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## RESEARCH ARTICLE

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

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## Abstract

1. Indirect interspecific effects (IIEs) occur when one species affects another through a third intermediary species. Understanding the role of IIEs in population dynamics is key for predicting community-level impacts of environmental change. Yet, empirically teasing apart IIEs from other interactions and population drivers has proven challenging and data-demanding, particularly in species-rich communities.
2. We used stochastic population models parameterized with long-term time series of individual data to simulate population trajectories and examine IIEs in a simple high-arctic vertebrate food chain consisting of the wild Svalbard reindeer, its scavenger (the Arctic fox) and the barnacle goose, a migratory prey of the fox.
3. We used the simulated population trajectories to explore co-fluctuations between the species within the food chain. Additionally, we adjusted the model in two ways: first, to isolate the impact of fluctuations in the abundance of a species by keeping its abundance constant; and second, to isolate the impact of a trophic interaction on the dynamics of other species by setting the abundance of the influencing species to zero.
4. We found that fluctuations in reindeer carcasses shaped fox abundance fluctuations, which subsequently affected goose population dynamics. Reindeer and goose population growth rates were nevertheless only weakly correlated, probably in part due to demographic and environmental stochasticity, density dependence and lagged dynamics in the geese. However, removing the fluctuations in

Brage B. Hansen, Aline M. Lee and Vidar Gr tan co-senior authorship.

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reindeer abundance or setting reindeer abundance to zero indeed demonstrated strong underlying IIEs on goose population dynamics and extinction probability. 5. This study thus highlights the importance of species interactions, including IIEs, on species coexistence and communities in the long-term, that is beyond immediate effects and covariation in short-term fluctuations.

#### KEYWORDS

Arctic fox, barnacle goose, food chain, high-Arctic Svalbard, indirect species interactions, stochastic model, Svalbard reindeer

## 1 | INTRODUCTION

Interspecific interactions influence population dynamics (Bengtsson, 1989; Bonsall & Hastings, 2004; Holland et al., 2002; Pettorelli et al., 2011; Rosenzweig & MacArthur, 1963) and how communities respond to disturbances or environmental variation (Casas Goncalves & Amarasekare, 2021; Gilman et al., 2010; 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). IIEs occur when 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 the indirect effect is the sum of two direct effects (Wootton, 1993). For example, IIEs occurred between two prey species (a gastropod and a bivalve) sharing the same invertebrate predators (Schmitt, 1987). The predator density was correlated with the gastropod density, resulting in higher bivalve mortality in areas with abundant gastropods. Thus, 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 is challenging due to their potential masking by interspecific effects (Martorell & Freckleton, 2014; Menge, 1997), especially in complex ecosystems with many species (Bascompte & Jordano, 2007; Holt, 1977). Additionally, demographic and environmental stochasticity, along with life history characteristics, can impact our assessment of IIEs on population dynamics (e.g. causing delayed dynamics; Thompson & Ollason, 2001; Warner & Chesson, 1985). Thus, empirically teasing apart IIEs within communities, requires high-quality, long-term data sets and a holistic modelling perspective involving all key species and interaction chains (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 population dynamics 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., 2010). However, accurate estimates of stochastic population parameters from multiple species are demanding and require monitoring of, for example 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 focussed 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 the 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 (Chesson, 2012; Holt, 1977; Holt & Bonsall, 2017), the fox. 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 shift in abundance of all three species due to direct effects of reindeer carcass abundance fluctuations on fox reproduction (scavenging reindeer), and of fox abundance on goose reproduction (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. The IIE in this system (reindeer–goose) involves two direct interactions (reindeer–fox and fox–goose). Prior research on the fox–goose interaction (Layton-Matthews et al., 2019, 2020) motivated us to explore its role in the reindeer–goose interaction pathway. Understanding the interplay between all components of the IIE provides a more comprehensive view of the complex dynamics. We therefore developed four adjusted models to compare with the dynamics under observed environmental characteristics and trophic interactions. In two adjusted models, we studied the impacts caused by fluctuations in the abundance of interacting species by keeping a constant abundance of one species through time. In the other models, we examined the importance of each trophic interaction by setting the abundance of a species to zero. For each case, we compared population dynamics using summary statistics and extinction rates.

## 2 | MATERIALS AND METHODS

### 2.1 | Study system and species

We focussed 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), that is 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 carcass availability 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 reindeer carcasses, 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 Solway Firth (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 & Bergersen, 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.

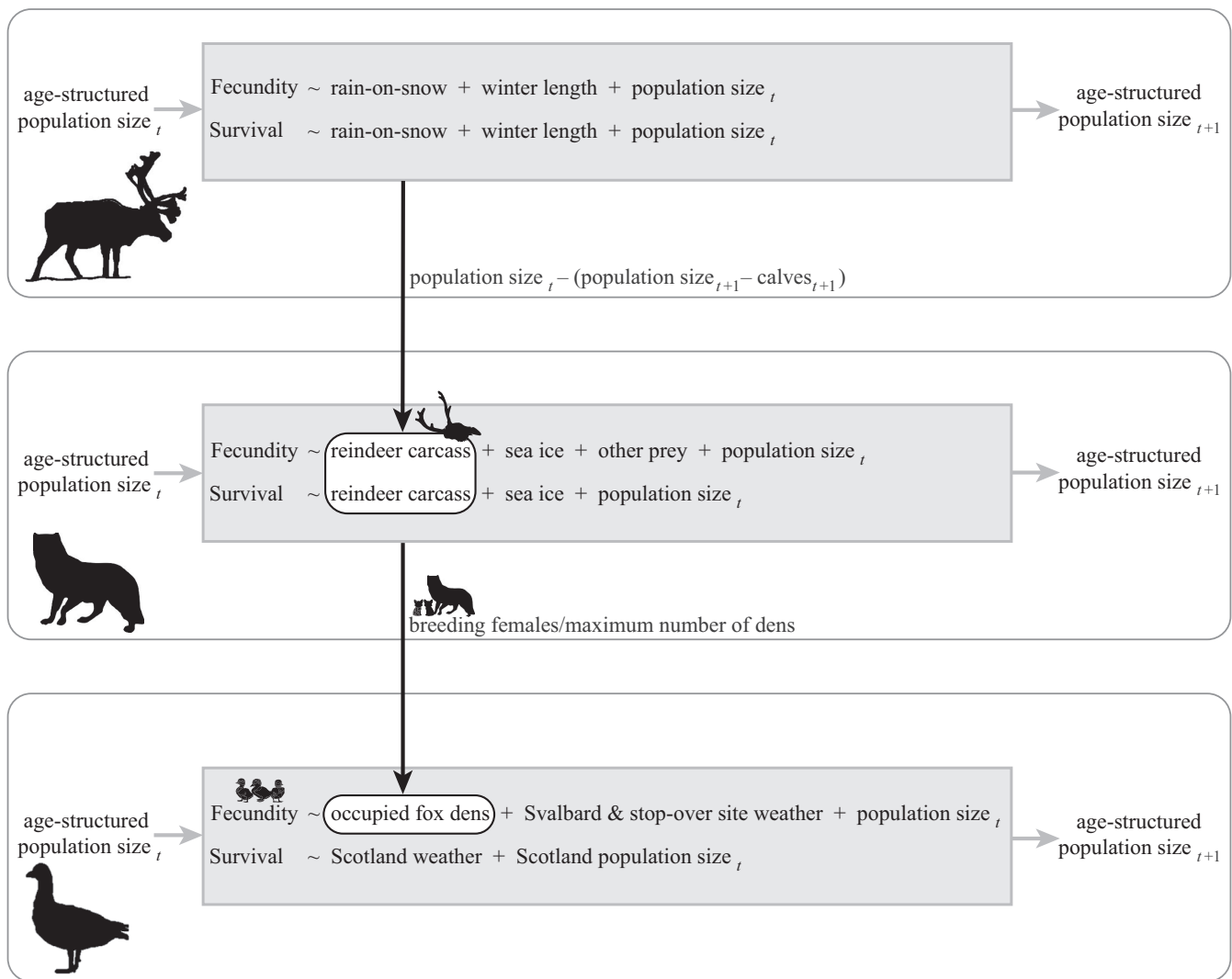
### 2.2 | Model structure

Single-species 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). Each model has been fitted with data from different geographical 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 inter-specific interactions support our key assumption that interaction effects remain consistent across Svalbard. Here, we built a multi-species community model by modifying and combining these single-species population models (Supporting Information S1). Permission for access of bird reserves and catching of barnacle geese was given by the governor of Svalbard, while permission for bird ringing was given by the Stavanger Museum. Ethics approval was not required for the Svalbard reindeer and Arctic fox data as we did not use collected data from these species (Supporting Information S1).

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). The first trophic link was the reindeer carcass effect on fox survival and reproduction (Eide et al., 2012; Hansen et al., 2013), operating through scavenging. We obtained reindeer carcass abundance by calculating reindeer mortality (population size the previous year minus population size the current year (excluding calves), Supporting Information S1, equation 1.0.7). The second modelled trophic link was between the fox and barnacle goose, that is fox abundance effect in early summer on goose reproductive rates. We calculated the proportion of active fox dens by dividing the number of fox breeding females by the total number of available dens (Supporting Information S1, equation 2.1.1). Specifically, in accordance with Layton-Matthews et al. (2020), we modelled goose

fledging probability as dependent on the proportion of fox dens occupied in early summer (i.e. active dens with cubs). This factor has previously been linked to fledging probability and 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 geese on fox; thus, we assumed here that barnacle geese do not directly affect annual fox dynamics. 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



**FIGURE 1** Diagram of the simplified study system, links between the three species in the model (the residents Svalbard reindeer and Arctic fox, and the migratory barnacle goose) and covariates affecting reproductive and survival rates. The model was composed of three single-species models (white boxes) connected by interspecific effects (black arrows). Covariate effects were extracted from the literature and introduced in the model to estimate reproductive and survival rates. Grey and black arrows represent the models' inputs and outputs. Data and models are based on/extracted from published literature (reindeer: Hansen et al., 2019, fox: Nater et al., 2021, and goose: Layton-Matthews et al., 2019, 2020).

age-specific population abundances of the three species (Supporting Information S1 and S3). Reindeer survival and reproductive rates depended on winter length and ROS. Fox survival and reproductive rates both depended on sea ice extent and survival also depended on pink-footed goose abundance 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), that is a direct negative effect of population size on both survival and reproduction. For the Arctic fox, we remodelled the survival and reproductive rates (Supporting Information S1), 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). The goose models in Layton-Matthews et al. (2019, 2020) found a first-order negative density-dependent effect of population size in the wintering grounds on survival and on number of goslings (due to model selection). Based on findings from Layton-Matthews et al. (2019), highlighting density dependence's role in regulating reproductive success, we revisited the model. Some simulations showed (unrealistically) large populations, indicating weak density dependence. Thus, we chose to include a negative density dependence in other goose reproductive components (hatching success and fledging probability, Supporting Information S1). Goose survival rates depended on barnacle goose population abundance in Scotland.

## 2.3 | Simulations

We simulated time series of age-specific abundances ( $N$ , only female individuals) for Svalbard reindeer, Arctic fox and barnacle goose (Supporting Information S1). 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 (reindeer: Hansen et al., 2019; Peeters et al., 2022; fox: Nater et al., 2021; Supporting Information S1). For barnacle goose, survival rates were estimated using the same capture-mark-recapture as described in Layton-Matthews et al. (2019), which provided posterior distributions of parameters through Markov Chain Monte Carlo simulations (implemented in JAGS, Plummer, 2003). However, here, their model was re-run including scaled covariates (Scotland temperature and population sizes, Supporting Information S1). The reproductive components were available as point estimates, that is mean values obtained from generalized linear mixed models (GLMMs, as done in Layton-Matthews et al., 2020); thus, parameter uncertainty was only accounted for in survival for this species.

For each species and each year, values of environmental covariates (and goose overwintering population size) were simulated by drawing from the historical (i.e. observed) values distribution. Historical values were extracted from the literature or from public sources online

(Supporting Information S3). 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 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 (Supporting Information S1). 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 species, we simulated one time series of 130 years. Starting population sizes were the same in all simulated trajectories and matched the mean population sizes for each species estimated for 1994 (Supporting Information S1). Yet, we removed the initial 30 years, to eliminate any bias from the given starting population sizes, that is transient effects. We simulated a total of 9090 stochastic population size trajectories for each species. We used the 9090 posterior model estimates available from the reindeer population model (Hansen et al., 2019). For the fox model, we randomly sampled 9090 from 45000 available posterior samples (Nater et al., 2021). For the goose survival model, we approximated 9090 samples from a posterior distribution of 3000 samples (Layton-Matthews et al., 2019) by sampling with replacement. Parameter sets leading to extinction for one of the species within the 30 initial years were excluded from further analysis.

### 2.3.1 | Baseline model simulations

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 pairwise correlations between population growth rates  $[\log(N_{t+1}) - \log(N_t)]$  of the three species and the key population parameters; reindeer carcass abundance (affecting fox survival and reproduction); number of fox breeding females (affecting goose reproduction); and barnacle goose recruits (fledglings per female, affected by fox predation). We also investigated delayed pairwise correlations between reindeer and the other two species, as in this study system, lagged co-fluctuations among species can occur because intrinsic population-dynamic properties, with reindeer density-dependent and age-structured mechanisms causing, for example, low mortality following crash years (Hansen et al., 2019).

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. We excluded trajectories where any species went extinct to mitigate biases when calculating distributions.

### 2.3.2 | Effects of interspecific interactions on equilibrium distributions

We evaluated, by simulations, the effects of interspecific interactions on equilibrium distributions of population sizes by comparing the output of adjusted models versus the output from the baseline model. Adjusted models I and II were implemented to isolate the impact of the fox on the goose equilibrium population size. In adjusted model I, we removed the impact of variation in fox breeding females by setting the abundance of fox breeding females at the average obtained from the baseline model simulations. In adjusted model II, we completely removed the fox impact on goose population dynamics by setting the abundance of fox breeding females to zero. These simulations allowed for estimating potential changes of fluctuations in fox breeding females (e.g. mean and variance) compared with the baseline model, and how this subsequently affected goose equilibrium population sizes. Focussing on the direct impact of the fox on the goose, results from adjusted models I and II could potentially allow for a more comprehensive understanding of how changes in fox abundance caused by changes in reindeer carcass numbers, ultimately affected goose dynamics. Similarly, in adjusted models III, we evaluated the impact of reindeer variation by setting reindeer carcass abundance at the average obtained from the baseline model simulations. In adjusted model IV, we removed the reindeer impact by setting the reindeer abundance to zero.

To implement models I and III, we calculated the mean percentage of occupied Arctic fox dens (calculated from fox breeding females as a proxy of fox abundance, [Supporting Information S1](#)) and reindeer carcass abundance from each simulated trajectory from the baseline model. As the models are fitted for scaled covariates, we scaled the covariates as done for the baseline model (according to the modelling approach, [Supporting Information S1](#)). We then incorporated the scaled mean of each trajectory as a constant covariate value in the corresponding adjusted models. We implemented models II and IV, respectively, by setting the reindeer carcasses numbers and fox breeding females abundance to zero when performing simulations. We scaled the covariates and incorporated them into the corresponding adjusted models.

To ensure comparability among these adjusted models and with the baseline model, we used the same parameter sets, and simulated covariates as in the baseline model. Consequently, each simulated trajectory from each adjusted model was paired with the corresponding simulated trajectory for the baseline model, that is 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 quantified the area of overlap between these two distributions and reported it as percentage overlap. This approach was adopted to ensure 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. When calculating extinction rate ratios, we excluded trajectories where at least one species went extinct during the burn-in in the baseline model or the corresponding adjusted model. For other ratios, we also excluded trajectories with species extinctions after the burn-in in the baseline model or the corresponding adjusted model.

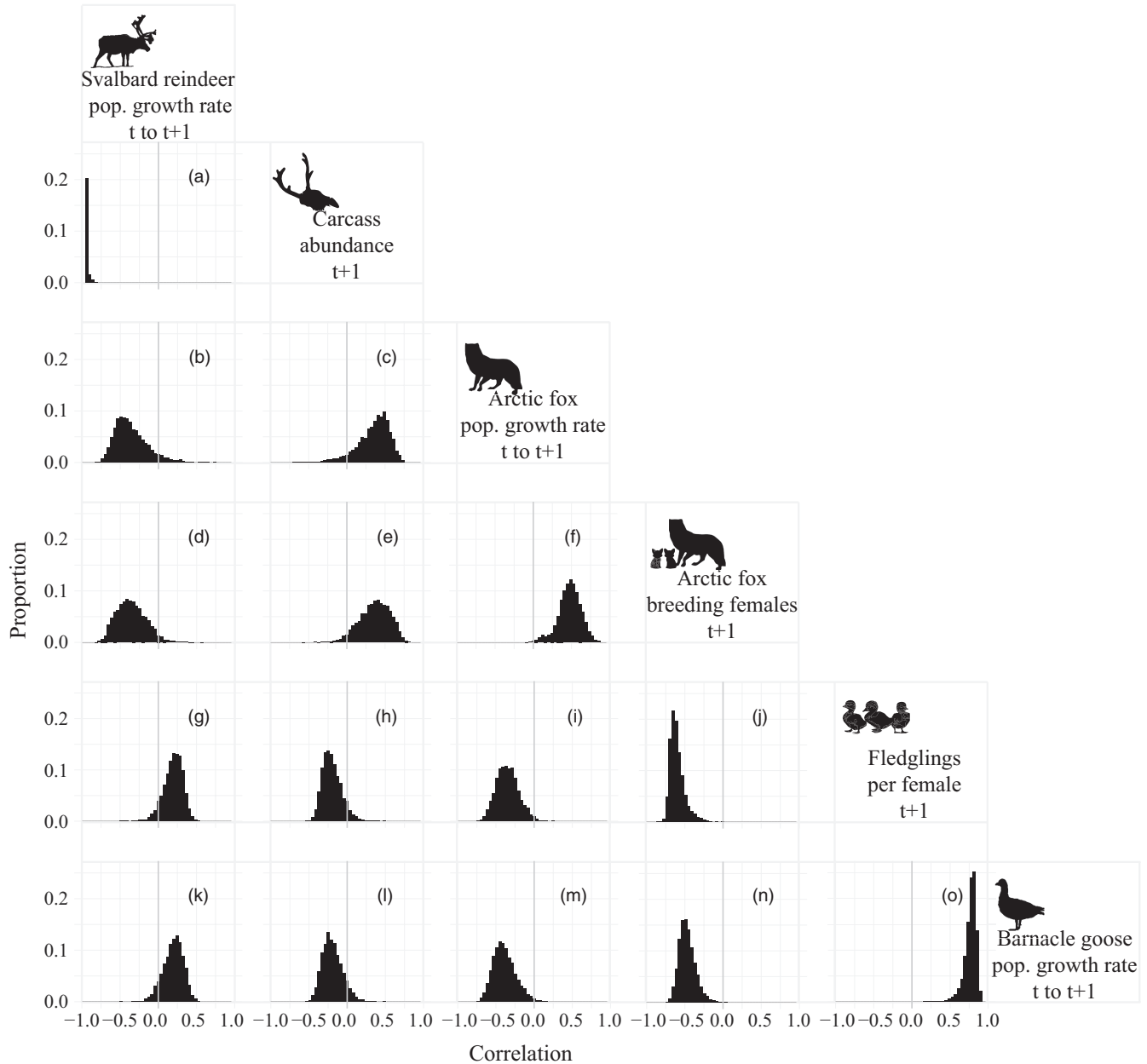
All modelling, simulations and analyses were performed using R version 4.3.1 (R Core Team, 2021).

## 3 | RESULTS

### 3.1 | Cross-species correlations

Out of 9090 simulations using the baseline (empirical) model, we included 5667 trajectories per species without any species extinctions. We found 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 2B,C](#)). 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 with 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 2I,J](#)). 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 2K,L](#)).

Reindeer population growth rates (from year  $t - 1$  to  $t$ ) were positively correlated with carcass abundances the following year (in year  $t + 1$ ,  $r = 0.31$  [0.13, 0.49]) as well as with fox population growth rates the following year ( $r = 0.32$  [-0.12, 0.63]), but correlations with goose population growth rates the following year were weak ( $r = -0.16$  [-0.43, 0.11]; [Supporting Information S4](#)).



**FIGURE 2** Distribution of estimated correlations between various simulated parameters for Svalbard reindeer, Arctic fox and the migratory barnacle goose. Correlations were calculated for each set of jointly simulated trajectories ( $n = 5667$ ). Variation in correlation is caused by parameter uncertainty and 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 that went extinct for at least one species were excluded from the distributions.

**FIGURE 3** Parameter summaries of Svalbard reindeer, Arctic fox, and barnacle goose population parameters (within-simulations) outputs of the baseline model (based on observed empirical relationships between species). For models I to IV we display the ratio of change (Median [2.5% quantile; 97.5% quantile]) compared to the baseline model (adjusted model/baseline model) and below, area of overlap (% overlap in ratio of change distribution with the baseline model). The baseline model was based on observed empirical relationships between species, model I assumed constant fox population size, model II assumed no impact of the fox on the goose, model III assumed constant reindeer carcass numbers, and model IV assumed no impact of reindeer carcass on fox. Trajectories that went extinct for a species were excluded from the summary of that species (except summary of extinctions).  $n^*$ , number of trajectories used after removing species-specific extinctions;  $n$ , number of trajectories used in the summary of each model after removing “burn-in” extinctions and to calculate extinction rates;  $\bar{x}$ , mean;  $\tilde{x}$ , mean median (within simulations);  $\sigma^2$ , mean variance (within simulations); CV, mean coefficient of variation (within simulations).



### 3.2 | Effects of interspecific interactions on equilibrium distributions

When calculating summary statistics from the baseline model 7999 trajectories were included after excluding burn-in extinctions (Figure 3).

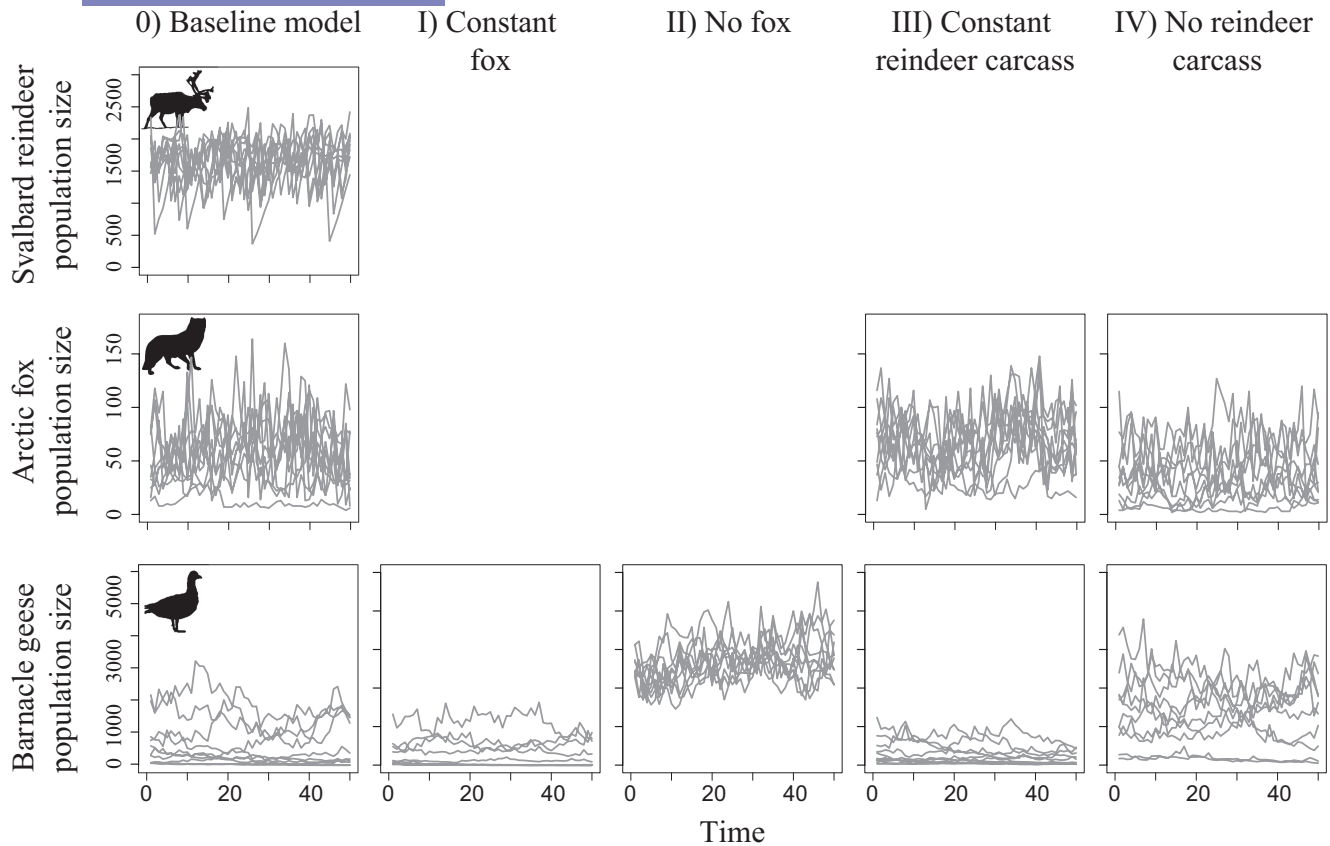
Removing the fluctuations in Arctic fox population sizes (model I) caused a reduction in the mean ( $\bar{x}$ ) and variation (CV) in the barnacle goose fledgling production (per female) and population sizes, while the extinction probability increased compared with the baseline model (Figure 3). Note,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

		Baseline
		$n = 7999$
		$n^* = 7981$
Svalbard reindeer	Population size	
	$\bar{x}$	1558
	$\tilde{x}$	1595
	$\sigma^2$	134,114
	CV	0.24
	Carcass abundance	
	$\bar{x}$	241
	$\tilde{x}$	118
	$\sigma^2$	100,648
	CV	1.28
Extinction rate (%)		0.23
		$n^* = 6578$
Arctic fox	Population size	
	$\bar{x}$	55.8
	$\tilde{x}$	52.1
	$\sigma^2$	724
	CV	0.49
	Breeding females	
	$\bar{x}$	12.2
	$\tilde{x}$	11.5
	$\sigma^2$	35.1
	CV	0.50
Extinction rate (%)		17.8
		$n^* = 7093$
Barnacle goose	Population size	
	$\bar{x}$	1087
	$\tilde{x}$	1031
	$\sigma^2$	311,084
	CV	0.574
	Fledglings per female	
	$\bar{x}$	0.532
	$\tilde{x}$	0.36
	$\sigma^2$	0.277
	CV	1.01
Extinction rate (%)		11.3

I	II	III	IV
Constant fox	No fox	Constant carcass	No carcass
$n = 7998$	$n = 7999$	$n = 7746$	$n = 6851$

Median ratio (2.5% q, 97.5% q) [% Area of overlap]

	$n^* = 6160$	$n^* = 5129$		
	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		
	$n^* = 5850$	$n^* = 7091$	$n^* = 5639$	$n^* = 5784$
	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



**FIGURE 4** 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). The baseline model was based on observed empirical relationships between species, model I assumed constant fox population size, model II assumed no impact of the fox on the goose, model III assumed constant reindeer carcass numbers, and model IV assumed no impact of reindeer carcass on fox.

With 0 fox abundance (model II), increased mean goose population sizes ~fourfold, while their variation (in terms of CV) was greatly reduced (Figures 3 and 4). Mean fledgling production was approximately identical to the baseline model, but the year-to-year variation was reduced. In this model, extinction probability was zero, that is no population trajectories went extinct.

Constant reindeer carcass abundances (model III) caused only a slight increase in Arctic fox mean breeding females and population sizes (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.

With no reindeer carcasses (model IV), Arctic fox mean number of breeding females and population sizes decreased (Figures 3 and 4). Despite a notable reduction in variability (as indicated by the lower variance, Figure 3), the changes in the CV were relatively minor. 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 population sizes variance because of a mean increase), causing a reduction in goose extinction rates (Figure 3).

## 4 | 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 rates time series to simulate population trajectories and examine the role of IIEs in a simple high-arctic vertebrate food chain. Specifically, we modelled the Svalbard reindeer, a scavenger of the reindeer (Arctic fox), and a migratory prey of the fox (barnacle goose). Population growth rates of directly interacting species were correlated due to the influence of reindeer carcass availability on fox abundance fluctuations, which, in turn, affected goose fledgling production through predation (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 setting species abundances to zero or removing carcass or fox variability revealed reindeer IIE 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. Short-term fluctuations in species abundance can cause co-fluctuations in other species, allowing environmental stochasticity and perturbations to cascade through the whole system (Abbott et al., 2009; Layton-Matthews et al., 2023; Menge, 1995). This leads to correlated dynamics between non-directly interacting species. The lack of long-term strong annual co-fluctuations in our study does not imply IIEs effects are negligible. Species' presence and their (direct and indirect) interactions contribute to establishing 'equilibrium distributions' (i.e. population abundances allowing coexistence) within communities (Chesson, 2000; McCann et al., 1998). Removing a single species can disrupt this equilibrium, altering the dynamics of another species in the same trophic chain, even when not directly interacting. Consequently, species long-term dynamics and abundances are expected to differ in the absence of these interactions. For instance, when removing reindeer carcasses (model IV) we found similar, yet less extreme, consequences for the goose dynamics (i.e. mean and variability in abundances and recruitment, and extinction risk) as when we removed fox abundance (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 is not limited to directly linked species but extends to indirectly connected ones as well.

Removing the presence of one species thus clearly demonstrated how IIEs impact 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 goose long-term dynamics, as did removal of fluctuations in fox abundance (model I). With no fox variation, goose mean abundances were reduced and extinction rates increased, while there was only a slight reduction in abundance variability. In typical conditions, goose 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 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 goose's ability to coexist with high predation pressure is at least partly because of 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 fox abundance variability 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 affecting 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, barnacle goose is a long-lived species (Black et al., 2014) where, for example, 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. Although our simulations showed negligible delayed co-fluctuations between reindeer and geese, there were delayed co-fluctuations between reindeer and foxes. This suggests that multi-year processes may influence the direct co-fluctuations between reindeer and geese. IIEs might also be overshadowed by other sources of demographic and environmental stochasticity, or by density dependence, factors known to drive population dynamics (Des Roches et al., 2018; Lande et al., 2003; Layton-Matthews et al., 2020; Sandal et al., 2022) and affecting survival and reproduction in both the fox and goose (Layton-Matthews et al., 2019, 2020; Nater et al., 2021). In short-term dynamics, impacts of IIEs are masked by the direct or delayed effects of internal or other external drivers on fox and goose dynamics. This masking effect results in weak correlations in population growth rates.

Despite our results showing little evidence of strong effects of IIEs on annual co-fluctuations when averaging over many years and simulations, specific combinations of conditions or parameters (such as those leading to a massive reindeer die-off) can lead to strong co-fluctuations in the shorter term. For instance, an extreme ROS 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). Given our focus on long-term dynamics, any strong short-term interactions between species might have been overlooked. Yet, 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).

When studying IIEs empirically, it is thus crucial to consider the different levels at which they can act. Yet, many studies attempt to estimate presence or strength of interactions from time

series analysis of only two species, usually co-fluctuations in abundance (Ives et al., 2003; Raffaelli & Hall, 1996; Sandal et al., 2022; Wootton, 1997). Because of factors mentioned above, as well as complexities related to potential nonlinearity (Ruesink, 1998; Sarnelle, 2003), (co-)fluctuations may seem relatively weakly 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, that is short-term changes or fluctuations in population size, versus press perturbations, that is 'permanent' changes in population size (Bender et al., 1984).

Our findings provide a rare empirical-based example of the role of IIEs in population dynamics, acting through the mean and variance in long-term population abundances, and extinction probabilities. However, detecting IIEs in between-species population co-fluctuations remains challenging due to other population-dynamic factors. For instance, our model did not account for the potential feedback effect a prey species might have on its predator. Additionally, our model did not include interactions with other species, but these effects are likely to be accounted for by the environmental noise component in our model. We investigated a food chain with unidirectional apparent competition (Holt, 1977), setting our system apart from others with apparent competition effects going in both directions. While we studied a simple trophic chain, more complex food webs with diverse interactions could exhibit greater robustness 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), that is beyond immediate impacts and short-term co-fluctuations in abundances of species.

#### AUTHOR CONTRIBUTIONS

Laura Bartra Cabré, Brage B. Hansen, Aline M. Lee and Vidar Grøtan conceived the original idea for the study. Leif E. Egil (reindeer), Eva Fuglei (fox) and Maarten J. J. E. Loonen (goose) collected monitoring data necessary for the original population models that were merged in this study. Laura Bartra Cabré and Vidar Grøtan developed the model and performed the analysis, with input from Aline M. Lee and Brage B. Hansen. Laura Bartra Cabré wrote the manuscript, with main contributions from Brage B. Hansen, Aline M. Lee and Vidar Grøtan, and additional contributions from all other authors. All authors provided critical input to the drafting process and collectively approved the final version for publication.

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#### CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.









#### DATA AVAILABILITY STATEMENT

All data and code needed to replicate the simulations are openly available in the DRYAD repository <https://doi.org/10.5061/dryad.zcrjdfnm4> (Bartra-Cabré et al., 2024).

#### STATEMENT ON INCLUSION

This study brings together authors from several countries and includes scientists based in the country where the study is based.

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## SUPPORTING INFORMATION

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

**Supporting Information S1.** Models for demographic parameters.

**Supporting Information S2.** Tables with covariates and parameter summaries.

**Supporting Information S3.** Covariates description and data sources.

**Supporting Information S4.** Distribution of estimated lagged correlations among various simulated parameters for Svalbard reindeer, Arctic fox and the migratory barnacle goose.

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