study was to investigate co-occurrence probabilities and not, for instance, temporal trends or estimating colonization or extinction. Thus, we stacked all sites and years in our analysis for a total of 314 site-years, that is, the number of active camera trap sites \times active camera trap years, in the alpine region and 354 site-years in the Arctic region. Each stack was constructed as a matrix ($x \times y$) of daily detection (1) and non-detection (0) of each species (x) per site-year (y). We assumed that each year and camera station represented an independent replicate of species assemblages.

Multi-species occupancy models can be complex as they require the specification of detection (ρ) and occupancy (ψ) parameters for each species, as well as parameters associated with the interactions between species. Our data, although including a fairly long time series, only included 98 distinct camera trap sites, which provided a challenge in estimating co-occurrence while simultaneously correcting for environmental noise and avoiding overparameterization. Hence, we defined six models for multi-species occupancy in response to our predictions (two models for each prediction; with and without rodent abundance), each of which included all four of our species of interest (Table 1). All models included *latitude* \times *longitude* as a covariate on the marginal occupancy of each species, and *carcass availability* and *day of the year* as covariates on the probability of detection for each species. The first model (1) included no additional covariates on the marginal occupancy of each individual species and assumed no interaction between species (all species interaction terms were fixed at 0). The second model (2) was identical to the first but included rodent abundance as a covariate on the marginal occupancy probability of each species. The third model (3) included no covariates on the marginal occupancy of each individual species and assumed interactions between each pair of species (no covariates, and higher-level interaction terms fixed at 0). The fourth model (4) was identical to the third but included rodent abundance as a covariate on the pairwise interactions between species. The fifth model (5) included no covariates on marginal occupancy and no covariates on the pairwise or higher-level interactions between species (all interaction terms at intercept). The sixth model (6) was identical to the fifth but included rodent abundance as a covariate on the interaction between three and four species. Each model was validated with a fivefold cross-validation process with a holdout of 25%, assessing how close the simulated (predicted) and observed data are to each other. From this validation process, we provide two measures of model accuracy, the root mean square error and the mean absolute error, where values closer to zero indicate a better fit to the observed data. In addition, we inspected parameter estimates and confidence limits to avoid the effects of overparameterization. 95% confidence limits for predicted probabilities were estimated using parametric bootstrapping with 5000 samples. Model parameters

TABLE 1 A simplistic definition of the six models for multi-species occupancy, along with a goodness-of-fit test for each model from a fivefold cross-validation. Species are represented by letters (R = red fox, A = Arctic fox, W = wolverine, G = golden eagle), where a combination of letters represents species interactions. α is the marginal intercept, β and γ are slope parameters for longitude \times latitude and rodent index, respectively. δ and ε are the conditional intercepts for pairwise and three- and four-way interactions, respectively, whereas η is the slope parameter for rodent index. RMSE is the root mean square error and MAE is the mean absolute error

Model	Marginal	Conditional	Alpine		Arctic	
			RMSE \pm SD	MAE \pm SD	RMSE \pm SD	MAE \pm SD
1	$\alpha_{R,A,W,G} + \beta_{R,A,W,G} \text{longlat}$	0	0.291 \pm 0.012	0.160 \pm 0.009	0.271 \pm 0.012	0.142 \pm 0.006
2	$\alpha_{R,A,W,G} + \beta_{R,A,W,G} \text{longlat} + \gamma_{R,A,W,G} \text{rodents}$	0	0.291 \pm 0.004	0.161 \pm 0.002	0.269 \pm 0.010	0.140 \pm 0.004
3	$\alpha_{R,A,W,G} + \beta_{R,A,W,G} \text{longlat}$	$\delta_{R,A,RW,RG,AW,AG,WG}$	0.286 \pm 0.008	0.157 \pm 0.006	0.269 \pm 0.009	0.141 \pm 0.004
4	$\alpha_{R,A,W,G} + \beta_{R,A,W,G} \text{longlat}$	$\delta_{R,A,RW,RG,AW,AG,WG} + \eta_{R,A,RW,RG,AW,AG,WG} \text{rodents}$	0.289 \pm 0.008	0.160 \pm 0.004	0.270 \pm 0.005	0.142 \pm 0.005
5	$\alpha_{R,A,W,G} + \beta_{R,A,W,G} \text{longlat}$	$\delta_{R,A,RW,RG,AW,AG,WG} + \varepsilon_{R,A,W,RAG,AW,AG,WG}$	0.288 \pm 0.016	0.159 \pm 0.010	0.267 \pm 0.015	0.140 \pm 0.007
6	$\alpha_{R,A,W,G} + \beta_{R,A,W,G} \text{longlat}$	$\delta_{R,A,RW,RG,AW,AG,WG} + \eta_{R,A,W,RAG,AW,AG,WG} \text{rodents}$	0.289 \pm 0.007	0.160 \pm 0.004	0.268 \pm 0.009	0.140 \pm 0.003

and confidence intervals were estimated as log-odds ratio and back-transformed to probabilities presented as a proportion (0–1) with associated lower 2.5% and upper 97.5% confidence limits.

3 | RESULTS

Of the combined 12,914 camera trap days in the alpine region, Arctic foxes were detected on 1395 days and at 48% of the combined site-years. Red foxes were detected on 1938 days and 75% of the site-years, wolverines on 726 days and 60% of site-years, and golden eagles on 650 days and 54% of site-years. In the Arctic region, Arctic foxes were detected on 399 days out of a combined 10,558 camera trap days, and at 24% of the site-years. Red foxes were detected on 2162 days and at 84% of the site-years, wolverines on 418 days and at 41% of the site-years and golden eagles on 530 days and at 40% of the site-years.

3.1 | Probability of detection and marginal occupancy covariates

The predicted average probability of detection (model 1 in Table 1; Table S1a,b) varied between species within both regions, where the Arctic and red fox had an overall higher probability of detection than wolverine and golden eagle (Table 2). The predicted probability of detection in both regions was higher when the *carcass* was present compared with absent, and increased throughout the study period, except for golden eagle in the Arctic region (Figure S1a,b). In the alpine region, the predicted average marginal occupancy probability (model 1) of the Arctic fox increased from the southwestern parts of the study area towards the northeastern parts, with an opposite pattern for the other species (Figure S2a). In the Arctic region, the predicted average marginal probability of occupancy of the Arctic fox increased from west to east, but with no clear pattern for the other species (Figure S2b).

3.2 | Single-species response to rodent abundance

Based on the marginal occupancy analysis including rodents (model 2 in Table 1; Table S2a,b), the Arctic fox responded, as we predicted,

more strongly than the other species to rodent abundance, which was particularly evident in the alpine region where occupancy of Arctic fox declined steeply with increasing rodent abundance (Figure 2a). In the Arctic region, occupancy of both the Arctic and red fox declined slightly with increasing abundance of small rodents (Figure 3a). For both regions, wolverine showed no clear response to rodent abundance, whereas the occupancy of golden eagle increased slightly with increasing abundance of small rodents (Table S2a,b).

3.3 | Pairwise co-occurrence

The conditional pairwise analysis (model 3 in Table 1; Table S3a,b) in the alpine region revealed that the mean probability of Arctic fox occupancy was similar with both the presence and absence of red fox and wolverine, respectively, but was lower with presence compared with the absence of golden eagle (Table 3a). When including rodents (model 4 in Table 1; Table S4a,b), the probability of Arctic fox occupancy in the alpine region declined with increasing rodent abundance in the presence of red fox and wolverine, respectively, and was consistently lower in the presence of golden eagle (Figure 2a). Red fox occupancy was higher when co-occurring with golden eagle, independent of rodent abundance (Table 3a; Figure 2a).

In the Arctic region, the mean probability of occupancy was higher for Arctic foxes in co-occurrence with wolverine (Table 3b). This relationship was relatively constant with increasing rodent abundance. Occupancy of Arctic foxes declined with increasing rodent abundance when co-occurring with the red fox (Figure 3a). Red fox occupancy was consistently high, independent of the absence or presence of larger predators (Table 3b; Figure 3a).

3.4 | Multi-species co-occurrence

In both regions, the mean predicted probability of occupancy (model 5 in Table 1; Table S5a,b) of Arctic fox was relatively higher in co-occurrence with the larger predators when the red fox was absent compared with when all four species were present (Table 4). The absence of wolverine lowered the probability of occupancy of Arctic fox when co-occurring with red fox and golden eagle, compared with when wolverine was present and either red fox or golden eagle was absent (Table 4). The mean predicted probability of occupancy for

TABLE 2 Predicted average probabilities of detection and marginal occupancy from the marginal occupancy analysis (model 1 in Table 1) for each species within the alpine and Arctic regions. *Site-years* refers to the number of camera trap sites × years where each species was detected. Numbers in brackets are the 95% confidence interval

Species	Alpine			Arctic		
	Site-years	Detection	Occupancy	Site-years	Detection	Occupancy
Arctic fox	149	0.22 [0.20, 0.23]	0.48 [0.38, 0.58]	85	0.13 [0.11, 0.16]	0.25 [0.18, 0.35]
Red fox	236	0.19 [0.18, 0.20]	0.77 [0.66, 0.84]	296	0.24 [0.23, 0.26]	0.84 [0.75, 0.90]
Wolverine	189	0.09 [0.08, 0.10]	0.64 [0.53, 0.74]	146	0.08 [0.07, 0.10]	0.48 [0.37, 0.60]
Golden eagle	170	0.09 [0.08, 0.10]	0.58 [0.46, 0.68]	141	0.12 [0.10, 0.13]	0.42 [0.32, 0.53]

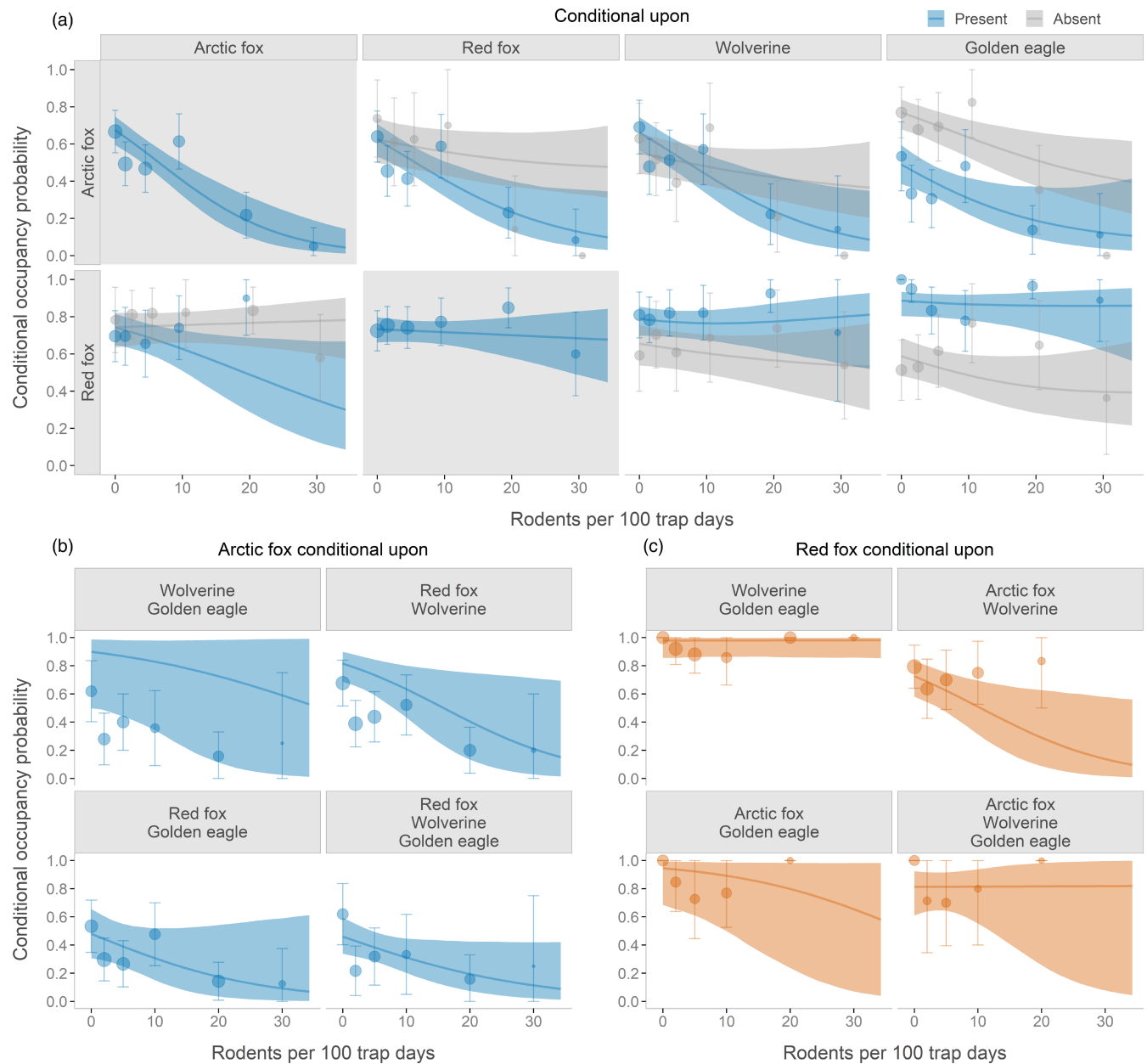


FIGURE 2 Alpine. Predicted marginal and conditional occupancy probability in relation to the abundance of small rodents (rodents per 100 trap days); (a) predicted marginal occupancy of Arctic fox and red fox (grey panels; model 2 in Table 1), with white panels showing the predicted probability of occupancy of the species in each row conditional on the presence and absence of the species in each column, based on the conditional pairwise analysis (model 4 in Table 1); (b, c) predicted probability of Arctic fox (b) and red fox (c) occupancy conditional on the presence and absence of Arctic/red fox, wolverine and golden eagle, based on the three- and four-way conditional occupancy analysis (model 6 in Table 1). Panel strip labels indicate which species are present. For all panels, solid lines indicate the predicted probability of occupancy, and shaded areas represent 95% confidence limits. Predictions were made with *longitude* × *latitude* fixed at the observed median. Circles show the mean naïve occupancy for single species (grey panels) and co-occurrences, grouped by rodent index at intervals 0, 0–2, 2–5, 5–10, 10–20 and 20–35. Error bars represent 2 × standard error. The size of the circles indicates the relative number of site-years occupied per group.

red fox was slightly lower in co-occurrence with Arctic fox and wolverine when golden eagle was absent, compared with when all species were present (Table 4).

When including rodents (model 6 in Table 1; Table S6a,b), Arctic fox occupancy in the alpine region declined with increasing rodent abundance for all predator assemblages and was highest at low rodent abundance in the absence of red fox and golden eagle, respectively (Figure 2b). The Arctic fox showed an overall similar pattern

in the Arctic region, although occupancy increased with increasing rodent abundance in co-occurrence with wolverine and golden eagle when the red fox was absent (Figure 3b). In both regions, red fox occupancy declined with increasing rodent abundance when the golden eagle was absent, with a steeper decline in the alpine region (Figures 2c and 3c). In other species assemblages, red fox occupancy was relatively high and to a lesser degree affected by rodent abundance.

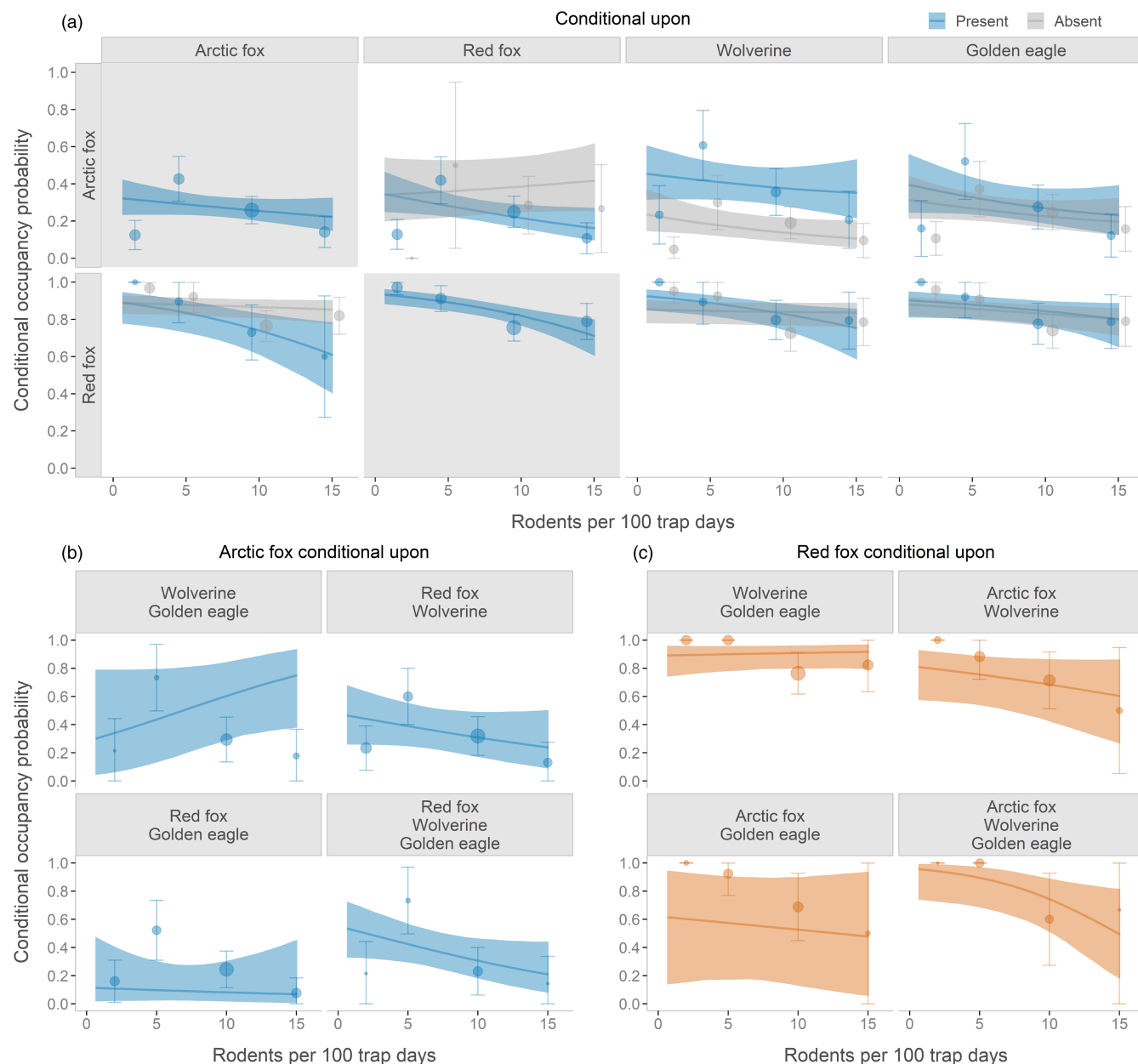


FIGURE 3 Arctic. Predicted marginal and conditional occupancy probability in relation to the abundance of small rodents (rodents per 100 trap days); (a) predicted marginal occupancy of Arctic fox and red fox (grey panels; model 2 in Table 1), with white panels showing the predicted probability of occupancy of the species in each row conditional on the presence and absence of the species in each column, based on the conditional pairwise analysis (model 4 in Table 1); (b, c) predicted probability of Arctic fox (b) and red fox (c) occupancy conditional on the presence and absence of Arctic/red fox, wolverine and golden eagle, based on the three- and four-way conditional occupancy analysis (model 6 in Table 1). Panel strip labels indicate which species are present. For all panels, solid lines indicate the predicted probability of occupancy, and shaded areas represent 95% confidence limits. Predictions were made with *longitude* × *latitude* fixed at the observed median. Circles show the mean naïve occupancy for single species (grey panels) and co-occurrences, grouped by rodent index at intervals 0–2, 2–5, 5–10 and 10–15. Error bars represent 2× standard error. The size of the circles indicates the relative number of site-years occupied per group.

4 | DISCUSSION

Co-occurrence between the meso-carnivores at simulated carcasses was impacted both negatively and positively by the occurrence of larger predators. Interestingly, this contradicts our expectation that meso-carnivores would overall avoid larger carnivores. Even the smaller Arctic fox exhibited contrasting patterns in co-occurrence

with larger carnivores. The Arctic fox tended to occupy sites with golden eagle less often, whereas the presence of wolverine seemed to some extent to mitigate the negative co-occurrence between Arctic fox and golden eagle. The degree of co-occurrence between the two meso-carnivores shifted, as predicted, with prey density, where the Arctic fox co-occurred more often at sites with the red fox when rodent abundance was low compared with when rodent

TABLE 3 Predicted average probabilities of species occupancy in alpine (a) and Arctic (b) study regions. Probabilities are from the conditional pairwise analysis (model 3 in Table 1) of the species in each row conditional on the presence and absence of the species in each column. Numbers in brackets are the 95% confidence intervals. Bold cells indicate statistically significant differences between presence and absence

	Pres./Abs.	Arctic fox	Red fox	Wolverine	Golden eagle
(a) Alpine					
Arctic fox	Present		0.46 [0.38, 0.54]	0.49 [0.41, 0.58]	0.35 [0.27, 0.44]
	Absent		0.53 [0.40, 0.66]	0.45 [0.35, 0.56]	0.65 [0.55, 0.75]
Red fox	Present	0.74 [0.64, 0.81]		0.81 [0.73, 0.87]	0.90 [0.82, 0.94]
	Absent	0.79 [0.70, 0.85]		0.68 [0.56, 0.77]	0.60 [0.48, 0.69]
Wolverine	Present	0.66 [0.56, 0.75]	0.68 [0.59, 0.76]		0.66 [0.56, 0.74]
	Absent	0.62 [0.51, 0.71]	0.50 [0.36, 0.64]		0.62 [0.51, 0.71]
Golden eagle	Present	0.41 [0.32, 0.51]	0.67 [0.58, 0.75]	0.59 [0.50, 0.67]	
	Absent	0.72 [0.62, 0.80]	0.25 [0.15, 0.39]	0.55 [0.43, 0.65]	
(b) Arctic					
Arctic fox	Present		0.24 [0.18, 0.31]	0.35 [0.27, 0.45]	0.28 [0.20, 0.37]
	Absent		0.34 [0.22, 0.48]	0.16 [0.11, 0.24]	0.23 [0.18, 0.31]
Red fox	Present	0.78 [0.65, 0.87]		0.86 [0.77, 0.91]	0.85 [0.76, 0.91]
	Absent	0.87 [0.79, 0.91]		0.83 [0.75, 0.89]	0.84 [0.76, 0.89]
Wolverine	Present	0.69 [0.56, 0.80]	0.49 [0.40, 0.57]		0.65 [0.54, 0.75]
	Absent	0.40 [0.32, 0.50]	0.44 [0.29, 0.60]		0.35 [0.27, 0.45]
Golden eagle	Present	0.47 [0.34, 0.59]	0.43 [0.35, 0.51]	0.58 [0.47, 0.67]	
	Absent	0.41 [0.33, 0.49]	0.40 [0.26, 0.55]	0.28 [0.20, 0.38]	

TABLE 4 Predicted average probabilities of occupancy from the higher-level conditional occupancy analysis (model 5 in Table 1) of the species in each row conditional on the presence of all other species, except the species in each of the middle columns

Region	Species	All species present, except				
		Red fox	Arctic fox	Wolverine	Golden eagle	All present
Alpine	Arctic fox	0.83 [0.38, 0.98]		0.34 [0.22, 0.50]	0.67 [0.54, 0.81]	0.33 [0.24, 0.45]
	Red fox		0.98 [0.89, 0.99]	0.94 [0.65, 0.99]	0.68 [0.53, 0.80]	0.84 [0.68, 0.93]
Arctic	Arctic fox	0.47 [0.24, 0.71]		0.09 [0.03, 0.27]	0.32 [0.21, 0.45]	0.34 [0.23, 0.45]
	Red fox		0.90 [0.78, 0.96]	0.52 [0.15, 0.87]	0.72 [0.48, 0.87]	0.81 [0.60, 0.92]

abundance was high. Site occupancy of the larger red fox was less affected by the occurrence of larger predators than the Arctic fox, as expected. We did, however, not expect that the red fox co-occurred more often at sites with both wolverine and golden eagle. Our results confirm that the interactions between species within this tundra predator guild are surprisingly intricate, most likely driven by facets of fear of predation, interspecific facilitation, and resource availability.

Resource availability is a major driver of predator abundance and intraguild interactions in marginal tundra habitats (Henden et al., 2010; Ims & Fuglei, 2005; Killengreen et al., 2011). For example, Stoessel et al. (2019) found that bottom-up constraints were the main determinant of species interactions during winter in Northern Sweden, where unpredictable food resources shaped the predator community structure of the alpine tundra. Many tundra species, such as the Arctic fox, depend on cyclic rodent peaks for successful reproduction and survival (Angerbjörn et al., 1999; Ims et al., 2017).

Indeed, the Arctic fox had the most pronounced response to fluctuations in small rodent abundance during our study, with a lower probability of occupancy at simulated carcasses when rodents were abundant, thus verifying our predictions. The red fox was ubiquitous within both our study regions, seemingly independent of small rodent abundance, in contrast with other studies (Henden et al., 2010). This may indicate that red foxes in our study to a larger degree could use alternative food sources such as carcasses in late winter in the tundra, or that the overall abundance of red foxes was possibly sustained by immigration from more productive ecosystems (boreal forest or coastlines). Expectedly, the Arctic fox co-occurred more often with the red fox at carcasses when the abundance of small rodents was low, likely as they are willing to risk intensified competition with the red fox for carrion resources. This pattern abated with increasing rodent abundance, when also co-occurrence with larger predators decreased, as we predicted. The influence of rodent abundance on the Arctic fox, and the co-occurrence with the red fox, was not as

pronounced in the Arctic region as in the alpine region. This could be related to a low abundance of Arctic foxes and a high abundance of red foxes within the Arctic region as a result of overall high levels of interspecific competition (Elmhagen et al., 2017), or different availability of rodents between regions and/or seasons (i.e. the predators were recorded in late winter, while the rodent data stemmed from the summer). The Arctic region also has a higher availability of reindeer carcasses (Henden et al., 2014; Tveraa et al., 2014), and provides close access to alternative food sources through coastal and marine habitats (Killengreen et al., 2011), which may particularly benefit the red fox due to its generalist and opportunistic nature.

Overall, the large predators within our study seemed to exert a structuring role through interactions with the two meso-carnivores. Surprisingly, both the red and Arctic fox were to some extent positively associated with the occurrence of wolverine in our study, particularly in the Arctic region. Wolverines roam vast areas and use a broad niche spanning both tundra, subalpine and boreal forest habitats (Landa et al., 1998). They may follow tracks of other species such as the red fox during foraging activities (van Dijk et al., 2008), and also scavenge on kills by other predators at lower elevations where they overlap with lynx *Lynx lynx* (Mattisson, Andr en, et al., 2011). As such, wolverines may both provide resources in the form of kills and provide information on the location of resources for both fox species. Such interspecific transmission of information on resource locations between scavenging species is more likely to occur when the availability of resources is low (Kane & Kendall, 2017; Orr et al., 2019), such as the winter in our study areas. Furthermore, our results reveal increased wolverine occupancy in areas with occurrence of golden eagle within the Arctic region, whereas no significant pattern was observed within the alpine region. Golden eagles, particularly young birds, roam tundra areas to a great extent during winter before nesting in March/April (Dahl et al., 2015). As such, the rate of locating carcasses used by wolverines may increase, and wolverines may also use golden eagles as visual cues for locating food (Orr et al., 2019), benefiting both species.

Although both fox species likely benefit from the interspecific transfer of information about food resources from golden eagles, the Arctic fox rarely co-occurred with golden eagles in the alpine region, whereas red fox occurrence was positively associated with golden eagles in both regions. There could be several explanations for these differences. The Arctic fox, being smaller (hare-sized) compared with the red fox, likely has a stronger fear response to golden eagles. Its larger body size may allow the red fox to use carcasses to a greater extent, strengthening the asymmetry between the two fox species. The more resource-limited red fox (Hersteinsson & Macdonald, 1992) may also need to take larger risks than the Arctic fox to cover its daily energy demands for survival in marginal tundra habitats. Lyly et al. (2015) found a positive association between red foxes and golden eagles in northern Finland and suggested that co-occurrence could be explained by the red fox' access to shelter in the forest, allowing the red fox to scavenge on golden eagle kills and increase its success in escaping predation. Occurring in the more open landscapes, the Arctic fox is likely more at risk of predation from avian predators, thus avoiding

carcasses occupied by golden eagles. This illustrates how an apex predator has a differential influence on meso-carnivores. In our case, the occurrence of golden eagles strengthened an already skewed intraguild competition between the two meso-carnivores in favour of the red fox.

The marginal occupancy probabilities of red foxes were relatively higher than Arctic foxes within both our study regions, although more so in the Arctic region. The consistent near-saturated red fox occupancy in the Arctic region may have had a persistent region-wide negative impact on the Arctic fox during the study period (Elmhagen et al., 2017). In contrast, the slightly lower and more variable site occupancy of the red fox within the alpine regions, combined with a relatively high site occupancy of the Arctic fox, may have increased the Arctic fox's access to carrion resources. This could indicate that the red fox may be a lesser threat to the Arctic fox when occurring at low densities, consistent with the findings of Lai et al. (2022) in the Canadian Arctic. When red fox abundance is relatively low, the Arctic fox may even benefit from following the red fox to locate carrion resources, especially when the abundance of rodents is low.

5 | CONCLUSIONS

Overall, our findings suggest that larger carnivores may have a structuring role on meso-carnivores by modifying their relationship through resource provisioning, but also by imposing a risk of predation. The relative strength of the interspecific interactions was indeed modified by resource availability through the natural dynamics of small rodents. Forecast climate-driven changes in the abundance of rodents may increase the future reliance on alternative food such as carrion for meso-carnivores, resulting in increased interference and predation risk from the larger carnivores, particularly for the Arctic fox. Conversely, the recovery of larger carnivores might contribute to reestablishing the natural densities of meso-carnivores, allowing them to co-exist. Although larger carnivores are slowly recolonizing Fennoscandia (Chapron et al., 2014), their current densities in many areas are likely too low to exert a regulating pressure on the meso-carnivores.

This study interestingly indicates that the recovery of one species could negatively impact another species. The recovery of the golden eagle may pose a direct threat to the recovery of the Arctic fox in Fennoscandia. This negative relationship could be density dependent, and likely less negative when the Arctic fox population occurs at viable densities. The role of the wolverine remains unclear: its current densities are likely too low to release its full structuring potential on meso-carnivores within the Scandinavian tundra ecosystem. This is also the case for the grey wolf, likely the most suppressive apex predator in northern ecosystems (Prugh & Sivy, 2020), however functionally extinct from the tundra biome in Scandinavia. As our study suggests, larger predators may currently have a low suppressive population-wide effect on the red fox, and continued boreal invasion of red fox into tundra habitats (Elmhagen et al., 2015) may therefore remain a threat to the conservation of the endangered

Arctic fox in Scandinavia. New insights into the complexity of predator interactions obtained from this study may contribute to developing knowledge-based ecosystem management practices.

AUTHOR CONTRIBUTIONS

Lars Rød-Eriksen and Nina E. Eide conceived the idea. Nina E. Eide, Siw T. Killengreen and Rolf A. Ims designed the study. Siw T. Killengreen, Dorothee Ehrich, Lars Rød-Eriksen and Nina E. Eide collected and compiled the data. Lars Rød-Eriksen analysed the data with input from Ivar Herfindal, Dorothee Ehrich and Siw T. Killengreen. Lars Rød-Eriksen led the writing of the manuscript with substantial input from all authors. All authors gave final approval for publication.

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CONFLICT OF INTEREST

The authors have no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available from Dryad Digital Repository <https://doi.org/10.5061/dryad.63xsj3v66> (Rød-Eriksen et al., 2022).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1. Alpine.

Table S1b. Arctic.

Figure S1a. Alpine.

Figure S1b. Arctic.

Figure S2a. Alpine.

Figure S6b. Arctic.

Table S2a. Alpine.

Table S2b. Arctic.

Table S3a. Alpine.

Table S3b. Arctic.

Table S4a. Alpine.

Table S4b. Arctic.

Table S5a. Alpine.

Table S5b. Arctic.

Table S6a. Alpine.

Table S6b. Arctic.

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