

# **The role of indirect interspecific effects in the stochastic dynamics of a simple trophic system**

Authors: Laura Bartra-Cabr <sup>1</sup>, Brage B. Hansen<sup>1,2,3</sup>, Aline M. Lee<sup>1,3</sup>, Kate Layton-Matthews<sup>4</sup>, Maarten J.J.E. Loonen<sup>5</sup>, Eva Fuglei<sup>6</sup>, Leif E. Loe<sup>7</sup>, Vidar Gr tan<sup>1</sup>.

Affiliations:

<sup>1</sup> Centre for Biodiversity Dynamics, Dept. of Biology, Norwegian University of Science and Technology, 7491 Trondheim, Norway

<sup>2</sup> Norwegian Institute for Nature Research, Dept. of Terrestrial Ecology, Trondheim, Norway

<sup>3</sup> Gj revoll Centre for Biodiversity Foresight Analyses, Norwegian University of Science and Technology, 7491 Trondheim, Norway

<sup>4</sup> Norwegian Institute for Nature Research, FRAM Centre, Troms , Norway

<sup>5</sup> Arctic Centre, University of Groningen, Groningen, the Netherlands

<sup>6</sup> Norwegian Polar Institute, Troms , Norway

<sup>7</sup> Norwegian University for Life Sciences, Faculty of Environmental Sciences and Natural Resource Management, H gskoleveien 12, 1432  s, Norway

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Laura Bartra Cabré

+47 973 344 02

[laurabc9@gmail.com](mailto:laurabc9@gmail.com)

## **Abstract**

Understanding indirect interspecific effects (IIEs) on population dynamics is key for predicting community dynamics. Yet, empirically teasing apart IIEs from other interactions and population drivers is data-demanding. We used stochastic population models parameterized with long-term vital rate time series to simulate population trajectories and examine IIEs in a high-arctic vertebrate trophic chain: Svalbard reindeer, its scavenger (Arctic fox), and a migratory fox prey (barnacle goose). Reindeer carcass supply shaped fox abundance fluctuations, subsequently affecting goose fluctuations. Yet reindeer and goose population growth rates were only weakly correlated, probably due to stochasticity, density dependence and life history traits. However, by isolating the effects of individual processes within our simulation model, we demonstrate the presence of strong IIEs on goose population fluctuations and extinction probability. Thus, we highlight the long-term impact of species interactions, including IIEs, on species coexistence and communities, beyond immediate effects and short-term fluctuations.

## Introduction

Interspecific interactions influence population dynamics (Bengtsson 1989; Bonsall & Hastings 2004; Holland *et al.* 2002; Pettoirelli *et al.* 2011; Rosenzweig & MacArthur 1963) and how communities respond to disturbances or environmental variation (Casas Goncalves & Amarasekare 2021; Gilman *et al.* 2010a; Novak *et al.* 2011). The mean, variability, and trends in a species' abundance can depend on the (changes in) abundance of another, directly interacting species (Abrams *et al.* 1996). This can have community-wide implications if part of an interaction chain (Wootton 1993), causing an indirect interspecific effect (IIE) where the presence or activity of a species A affects the abundance of another species B through a third intermediary species C (e.g., Figure 1). C interacts with both A and B, meaning that the indirect effect is the sum of the two direct effects (Wootton 1993). IIEs are likely to exert significant impacts on some populations' and communities' dynamics (Abrams *et al.* 1996; Menge 1997; Wootton 1993, 2002; Yodzis 2000). However, quantifying the importance of IIEs in natural systems has proven challenging. This is partly because they can be masked or counteracted by other interspecific effects (Martorell & Freckleton 2014; Menge 1997) – especially in complex ecosystems with many species (Bascompte & Jordano 2007; Holt 1977) – and impacts of demographic and environmental stochasticity (Abbott *et al.* 2009; Adler & Drake 2008; Bonsall & Hastings 2004) and life history characteristics (e.g., causing delayed dynamics; Thompson & Ollason 2001; Warner & Chesson 1985). Thus, empirically teasing apart IIEs in population dynamics requires high-quality, long-term datasets and a holistic modelling perspective involving all key species and chains of interactions (Ives & Jansen 1998; Novak *et al.* 2011).

Multispecies population modelling is a suitable approach to simultaneously account for stochasticity and the direct and indirect interactions between multiple key species in communities (Delmas *et al.* 2019). When based on empirically derived population

parameters, this approach can be used to understand the dynamics of populations over time and under different environmental and ecological conditions, also enabling predictions (e.g., through simulations) of how populations may respond to future scenarios (Gilman *et al.* 2010b). However, accurate estimates of stochastic population parameters from multiple species are demanding and require monitoring of e.g., abundances, reproductive rates, and survival rates over a considerable time frame. This poses a significant challenge to building realistic multispecies population models (Zipkin *et al.* 2023), especially in complex ecosystems with many trophic interactions (Aufderheide *et al.* 2013).

We used a multispecies stochastic modelling approach to explore the influences of direct and indirect interactions on population dynamics within a well-studied and simple vertebrate community. The model was constructed based on existing population models and established trophic linkages from long-term monitoring time series data, allowing us to simulate linked population trajectories. Our main objective was to investigate the role of IIEs in the species' population dynamics and co-fluctuations, and its structuring effect on long-term means and fluctuations in abundances. We focused on the three key species of the simple vertebrate community on the high-arctic tundra of Ny-Ålesund (Pedersen *et al.* 2022), Svalbard, a study system with few species and a comprehensive understanding of their dynamics and direct interactions (Albon *et al.* 2017; Fuglei *et al.* 2003; Hansen *et al.* 2013, 2019; Layton-Matthews *et al.* 2020; Tyler 1987). We built a joint multispecies model based on single-species population models for wild Svalbard reindeer *Rangifer tarandus platyrhynchus* (Hansen *et al.* 2019), Arctic fox *Vulpes lagopus* (Nater *et al.* 2021), and barnacle goose *Branta leucopsis* (Layton-Matthews *et al.* 2019, 2020), thus enabling simulation of linked population dynamics accounting for both deterministic and stochastic processes.

We were particularly interested in assessing implications of IIEs of the large herbivore, the resident reindeer, on the dynamics of the migratory barnacle goose, acting through

unidirectional ‘apparent competition’ due to a shared predator/scavenger, the fox (Chesson 2012; Holt 1977; Holt & Bonsall 2017). Short-term implications of this IIE were observed following a dramatic reindeer population crash during a harsh winter in 1994 (Fuglei *et al.* 2003). The crash led to a lagged shift in abundance of all three species due to direct effects of reindeer carcass abundance fluctuations on reproduction of foxes (scavenging reindeer), and of the abundance of foxes on reproduction of the goose (Layton-Matthews *et al.* 2023). Here, based on the existing stochastic population models, we simulated long-term, linked population trajectories and assessed co-fluctuations in the three species’ dynamics under observed environmental characteristics and trophic interactions. To disentangle different aspects of direct and indirect effects in this system we then compared these simulated population dynamics to the dynamics found in adjusted models. First, we isolated effects of fluctuations in the abundance of one species on the dynamics of other species by setting the parameters driving the interactions (reindeer carcasses or fox abundances) as constant. Then, we isolated the effect of each trophic interaction (carcass effect on foxes or fox effect on geese) being present or not in the system by removing it. In each case, we compared population dynamics using summary statistics and extinction rates.

## **Material and methods**

### **Study system and species**

We focus on three key species from the terrestrial vertebrate food chain in large parts of the Svalbard archipelago (74°–80°N): Svalbard reindeer, Arctic fox, and barnacle goose (Fuglei *et al.* 2003; Layton-Matthews *et al.* 2023; Pedersen *et al.* 2022). Across the Svalbard tundra, the overwintering (i.e., resident) tundra community consists of two herbivores, the Svalbard reindeer and the Svalbard rock ptarmigan (*Lagopus muta hyperborea*), and one carnivore, the

Arctic fox, a predator and scavenger. In spring and summer, migratory birds such as barnacle geese arrive in the archipelago to breed. In addition, the polar bear (*Ursus maritimus*), a marine top predator, is occasionally present on the tundra. Although the community modelled here thus represents a simplification, it includes the three key species in Ny-Ålesund (Pedersen *et al.* 2022), i.e., the study area for the barnacle goose monitoring and population modelling (see below).

Svalbard reindeer is the only large herbivore on the archipelago and plays a crucial role in the tundra ecosystem. In Svalbard, there are no effective predators of reindeer (with some rare exceptions of killings by polar bears; (Stempniewicz *et al.* 2021), and fluctuations in survival and reproduction are mainly shaped by interactions between density dependence and effects of snow conditions, including rain-on-snow (ROS) and associated icing events, as well as the length and productivity of the snow-free season (Albon *et al.* 2017; Hansen *et al.* 2019; Loe *et al.* 2021; Stien *et al.* 2012; Tyler 1987). Fluctuations in the number of reindeer carcasses are known to affect reproduction and population size of its scavenger, the Arctic fox (Eide *et al.* 2012; Fuglei *et al.* 2003; Nater *et al.* 2021), while predation by foxes on neonatal reindeer calves is rare (Prestrud 1992). Reindeer population declines due to density-dependent weather effects can result in high availability of carcasses during and following the fox breeding season, potentially leading to an increase in the Arctic fox population size for 1-2 years (Fuglei *et al.* 2003; Hansen *et al.* 2013; Layton-Matthews *et al.* 2023; Nater *et al.* 2021).

The Svalbard Arctic fox is an opportunistic predator and scavenger that feeds on a variety of prey, with no natural competitors (Eide *et al.* 2005; Prestrud 1992). During winter, the main food source is carcasses of reindeer, and occasionally seals (on the sea ice; Eide *et al.* 2012; Lai *et al.* 2017; Nater *et al.* 2021), as well as stored food (Frafjord 1993; Fuglei *et al.* 2003). In summer and spring, the Arctic fox is limited by territorial behaviour and a finite number of available den sites (Prestrud 1992). Their prey during summer mainly consists of migratory

bird species such as geese, alcids, gulls and fulmars (Prestrud 1992). In addition, Svalbard rock ptarmigans are available year-round but are of unknown importance.

The barnacle goose is one of two abundant goose species breeding in Svalbard in summer. The Svalbard barnacle geese winter in Scotland, UK, with a spring stopover at Helgeland and Vesterålen, islands along the Norwegian coast (Tombre *et al.* 2019). After the goslings have fledged in August, geese migrate to their wintering grounds. The Arctic fox plays a critical role in influencing the barnacle goose population by preying mainly on goslings (Fuglei *et al.* 2003; Layton-Matthews *et al.* 2020; Loonen *et al.* 1998; Stahl & Loonen 1998). While barnacle geese (Fox *et al.* 2005) and Svalbard reindeer (Bjørkvoll *et al.* 2009; Hansson *et al.* 2013) indeed share some food sources, particularly graminoids, their overlap in diet and habitat use is low during the short summer season when geese are present in Svalbard (Ravolainen *et al.* 2024), suggesting low competition for resources.

## Model structure

Individual population models have previously been developed for all three study species (Svalbard reindeer: Hansen *et al.* 2019; Arctic fox: Nater *et al.* 2021; Barnacle goose: Layton-Matthews *et al.* 2019, 2020). Here, we built a multispecies community model by modifying and combining these single-species population models (Supplementary material I). Our model was stochastic (i.e., including environmental and demographic stochasticity), density-dependent and age-structured, and included the two major trophic links among the three species (Figure 1). We employ population models for the three species in distinct geographic areas in Svalbard (Svalbard reindeer in Reindalen, Semmeldalen and Colesdalen; Arctic fox in Adventdalen and Sassendalen; and barnacle goose in Ny-Ålesund). This is the best combination of available empirical population models representing the system,



recognizing the inherent simplifications and assumptions involved. Yet, the similarities in environmental conditions and interspecific interactions support our key assumption that interaction effects remain consistent across Svalbard. The first trophic link was the effect of reindeer carcass abundance on fox survival and reproduction (Eide *et al.* 2012; Hansen *et al.* 2013), operating through scavenging. The second modelled trophic link was between the fox and barnacle goose, i.e., the effect of fox abundances in early summer on goose reproductive rates. More specifically, in accordance with Layton Matthews *et al.* (2020), we modelled the goose fledging probability as dependent on the proportion of fox dens occupied in early summer, i.e., the proportion active dens with cubs, which has previously been linked to fledging probability and resultant overall goose abundance in late summer (Layton-Matthews *et al.* 2020, 2023). Due to the absence of data in the literature, we were unable to parameterize the potential feedback effect of the geese on the fox., thus we assumed here that the barnacle geese do not directly affect the annual dynamics fox. Although the fox in part relies on breeding bird populations, such as geese and sea birds, over the summer, reindeer carcasses become a key resource in winter and spring due to the scarcity of alternative food sources, making this a reasonable assumption.

We used the previously published population models (Hansen *et al.* 2019; Layton-Matthews *et al.* 2019, 2020; Nater *et al.* 2021) to guide our choice of density-independent effects to include in modelling the variation in expected age-specific vital rates and annual age-specific population abundances of the three species (Supplementary material I and III). Reindeer survival and reproductive rates depended on winter length and rain-on-snow (ROS). Fox survival and reproductive rates both depended on sea ice extent and survival also depended on abundance of pink-footed goose at the wintering grounds. Barnacle goose survival and reproductive rates depended on weather conditions in both the breeding ground (i.e., Ny-

Ålesund area of Svalbard, for reproductive rates) and the overwintering/spring staging ground (Scotland/mid-Norway for survival rates).

Finally, we accounted for density dependence in all three species. Reindeer density effects were modelled following Hansen *et al.* (2019), i.e., a direct negative effect of population size on both survival and reproduction. For the Arctic fox, we remodelled the survival and reproductive rates (Supplementary material I), to also include an empirically expected (cf. Hansen *et al.* 2013) first order negative density dependence, by using the posterior distribution of Nater *et al.* (2021). Likewise, for the goose model, which already included a first-order negative density-dependent effect of population size in the wintering grounds on survival rates (Layton-Matthews *et al.* 2019), we added first-order negative density dependence (an effect of annual number of adult geese in the breeding area) in all goose reproductive steps (Supplementary material I). Goose survival rates depended on barnacle goose population abundance in Scotland.

## Simulations

We simulated time series of age-specific abundances (N, only female individuals) for Svalbard reindeer, Arctic fox, and barnacle goose (Supplementary material I). To account for dependency in parameter uncertainty across vital rate parameters (within species), parameters influencing annual variation in vital rates were drawn from posterior distributions of estimates from previously published species-specific models where available (reindeer: Hansen *et al.* 2019; Peeters *et al.* 2022; fox: Nater *et al.* 2021; Supplementary material I). For the barnacle goose, survival rates were estimated using the same capture-mark-recapture model described in Layton-Matthews *et al.* (2019). However, here, their model was re-run including scaled covariates (Scotland temperature and population sizes, Supplementary

material I). The reproductive components were available as point estimates, i.e., mean values (Layton-Matthews *et al.*, 2020), thus parameter uncertainty was only accounted for in survival for this species.

For each species and each time step (year), values of environmental covariates (and the goose overwintering population size) were simulated by drawing from the historical (i.e., observed) distribution of values. Historical values were extracted from the literature or from public sources online (Supplementary material III). We accounted for potentially correlated residual environmental noise by simulating random samples from a multivariate normal distribution with zero mean and covariance matrices based on covariances among residuals from fitted models.

Given simulated covariates, simulated environmental noise and the number of individuals in different age classes, we obtained expected survival and reproductive rates for the three species. To also account for demographic stochasticity, we simulated the realized number of survivals and recruits by using a Poisson and/or binomial distribution (see Supplementary material I). The realized number of survivors and recruits provided the next age-specific population size needed for predicting the set of survival and reproductive rates for the next iteration of the simulation algorithm.

For each set of parameters obtained from the posterior distributions of each of the species, we simulated one time series of 130 time steps (years) and removed the initial 30 time steps, to remove any bias from the given starting population sizes i.e., transient effects. We simulated a total of 9090 stochastic population size trajectories (corresponding to the 9090 posterior model estimates in Hansen *et al.* 2019) for each species. Sets of parameters leading to extinction for one of the species within the 30 initial time steps were excluded from further analysis.

## Baseline model simulations

To assess the role of indirect interspecific effects (IIEs), we simulated long-term population trajectories and assessed covariances between the species' dynamics under observed ('natural') environmental characteristics and trophic interactions (hereafter referred to as the baseline model). Using these simulated population trajectories we calculated the correlations between population growth rates [ $\log(N_{t+1}) - \log(N_t)$ ] of the three species and the two key population parameters for the trophic linkages; abundance of reindeer carcasses and number of barnacle goose recruits (fledglings per female). For each run of simulated population trajectories, we also calculated population-dynamic summary statistics and extinction rates for the three species. Population-dynamic summary statistics included (for each simulated trajectory) the mean ( $\bar{x}$ ) and median ( $\tilde{x}$ , highly similar despite non-normal distributions), variance ( $\sigma^2$ ), and coefficient of variation (CV, to account for differences in the mean) across each trajectory. In addition, we calculated the mean of the summary statistics across all trajectories.

## Effects of interspecific interactions on equilibrium distributions

We then evaluated, by simulations, the role of direct and indirect interactions in the long-term community dynamics by adjusting this baseline model. We isolated indirect effects of fluctuations in population abundances by setting fox abundances (model I) or reindeer carcasses (model III) at a constant value. To do that, we calculated the mean percentage of occupied Arctic fox dens (proxy of fox abundance, Supplementary material I), and reindeer carcass abundance from each of the simulated trajectories from the baseline model. We then used the mean abundance of each trajectory as a constant covariate value in the corresponding adjusted models. Next, we removed the interaction effects (on foxes and geese, models II and IV respectively). By comparing the simulated barnacle goose dynamics with simulations from the baseline model, adjusted models I and II were thus used to explore

effects of the direct fox-goose interaction, while models III and IV explored the effects of indirect interspecific interactions (IIEs) between the reindeer and goose.

To ensure comparability among these adjusted models and with the baseline model, we used the same sets of parameters, simulated covariates, and simulated environmental residual noise as in the baseline model. Consequently, each simulated trajectory from each of the adjusted model was paired with the corresponding simulated trajectory for the baseline model, i.e., all covariate time series (except the one under investigation, reindeer carcass number or fox abundance, depending on the adjusted model) were identical.

For each of the adjusted models, we calculated the same population-dynamic summary statistics and extinction rates as for the baseline model. To evaluate effects of interspecific interactions on the long-term dynamics (i.e., for these summary statistics), we also calculated the ratio of change in each summary statistic (Adjusted model/Baseline model) for each paired simulated trajectory. Additionally, we simulated another set of trajectories from the baseline model and calculated the ratios with the original set of trajectories from the baseline model (Baseline model/Baseline model; these ratios were expected to be close to 1, given that they represent changes within the same model). We then quantified the area of overlap between these two distributions and reported it as percentage overlap. This approach was adopted to ensure that any differences in the ratios of change between the adjusted and baseline models are not merely a result of inherent randomness or variability within the models.

## **Results**

## Cross-species correlations

The simulated population trajectories from the baseline (empirical) model showed that correlated population growth rates between directly interacting species were higher than those among indirectly interacting species (Figure 2). Reindeer population growth rates were strongly negatively correlated with the annual reindeer carcass abundances (median correlation [2.5% quantile, 97.5% quantile]:  $r = -0.97[-99, -0.92]$ ; Figure 2A). Fox population growth rates were positively correlated with reindeer carcass abundances and negatively correlated with reindeer population growth rates ( $r = 0.38[-0.16, 0.65]$  and  $r = -0.39[-0.67, 0.16]$ , respectively; Figure 2C and 2B). Fox breeding females' abundance was positively correlated with fox population growth rates ( $r = 0.50[0.13, 0.76]$ ; Figure 2F). Goose fledgling abundance (strongly positively correlated with goose population growth rates,  $r = 0.78[0.56, 0.87]$ ; Figure 2O), was negatively correlated to fox breeding females' abundance and fox population growth rates ( $r = -0.62[-0.73, -0.34]$  and  $r = -0.36[-0.61, -0.05]$ , respectively; Figure 2J and 2I). Goose population growth rates were negatively correlated with fox population growth rates ( $r = -0.40[-0.63, -0.07]$ ; Figure 2M), yet less correlated with reindeer carcass abundances and reindeer population growth rates ( $r = -0.21[-0.09, 0.42]$  and  $r = 0.21[-0.09, 0.42]$ , respectively; Figure 2L and 2K).

In this study system, lagged co-fluctuations among species can occur due to intrinsic population-dynamic properties, with reindeer density-dependent and age-structured mechanisms causing, e.g., low mortality following crash years (Hansen *et al.* 2019). Reindeer population growth rates were thus positively correlated with carcass abundances ( $r = 0.31[0.13, 0.49]$ ) as well as next year's fox population growth rates ( $r = 0.32[-0.12, 0.63]$ ), but correlations with goose population growth rates were weak ( $r = -0.16[-0.43, 0.11]$ ; Supplementary material IV).

## Effects of interspecific interactions on equilibrium distributions

Removing the fluctuations in Arctic fox population sizes (model I) caused a reduction in the mean ( $\bar{x}$ ) and variation (CV) in the barnacle goose fledgling production (per female) and population sizes, while the extinction probability increased compared with the baseline model (Figure 3). Note, however, that the population-dynamic outcome for the geese varied widely between population trajectories (Figure 4).

Removing the effect of foxes on the barnacle goose (model II), increased mean goose population sizes ~four-fold, while their variation (in terms of CV) was greatly reduced (Figures 3 and 4). Mean fledgling production was approximately identical with the baseline model, but the year-to-year variation was reduced. In this model, extinction probability was close to zero, i.e., no population trajectories went extinct.

Constant reindeer carcass abundances (model III) caused only a slight increase in mean number of breeding females and population sizes of the Arctic fox (Figures 3 and 4), as well as slightly less variation (in terms of CV) in both parameters, reducing their extinction rate (Figure 3). The IIE was evident in terms of a resultant reduction in the mean (and a slight increase in the variation, CV) of barnacle goose population sizes (yet less so in fledglings per female) and, in turn, slightly increased goose extinction rates.

When the effect of reindeer carcasses on Arctic foxes was removed (i.e., simulating no effects of reindeer in the community dynamics, model IV), the mean number of breeding females and population sizes of the Arctic fox decreased (Figures 3 and 4). A reduction in variability was evident (Figure 3), yet mainly in terms of variance, and less so for CV, which accounts for changes in the mean. As a result, fox extinction rates increased. For the goose, the IIE was evident as an increase in population sizes. The variability in these goose

parameters was reduced (except for an increase in variance of population sizes due to the increase in mean), causing a reduction in goose extinction rates (Figure 3).

## Discussion

An empirical understanding of indirect interspecific interactions (IIEs) on both short- and long-term population dynamics is key for predicting community structure and dynamics (Higashi & Nakajima 1995; Novak *et al.* 2011). Here, we have applied stochastic population models parameterized from long-term vital rate time series to simulate population trajectories and examine the role of IIEs in a simple high-arctic vertebrate food chain. Specifically, we modeled the Svalbard reindeer, a scavenger of the reindeer (Arctic fox), and a migratory prey of the fox (barnacle goose). Because the availability of reindeer carcasses shaped fox abundance fluctuations, which, through predation, strongly influenced the production of goose fledglings, the population growth rates were correlated between directly interacting species (Figure 2). This follows empirical observations and expectations (Eide *et al.* 2012; Fuglei *et al.* 2003; Hansen *et al.* 2013; Layton-Matthews *et al.* 2020, 2023; Nater *et al.* 2021). However, reindeer and goose population growth rates were only weakly correlated (Figure 2). Despite this, simulations from adjusted models removing trophic interactions or carcass or fox variability revealed that the IIE of the reindeer indeed had a substantial impact on long-term goose abundances (i.e., mean and variance) and extinction probability (Figures 3 and 4). Strong IIEs can operate in a system but manifest differently at different levels. If short-term fluctuations in abundance of one species cause co-fluctuations in other species, environmental stochasticity and perturbations can in principle cascade through the whole system (Abbott *et al.* 2009; Layton-Matthews *et al.* 2023; Menge 1995), leading to correlated dynamics between species that do not interact directly with each other. The lack of strong



annual co-fluctuations (in the long-run) in our study does not dismiss the potential importance of IIEs acting through other species' presence or absence on longer-term abundances and dynamics (Suominen *et al.* 1999). Species' presence and their (direct and indirect) interactions contribute to establishing 'equilibrium distributions' (i.e., population abundances allowing coexistence) of communities (Chesson 2000; McCann *et al.* 1998). Thus, the long-term dynamics and abundances would be expected to differ in the absence of IIEs. Removing the effect of reindeer carcasses on the fox (model IV) showed similar, yet less extreme, consequences for the goose dynamics (i.e., the mean and variability in abundances and recruitment, and extinction risk) as when the fox effects on the goose were removed (model II). In model IV, fox population dynamics showed some decline in mean population size and increase in extinction rate (yet little change in variability, in terms of CV), whereas the goose population showed a doubled mean abundance, a reduction in abundance variability (in terms of CV), and halved extinction risk. Thus, the presence of interspecific interactions indeed has an important impact on the community in the long run and this impact isn't limited to directly linked species but extends to indirectly connected ones as well.

Removing the IIE thus clearly demonstrated how it impacts the multispecies equilibrium distribution, as expected by theory (Higashi & Nakajima 1995; Spiesman & Inouye 2015; Wootton 1994). Removing fluctuations in carcass abundance (model III) influenced the long-term dynamics of the goose, as did removal of fluctuations in fox abundance (model I). With no fox variation, goose mean abundances were reduced and extinction rates increased, while the reduction in abundance variability was only slight. In typical conditions, geese populations experience fluctuations in predation rates, with some years having high predation and others having low predation (Layton-Matthews *et al.* 2020). For long-lived species, only a few years of good recruitment may be enough to sustain their population. Goose adults are

not affected by fox predation, serving as a ‘storage’ for the population. However, if the variation in predation pressure is removed, and the predation rate remains constant (and considerable), the population will not be able to produce enough recruits to maintain the population, effectively removing the storage effect (Chesson & Huntly 1997; Warner & Chesson 1985), leading to reduced abundances and higher extinction risk in the long term. Thus, based on our results, we suspect that the goose’s ability to coexist with high predation pressure is at least partly due to this storage effect. Similar reductions in goose abundances occurred due to the IIE where carcass variability was removed (model III), despite no major changes to fox dynamics. Thus, even a slight increase in the mean and decrease in the variability of fox abundances was sufficient to cause reduced goose overall abundance and increased extinction risk.

Our results indicate that the strength of co-fluctuations in annual abundances of indirectly interacting species is the product of the co-fluctuations of the directly interacting species. Indirect co-fluctuations are influenced by multiple steps that affect population dynamics of all three species. Thus, even in this ‘simple’ system with strong direct interactions, co-fluctuations in indirectly interacting species are often weak, as some correlation is lost at each step of the process. For instance, the barnacle goose is a long-lived species (Black *et al.* 2014) where, e.g., fluctuations in age-structure may result in delayed effects on population abundance (Layton-Matthews *et al.* 2019), thus decoupling a portion of the annual changes in abundance from the direct impacts of predation. IIEs might also be overshadowed by other sources of demographic and environmental stochasticity, or by density dependence, factors known to drive population dynamics (Lande *et al.* 2003; Layton-Matthews *et al.* 2020; Des Roches *et al.* 2018; Sandal *et al.* 2022) and clearly affecting survival and reproduction in both the Arctic fox and the geese (Layton-Matthews *et al.* 2019, 2020; Nater *et al.* 2021). Hence, the direct or delayed effects of internal or other external drivers of the fox and goose

dynamics mask impacts of IIEs in short-term dynamics (i.e., causing weak correlations in population growth rates).

Despite little evidence of strong short-term effects of IIEs on annual co-fluctuations when averaging over many years and simulations, specific combinations of conditions or parameters can lead to strong co-fluctuations in the shorter-term. For instance, an extreme rain-on-snow event in this system in 1994 resulted in ice-locked pastures, a reindeer population crash (from overabundance), and a burst – and subsequent long-term reduction – in both reindeer carcasses and fox abundances (Fuglei *et al.* 2003). This led to strong immediate, yet lagged co-fluctuations in population growth rates, as well as a parallel, lagged shift in abundance across reindeer, fox, and goose, lasting over a few years (Layton-Matthews *et al.* 2023). Thus, sudden perturbations of key species may still cause strong impacts of IIEs on short-term co-fluctuations (Higashi & Nakajima 1995; Piovia-Scott *et al.* 2017), which could not be captured in our model framework.

When studying IIEs empirically, it is thus crucial to keep in mind the different levels at which they can act. Many studies attempt to estimate presence or strength of interactions from time series analysis, in principle co-fluctuations in abundance (Ives *et al.* 2003; Raffaelli & Hall 1996; Sandal *et al.* 2022; Wootton 1997). Because of intrinsic and extrinsic factors mentioned above, as well as complexities related to potential nonlinearity (Ruesink 1998; Sarnelle 2003), (co)-fluctuations may seem relatively little influenced by interspecific interactions (Adler *et al.* 2018; Barabás *et al.* 2016; Sandal *et al.* 2022), and particularly IIEs. Changes in the mean abundance or variability of a key species can still shape another species' long-term dynamics (Benedetti-Cecchi 2003; Berlow 1999; Butler Iv 1989). This dichotomy of 'impacts' can be related to pulse perturbations, i.e., short-term changes or fluctuations in population size, versus press perturbations, i.e., 'permanent' changes in population size (Bender *et al.* 1984).

Our findings provide a rare empirical-based example of the underlying role of IIEs in population dynamics, acting through the mean and variance in long-term population abundances, and extinction probabilities. Because of other extrinsic as well as intrinsic population-dynamic drivers, the IIE was only barely detectable in the between-species population co-fluctuations. These patterns will probably differ for communities characterized by other life histories, other trophic interactions, or larger, more complex food webs. For instance, the dynamics of larger food webs with more diverse interactions than in our simple high-arctic study system could be more robust to changing trophic interactions (Borrvall *et al.* 2000). Nevertheless, these insights highlight the significance of considering the long-term structuring impact of species interactions, including IIEs, on communities and species' stable coexistence (Chesson 2000, 2012), i.e., beyond immediate impacts and short-term co-fluctuations in abundances of species.

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## Figures

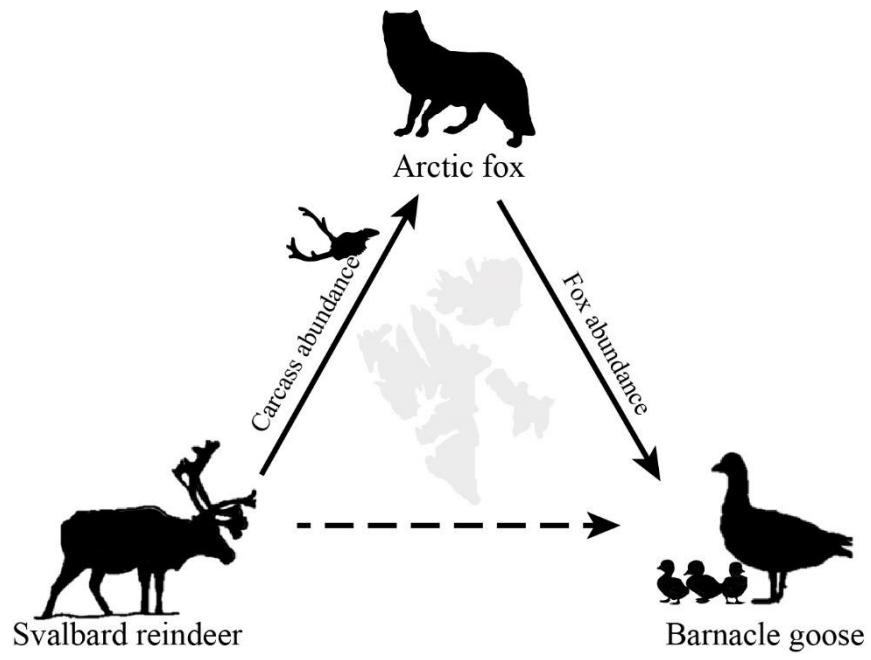
Figure 1 – Diagram of the simplified Svalbard system, links between the three species in the model (the residents Svalbard reindeer, Arctic fox and the migratory barnacle goose) and covariates affecting reproductive and survival rates. The model was composed of three species models split in the three sections: Svalbard reindeer model, Arctic fox model, and barnacle goose model. Direct interspecific effects represented with a bold arrow; indirect interspecific effects (IIEs) represented with a dashed arrow. Covariate effects were extracted from the literature and introduced in the model to estimate reproductive and survival rates of the species. Data and models based on/extracted from published literature (reindeer: Hansen *et al.* 2019, Arctic fox: Nater *et al.* 2021, and barnacle goose: Layton-Matthews *et al.* 2020).

Figure 2 – Variation in calculated correlation among various simulated quantities for Svalbard reindeer, Arctic fox and the migratory barnacle goose. Correlations were calculated for each set of jointly simulated trajectories ( $n = 4366$ ) for the three species. The variation in correlation is caused by parameter uncertainty as well as the simulated stochastic processes. Pairs described by column and row (e.g., plot A is the distribution of correlations between reindeer annual population growth rate from year  $t$  to  $t+1$  and annual reindeer carcass abundance at year  $t+1$ ). Trajectories with 0 (extinct during simulation time) were excluded from the distributions.

Figure 3 – Baseline model) Parameter summaries of Svalbard reindeer, Arctic fox, and barnacle goose population parameters (within-simulations) outputs of the baseline model (assuming no alterations to the community). I-IV) Ratio of change (Median [2.5% quantile; 97.5% quantile]) compared to the baseline model (Adjusted model/Baseline model). Baseline model was based on observed empirical relationships between species, model I assumed constant Arctic fox population size, model II assumed no effect of Arctic fox on barnacle

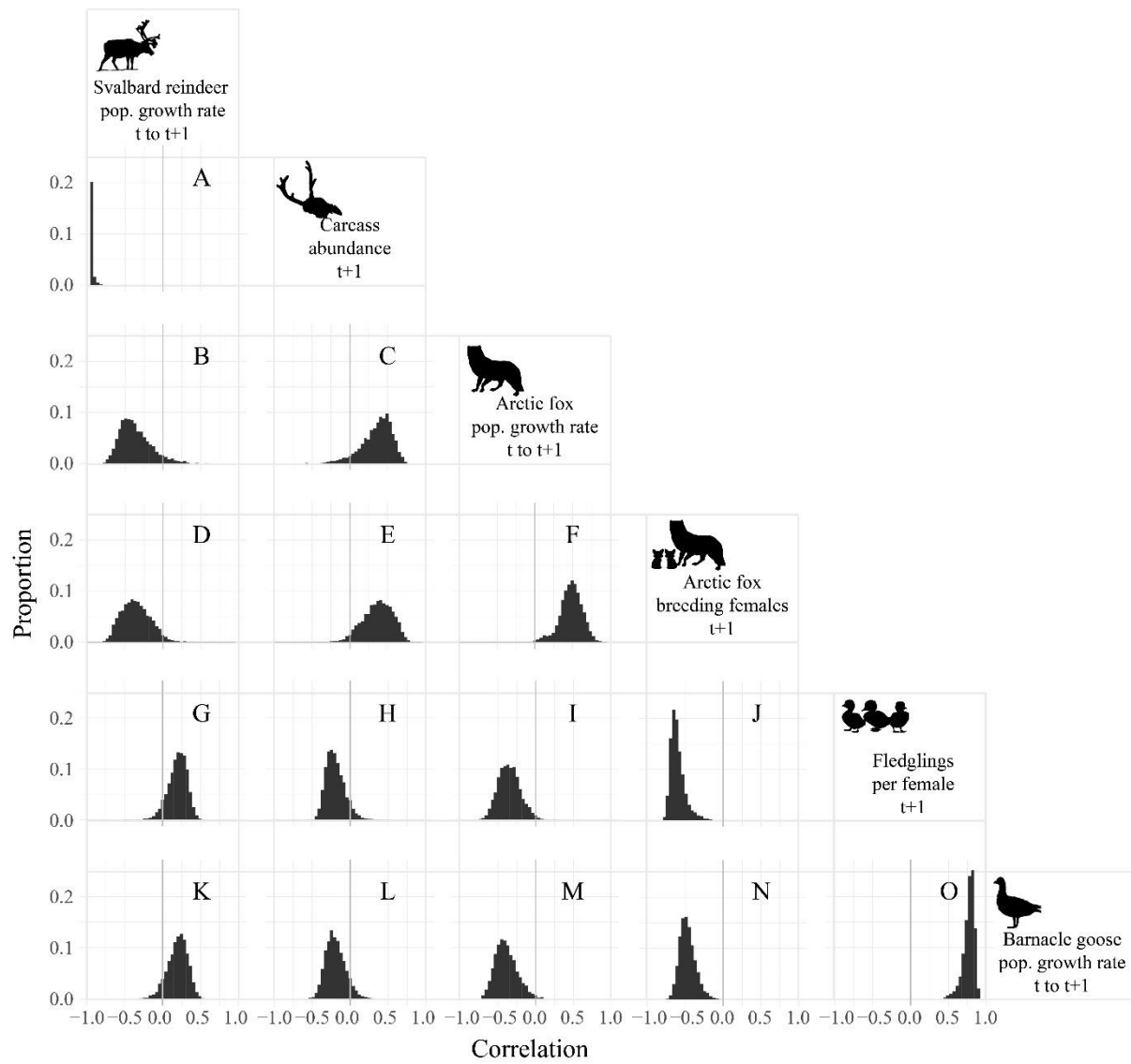
goose, model III assumed constant reindeer carcass, and model IV assumed no effect of reindeer carcass on Arctic fox. Trajectories that reached 0 for a species (extinction) were excluded from the summary of that species (except summary of extinctions). n: number of trajectories used in the summary of each model after removing “burn-in” extinctions (including extinct trajectories after “burn-in”),  $\bar{x}$ : mean,  $\tilde{x}$ : mean median (within simulations),  $\sigma^2$ : mean variance (within simulations), CV: mean coefficient of variation (within simulations).

Figure 41 – Example of simulated trajectories of (from top to bottom): Svalbard reindeer population size, Arctic fox population size, and barnacle goose population size (y-axis) over 50 years (x-axis, subset of the 100 years simulation). Baseline model was based on observed empirical relationships between species, model I assumed constant Arctic fox population size, model II assumed no effect of Arctic fox on barnacle goose, model III assumed constant reindeer carcass, and model IV assumed no effect of reindeer carcass on Arctic fox.



**Fig 1**





**Fig 2**

		Baseline model				
		n = 7,999				
Svalbard reindeer	Population size		I	II	III	IV
	$\bar{x}$		Constant fox abundance	No fox abundance effect	Constant carcass	No carcass effect
	$\bar{x}$		n = 7,998	n = 7,999	n = 7,746	n = 6,851
	$\sigma^2$					
	CV					
	Carcass abundance					
	$\bar{x}$					
	$\bar{x}$					
	$\sigma^2$					
	CV					
Extinction rate (%)		0.23				
Arctic fox	Population size					
	$\bar{x}$					
	$\bar{x}$					
	$\sigma^2$					
	CV					
	Breeding females					
	$\bar{x}$					
	$\bar{x}$					
	$\sigma^2$					
	CV					
Extinction rate (%)		17.8				
Barnacle geese	Population size					
	$\bar{x}$					
	$\bar{x}$					
	$\sigma^2$					
	CV					
	Fledglings per female					
	$\bar{x}$					
	$\bar{x}$					
	$\sigma^2$					
	CV					
Extinction rate (%)		11.3				

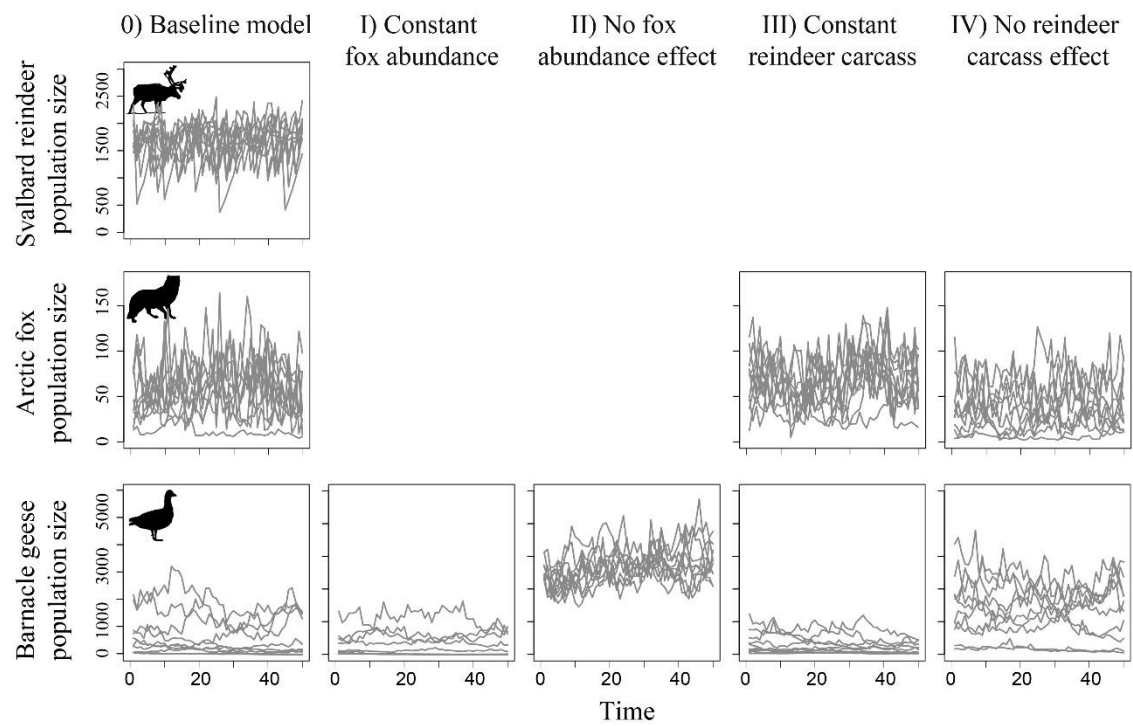
  

Median ratio (2.5% q, 97.5% q) [%Area of overlap of the distributions]	1.10 (0.86, 1.95) [69%]	0.75 (0.36, 1.13) [37%]
	1.13 (0.85, 2.19) [67%]	0.76 (0.36, 1.15) [42%]
	0.94 (0.46, 2.13) [90%]	0.49 (0.11, 1.28) [38%]
	0.86 (0.55, 1.23) [65%]	0.95 (0.66, 1.34) [85%]
	1.07 (0.86, 1.75) [73%]	0.79 (0.42, 1.11) [41%]
	1.09 (0.83, 2.00) [71%]	0.80 (0.42, 1.17) [49%]
	0.90 (0.52, 1.72) [81%]	0.55 (0.16, 1.20) [35%]
	0.87 (0.59, 1.17) [60%]	0.95 (0.72, 1.30) [83%]
	0.59	1.65

Median ratio (2.5% q, 97.5% q) [%Area of overlap of the distributions]	0.78 (0.11, 1.48) [69%]	3.86 (1.00, 71.1) [43%]	0.66 (0.04, 3.64) [75%]	1.95 (0.30, 19.4) [66%]
	0.79 (0.07, 2.04) [72%]	4.42 (0.99, 123.3) [45%]	0.62 (0.02, 4.55) [79%]	2.12 (0.25, 28.4) [65%]
	0.32 (0.02, 2.26) [71%]	2.46 (0.27, 322.9) [66%]	0.59 (0, 14.6) [86%]	1.84 (0.09, 121.9) [87%]
	0.85 (0.34, 2.51) [88%]	0.42 (0.15, 1.01) [38%]	1.21 (0.47, 3.42) [83%]	0.70 (0.27, 1.85) [73%]
	0.89 (0.63, 1.16) [72%]	1.00 (0.75, 1.50) [95%]	0.96 (0.61, 1.32) [89%]	1.02 (0.75, 1.46) [93%]
	1.00 (0.66, 1.55) [86%]	1.19 (0.73, 3.20) [78%]	0.90 (0.34, 1.69) [85%]	1.16 (0.66, 2.46) [81%]
	0.58 (0.25, 1.14) [46%]	0.57 (0.29, 1.19) [44%]	1.00 (0.53, 1.98) [97%]	0.79 (0.40, 1.53) [74%]
	0.85 (0.68, 1.09) [54%]	0.74 (0.51, 1.09) [41%]	1.06 (0.81, 1.53) [82%]	0.86 (0.63, 1.20) [62%]
	2.29	0	2.09	0.55

**Fig 3**



**Fig 4**