Received: 27 February 2019 | Accepted: 13 August 2019

DOI: 10.1111/1365-2656.13104

RESEARCH ARTICLE

Journal of Animal Ecology BRITISH ECOLOGICAL SOCIETY

Direct and indirect effects of regional and local climatic factors on trophic interactions in the Arctic tundra

Claire-Cécile Juhasz[1,2] | Bill Shipley[3] | Gilles Gauthier[2,4] | Dominique Berteaux[5] | Nicolas Lecomte[1,2]

[1]Canada Research Chair in Polar and Boreal Ecology, Université de Moncton, Moncton, NB, Canada

[2]Centre d'études Nordiques, Université Laval, Quebec, QC, Canada

[3]Département de Biologie, Université de Sherbrooke, Sherbrooke, QC, Canada

[4]Département de Biologie, Université Laval, Quebec, QC, Canada

[5]Chaire de recherche du Canada en biodiversité nordique and Centre d'Études Nordiques, Université du Québec à Rimouski, Rimouski, QC, Canada

Correspondence
Claire-Cécile Juhasz and Nicolas Lecomte
Emails: clrccljuhasz@gmail.com; Nicolas.Lecomte@umoncton.ca

Funding information
Canada Research Chairs; Canadian Wildlife Service; Canadian Network of Centres of Excellence ArcticNet; Canada Foundation for Innovation; Université de Moncton; Natural Sciences and Engineering Research Council of Canada

Handling Editor: Dave Koons

[Corrections added on 19 February 2020 after online publication: the author list and affiliations have been updated to include Dominique Berteaux; thus a citation to the date source, the Authors' Contributions statement, and citation to the reference list have been updated and included in this version.]

Abstract

1. Climate change can impact ecosystems by reshaping the dynamics of resource exploitation for predators and their prey. Alterations of these pathways could be especially intense in ecosystems characterized by a simple trophic structure and rapid warming trends, such as in the Arctic. However, quantifying the multiple direct and indirect pathways through which climate change is likely to alter trophic interactions and their relative strength remains a challenge.
2. Here, we aim to identify direct and indirect causal mechanisms driven by climate affecting predator–prey interactions of species sharing a tundra food web.
3. We based our study on relationships between one Arctic predator (Arctic fox) and its two main prey – lemmings (preferred prey) and snow geese (alternate prey) – which are exposed to variable local and regional climatic factors across years. We used a combination of models mapping multiple causal links among key variables derived from a long-term dataset (21 years).
4. We obtained several possible scenarios linking regional climate factors (Arctic oscillations) and local temperature and precipitation to the breeding of species. Our results suggest that both regional and local climate factors have direct and indirect impacts on the breeding of foxes and geese. Local climate showed a positive causal link with goose nesting success, while both regional and local climate displayed contrasted effects on the proportion of fox breeding. We found no impact of climate on lemming abundance. We observed positive relationships between lemming, fox and goose reproduction highlighting numerical and functional responses of fox to the variability of lemming abundance.
5. Our study measures causal links and strength of interactions in a food web, quantifying both numerical response of a predator and apparent interactions between its two main prey. These results improve our understanding of the complex effects of climate on predator–prey interactions and our capacity to anticipate food web response to ongoing climate change.

KEYWORDS
Arctic tundra, climate impacts, food web, path analysis, trophic interactions

Gilles Gauthier and Nicolas Lecomte are senior authors.

1 | INTRODUCTION

Impacts of climate change on species dynamics are already widespread across many ecosystems (Ims & Fuglei, 2005; Ockendon et al., 2014). Such impacts reshape species distributions redefining the functioning of ecosystems by changing resource availability and species interactions (Cahill et al., 2012; Walther et al., 2002). For instance, increased air temperatures can not only directly alter the number of prey and their predators but also indirectly facilitate predation or dampen predation risks by influencing both searching activities and handling time of prey (Sentis, Hemptinne, & Brodeur, 2012; Thakur, Künne, Griffin, & Eisenhauer, 2017). So far, few studies have measured the relative strengths of direct and indirect impacts of climate changes on trophic interactions (Antiqueira, Petchey, & Romero, 2018; Ogilvie et al., 2017) and especially among endotherm species. This knowledge gap is even more apparent when accounting for the fact that alteration of trophic interactions differs greatly according to the thermoregulatory capacity of animals (ectotherm predator and prey: Grigaltchik, Ward, & Seebacher, 2012; endotherm predator – ectotherm prey: Rodenhouse, 1992; ectotherm/endotherm predators and endotherm prey: Cox, Thompson, & Reidy, 2013; endotherm predator and prey: Creel, Creel, Creel, & Creel, 2016).

Climate change may affect species directly, via physiological impacts, and indirectly, through alterations in interactions between species. Indirect effects (such as phenological mismatch or changing food availability and predation) generally have a greater impact on species dynamics than direct ones (such as physiological stress; Cahill et al., 2012; Ockendon et al., 2014). The relative importance of direct and indirect impacts of ongoing climate change on trophic interactions could be particularly acute in ecosystems characterized by a simple trophic structure and rapid warming trends. As air temperatures and precipitation amounts rise rapidly across the Arctic tundra (IPCC, 2013), weather conditions have the potential to play a determinant role in species dynamics and interactions in this biome (e.g. Hansen et al., 2013). Despite the paucity of studies, some have already reported contrasting impacts of various climatic factors on species dynamics in various regions of the Arctic, from positive (geese: Jensen et al., 2008; Lecomte, Gauthier, & Giroux, 2009) to negative (geese: Doiron, Gauthier, & Lévesque, 2015; raptors: Lamarre et al., 2018; lemming: Ims, Henden, & Killengreen, 2008). At the ecosystem level, Legagneux et al. (2014) showed that warmer temperatures in the Arctic could increase predation intensity on herbivore prey. Nonetheless, quantifying the multiple direct and indirect pathways through which various climatic factors may alter trophic interactions and their relative strength remains a challenge that few studies have addressed in the Arctic.

Using a dataset ranging from 1996 to 2016, we examined direct and indirect mechanisms driven by climate that could potentially affect predator–prey interactions between a tundra top predator, the Arctic fox (*Vulpes lagopus*; terrestrial predator), their main prey, lemmings (*Lemmus trimucronatus* and *Dicrostonyx groenlandicus*) and their main alternative prey, greater snow geese (*Anser caerulescens atlantica*); together these form a hypothesized causal structure (Figure 1a). These links were defined by a series of a priori hypotheses based on known mechanisms specific to the Arctic ecosystem (see Table 1). Climate may influence goose nesting success in several ways: (a) when geese arrive at the breeding site, the snow cover (linked to weather conditions) impacts food and nest site availability (Dickey, Gauthier, & Cadieux, 2008). A delayed spring, associated with a late snowmelt, should decrease the body condition of breeding females and increase the stress linked to intraspecific competition for nest sites, resulting in decreased nesting success. (b) During incubation, temperature can influence the cooling of eggs, implying an increased risk of embryo mortality during cold days (Dickey et al., 2008; Poussart, Larochelle, & Gauthier, 2000). Rainfall, by modifying water accessibility through travelled distance for incubating females, should alter goose capacity to go back to nests and fend off predators during incubation recesses (Lecomte et al., 2009). Lemmings, the other major prey in this system, show 3- to 4-year population cycles, and their abundance during summer is linked to their winter breeding and possibly to winter climate conditions affecting snow quality (food access, predation pressure; Bilodeau, Gauthier, & Berteaux, 2013; Dominé et al., 2018). Arctic fox breeding success is dependent on lemming population fluctuations and is maximal during years of high lemming abundance (fox numerical response; Tarroux, Bêty, Gauthier, & Berteaux, 2012). During the decreasing and low phase of lemming abundance, foxes shift prey and heavily feed on goose eggs and goslings (fox functional response towards the alternative prey; Bêty, Gauthier, Giroux, & Korpimäki, 2001). Fox predation is the main cause of nesting failure in geese (Bêty et al., 2001; Lecomte et al., 2009), and it can lead to almost complete nesting failure during a lemming crash (Bêty et al., 2001; Bêty, Gauthier, Korpimäki, & Giroux, 2002; Lecomte, Careau, Gauthier, & Giroux, 2008).

Thus, we have good reasons to suspect that goose reproduction can be affected by both predation and local climatic conditions during the nesting period (Bêty et al., 2002; Lecomte et al., 2009). However, we do not know the relative strengths of these multiple biotic and abiotic effects on goose reproduction and how they interact with each other. Therefore, in this study, we examined (a) whether climate could positively or negatively affect lemming abundance, goose breeding success and the reproduction of their main predator, either directly or indirectly, and (b) whether these effects could result in an alteration of the prey–predator dynamics between the Arctic fox and snow goose (Table 1; Figure 1a). We used confirmatory path analysis (Shipley, 2009), also known as piecewise structural equation modelling (Lefcheck, 2016), to disentangle the direct and indirect effects of climate on the predator–prey interactions between foxes and geese. We based our hypothetical causal claims between observed and latent variables (i.e. non-measured variables) on our specific knowledge about this system (Table 1; Figure 1a). To do so, we analysed long-term data (21 years) on fox and goose breeding success, lemming abundance, as well as local (air temperatures and cumulative precipitations) and regional (Arctic oscillation, AO) climate indices.

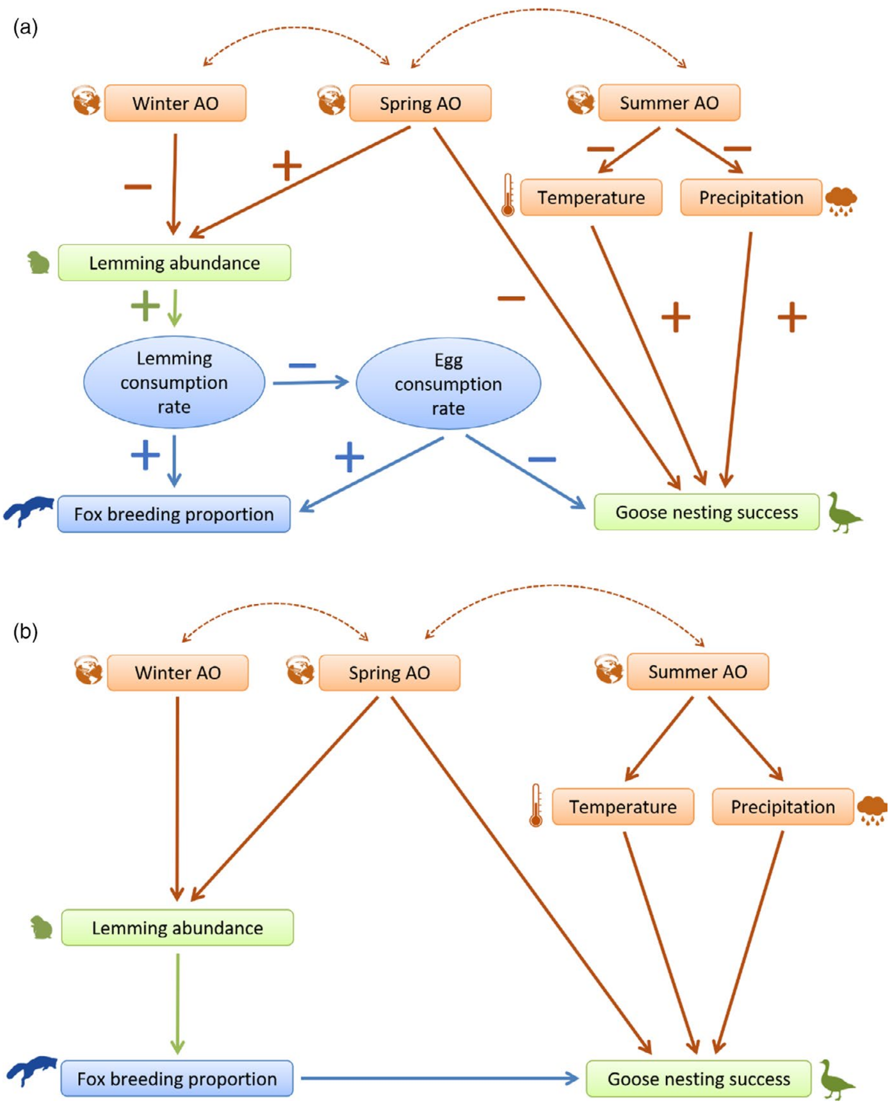

FIGURE 1 Hypothesized causal links between climate (orange boxes), one predator (Arctic fox; blue box) and two prey species (greater snow goose and lemming sp.; green boxes) specific to the high Arctic. Regional climate (i.e. winter and spring AO) may directly influence lemming abundance and goose nesting success, while summer AO may be directly linked with temperature and precipitation during goose nesting period. In turn, these local climate variables may directly influence goose nesting success. (a) Illustrates the path diagram with hypothesized causal links between latent variables (non-measured variables; blue circles) and other variables. Thus, lemming abundance may have an indirect causal link with goose nesting success and the proportion of active breeding fox dens through consumption rates of prey by foxes (latent variables; blue circles). (b) Corresponds to the directed acyclic graph with no latent variables and equivalent to the original path diagram (a). Double-headed stippled arrows represent a free covariance between exogenous variables (i.e. winter, spring and summer AO)

2 | MATERIALS AND METHODS

2.1 | Study system

The study was conducted at Bylot Island, Sirmilik National Park of Canada (73°N, 80°W), which contains the largest greater snow goose breeding colony (ca. 20,000 pairs; Reed, Hughes, & Boyd, 2002) in the Canadian Arctic. More than 95% of goose nests are concentrated in a high-density area (50–70 km^2). The landscape is dominated by mesic tundra in the upland and a mixture of mesic tundra and wetlands (primarily polygonal tundra) in the lowlands (Gauthier et al., 2013). Wetlands account for ca. 15% of the study area (Lecomte, Gauthier, & Giroux, 2008; Massé, Rochefort, & Gauthier, 2001). Between 1989 and 2011, Bylot Island experienced a warming trend during both spring and summer (from 0.3°C per decade in June to 1.1°C per decade in both May and August) and the average annual cumulative thawing degree-days (sum of the daily mean temperature above 0°C) increased by almost 40% (Gauthier et al., 2011, 2013). Although the entire Arctic has experienced a modest increase in the amount of summer precipitation since 1950 (+5%; AMAP, 2012), this period has witnessed an increase in extreme events, including the occurrence of the five wettest summers in the Arctic over the past 20 years (AMAP, 2012). Furthermore, climate models project precipitation increases of 30%–50% during the cold season over the coming decades, with an increasing proportion falling as rain instead of snow (AMAP, 2017; Bintanja & Andry, 2017).

2.2 | Goose nesting success

The monitoring of goose nesting activity took place annually since 1994 (see Bêty & Gauthier, 2001). Nest searches were conducted using two methods: (a) over an intensively studied area (ca. 50 ha) located in the centre of the colony every year and (b) within a variable number of 1 and 2-ha plots randomly located throughout the colony. Previous analyses showed that nesting success did not differ between those two samples of nests (Reed, Gauthier, & Pradel, 2005), which were combined in this study. In the field, nests were systematically found and marked during periods of laying and early incubation. Nests were revisited at least three times during the nesting season

TABLE 1 Hypothesized causal links between climate, a predator species and its two main prey hypothesized in our study and implied known mechanisms specific to the Arctic ecosystem

	Causal variable (*name*)	Affected variable (*name*)	Expected effect	Hypothesized mechanisms
1.	Winter AO (*winAO*)	Lemming abundance (*lmg*)	Negative	High winter AO index, which is linked to a decrease of precipitation and an increase of wind strength, decreases the quality of lemming subnivean habitat (access to food and cold protection) and lemming breeding during winter (Berteaux et al., 2017; Dominé et al., 2018) and influences their summer abundance (Fauteux et al., 2015; Ims et al., 2008)
2.	Spring AO (*sprAO*)	Lemming abundance (*lmg*)	Positive	High spring AO index, which is linked to a decrease in air temperature, prolongs the snow cover and a good quality subnivean habitat for lemmings (cold protection and reduced predation risk; Berteaux et al., 2017) and influences their summer abundance
3.	Spring AO (*sprAO*)	Goose nesting success (*goose*)	Negative	High spring AO, which is linked to a decrease in air temperature, delays spring and prolongs the snow cover, which have a negative effect on food and nest site availability for geese (Dickey et al., 2008)
4.	Summer AO (*sumAO*)	Average of air temperature during nesting (*temp*)	Negative	High summer AO index, which is linked to an increase of wind strength and a decrease of air temperature, is indicative of cold temperature during the goose nesting period (Mitchell, 2004; Thompson & Wallace, 2000)
5.	Summer AO (*sumAO*)	Cumulative summer rainfall during nesting (*prec*)	Negative	High summer AO index, which is linked to a decrease of precipitation, is indicative of a low cumulative rainfall during the goose nesting period (Mitchell, 2004; Thompson & Wallace, 2000)
6.	Average of air temperature during nesting (*temp*)	Goose nesting success (*goose*)	Positive	Warm temperature during incubation reduces embryo mortality (Dickey et al., 2008; Poussart et al., 2000)
7.	Cumulative summer rainfall during nesting (*prec*)	Goose nesting success (*goose*)	Positive	High rainfall increases water availability and goose ability of fending predators off (Lecomte et al., 2009)
8.	Lemming abundance (*lmg*)	Proportion of fox dens with breeding (*fox*)	Positive	High abundance of lemmings leads to high lemming consumption by foxes and a high number of fox dens with breeding (numerical response to the increased lemming abundance; Angerbjörn et al., 1999; Braestrup, 1941; Kaikusalo & Angerbjörn, 1995)
9.	Proportion of fox dens with breeding (*fox*)	Goose nesting success (*goose*)	Positive	High breeding activity of foxes occurs when lemming abundance is high. Consumption of lemmings by foxes then increases, which reduces the consumption of goose eggs by foxes and improves the nesting success of geese (functional response of fox to the high abundance of its main prey; Bêty et al., 2002)

to determine initiation and hatching dates and their success. A nest was considered successful if at least one egg hatched. Apparent nest survival (*goose*) was thus a binomial variable for each monitored nest over the years (with 1 for successful nest and 0 for failed nest; Table S1). As we monitored the majority of nests from the beginning of the nesting attempts, we used this apparent estimator in our analysis.

2.3 | Lemming abundance

Since 2004, lemming abundance (*lmg*) was annually estimated with live trapping and capture–mark–recapture methods during summer (Table S1) in two 11-ha permanent grids (one for each type of habitat – mesic tundra and wetland) for 3 consecutive days during 3 periods (mid-June, mid-July and mid-August). Each grid contained 100–144 trapping stations separated by 30 m and arranged in a Cartesian plane (see more details in Fauteux, Gauthier, & Berteaux, 2015). We used the average between grids to determine an overall lemming density. Before 2004, index of lemming abundance was estimated by using the relationship between annual lemming density obtained from the previous method and the abundance index obtained from snap-trapping (Gruyer, Gauthier, & Berteaux, 2008) over 2004–2014 (R^2_{adj} = 0.81; Gauthier et al., 2013).

2.4 | Fox breeding activity

Generally considered as a meso-predator in the Arctic ecosystem, the Arctic fox represents one of the top-predator species at Bylot

Island. We monitored Arctic fox dens opportunistically from 1993 to 2002 and systematically throughout the study area since 2003 (number of monitored dens ranged from 35 before 2003 to about 100 after 2003; Berteaux, 2019). Fox dens were checked at least twice during the summer (late May and early July; Table S1) to monitor signs of breeding activity (Szor, Berteaux, & Gauthier, 2008). Arctic fox breeding activity (*fox*) was estimated as the proportion of monitored dens from which an Arctic fox litter emerged during summer, hereafter called the proportion of fox dens with breeding (average date of pup emergence = 17 June; Morin, 2015).

2.5 | Climate data

2.5.1 | Regional climate

The Arctic oscillation (AO) represents fluctuations in atmospheric pressure between polar and middle latitudes (Thompson & Wallace, 1998) and has a strong influence on weather conditions in the Arctic (Comiso & Hall, 2014). In the eastern Canadian Arctic, including the North Baffin area, negative AO values are associated with weaker winds, higher precipitation and warmer temperatures than normal, while positive values correspond to opposite conditions (Thompson & Wallace, 2000). Dickey et al. (2008) already demonstrated the seasonal influence of AO (winter, spring and summer) on goose nesting success in the high Arctic. Moreover, winter AO, by influencing winter conditions, could impact survival and condition of resident species (i.e. lemmings, Arctic fox) and thus their ability to breed during spring and summer (Williams, Henry, & Sinclair, 2015). We therefore decided to consider these three seasonal periods (winter, spring and summer) to study the impact of AO on species interactions (Table S1). We obtained daily values for the AO index from the Climate Prediction Center of the National Weather Service (http://www.cpc.ncep.noaa.gov). For each year, we estimated three AO indexes (*winAO*, *sprAO* and *sumAO*) by averaging daily index AO of the interested period. We used the same period described in Dickey et al. (2008) (Table S1).

2.5.2 | Local climate

Temperature data were extracted from an automated weather station located in the south plain of Bylot Island (hourly basis record at 20 m above sea level a.s.l.; CEN, 2018). The daily air temperature was obtained by averaging data recorded every minute for 24 hr. Daily precipitation was recorded manually during the summer using a rain gauge. For each monitored nest, we computed the mean of daily air temperature (*temp*) and the cumulative precipitation (*prec*) experienced between its initiation date and hatching or failure date (Table S1).

2.6 | Statistical analysis

We used confirmatory path analyses to test our causal hypotheses describing how the variables are causally linked based on hypothesized direct and indirect effects. This kind of analysis is used to specify and test complex multivariate relationships among a suite of interrelated variables, which can be both predictors and responses. Links among variables are represented by a path diagram, and arrows illustrate hypothesized direct causal relationships, that is relationships that are not mediated by any other variable in the model. We associated several datasets (regional and local climate, nesting success of geese, breeding success of foxes, lemming abundance) over 21 years (1996–2016).

We first defined our multivariate causal hypotheses based on our knowledge specific to the studied system (Table 1) and then expressed these hypotheses into a directed acyclic path diagram (i.e. a graph describing the causal relationship between variables; Figure 1a, Grace et al., 2012). We specified hypothesized mechanisms (Table 1) by building the original path diagram with both observed and latent variables (Figure 1a). Latent variables were not measured in the field but are part of the hypothesized causal model. In our system, they represented predation behaviour on lemmings and geese by foxes (i.e. lemming and goose egg consumption rates). In order to test our causal hypothesis with our measured data, we translated the original path diagram (with latent variables) into an equivalent directed acyclic graph (only with observed variables; Figure 1b). This new directed acyclic graph is equivalent to the original one in its d-separation claims involving the observed variables and so allowed us to consider the hypothesized causal links between several variables (i.e. proportion of fox dens with breeding, goose nesting success and some climate variables; see results) as inducing paths involving these latent variables (Shipley, 2016). Specifically, we detailed how we proceeded in Method. S2. This path diagram implies a series of zero (partial) correlations (absence of correlation between two variables when fixing a third variable in the path diagram, to a constant value) which, together, can be tested using a d-sep test (Shipley, 2000). This method allows us to use data with non-normal distributions and that is hierarchically structured (Shipley, 2009, 2016).

We translated hypothesized causal links of the path diagram into a path model. The path model was composed of a set of statistical models: one statistical model for each variable having at least one causal parent in the tested path diagram (i.e. lemming abundance, proportion of fox dens with breeding and success/failure for each goose nest). Since it is biologically reasonable to hypothesize that a summer that is both warm and wet would favour nesting success in greater snow geese, we also included an interaction term in our models. Royer-Boutin (2015) previously found a weak lagged effect of lemming abundance on goose nesting success in our system, as success tended to be lower in the year following a lemming peak. In a preliminary analysis, we tested for a lagged effect of predation on goose nesting success, but this link was never significant. We therefore did not consider lagged effect any further in our analyses.

All statistical models in a path model were based on the same dataset. We used linear (LMs) or generalized linear mixed models (GLMMs) each with their appropriate distributions (normal or binomial) and their appropriate random effects (year). To overcome issues related to nonlinear relationships with the proportion of fox dens with breeding, we log-transformed lemming abundance data. For all models, the overdispersion was checked. We started by fitting the full path model to our data (Figure 1a) and then proceeded by fitting a series of path models derived from the original one, that is with different links among our variables (see Figure S3). We used the AIC statistic to select the best fitting model. In the presence of models having ΔAIC < 3 (Burnham & Anderson, 2010), we proceed with a model-averaging method (Shipley, 2013). Finally, each variable of the best path model was first standardized to unite variance and zero mean in order to obtain standardized path coefficients. These coefficients allowed us to compare the strength of direct and indirect causal links between variables in the model. The strength of an indirect path between two variables was obtained by multiplying path coefficients belonging to this path.

We used the package PIECEWISESEM (Lefcheck, 2016, package version 1.2.1, R version 3.3.2) to run the analyses.

3 | RESULTS

3.1 | Biotic and abiotic trends

During our 21-year study (1996–2016), lemming abundance, the proportion of fox dens with breeding and goose nesting success presented large fluctuations (Figure 2). Lemming abundance ranged from a minimum of 0.02 in 2013 to up to 9.35 lemming/ha in 2000 (mean ± *SD* = 2.19 ± 2.52 lemming/ha), with 7 years of low, intermediate and high abundance, respectively. The proportion of breeding fox dens ranged from 0 in 2002 to 0.33 in 2016 (mean ± *SD* = 0.14 ± 0.09). Finally, goose nesting success fluctuated between 0.14 in 1999 and 0.91 in 2014 (mean ± *SD* = 0.69 ± 0.18).

Between 1996 and 2016, winter, spring and summer AO ranged from −1.65 to +1.07 with no temporal trend (*winAO*, $F_{1,19}$ = 1.06, *p* = .32; *sprAO*, $F_{1,19}$ = 0.08, *p* = .78; *sumAO*, $F_{1,19}$ = 1.35, *p* = .26; Figure S4). During the same period, the mean temperatures measured between the annual mean initiation date and the mean hatching date of geese (i.e. the laying and incubation periods) was 4.6 ± 0.8°C, with annual values fluctuating from 3.3°C to +6.1°C (Figure S5). Between 1996 and 2016, the average cumulative precipitation during the goose nesting period was 21.6 ± 17.9 mm, with a maximal value in 2012 (69.0 mm) and a minimal one in 2016 (1.6 mm; Figure S5). There was no temporal trend in air temperature and cumulative precipitation during the goose nesting period (LMs, air temperature, $F_{1,19}$ = 0.23, *p* = .64; precipitation, $F_{1,19}$ = 0.86, *p* = .36), but climatic factors could aptly be described as being highly variable over time.

3.2 | Weather and climatic impacts on Arctic species

Among all path models tested, seven of them were not statistically rejected by our data (i.e. *p*-value > .05 for the C-statistic value; Figure S3 & Table S6) but only two were close competitors with a ΔAIC < 3 (Table S7). Both present the same causal links illustrating relationships between the local climate and any species, and between species themselves. The only difference was in the absence of a regional climate influence (i.e. winter AO) in the path model. We therefore calculated model-averaged estimators of each causal link present in these two path models (Table S8).

The proportion of fox dens with breeding, air temperature and cumulative precipitation during the period of goose nesting explained 72% of the variation in goose nesting success. According to the path coefficients (PC), local climate had the largest influence on goose nesting success, which increased when both temperature and precipitation were high, though with a stronger effect of the latter variable ($PC_{prec-goose}$ = 2.11 ± 0.12; $PC_{temp-goose}$ = 1.41 ± 0.10; Figure 3). Fox breeding also displayed a positive causal link with

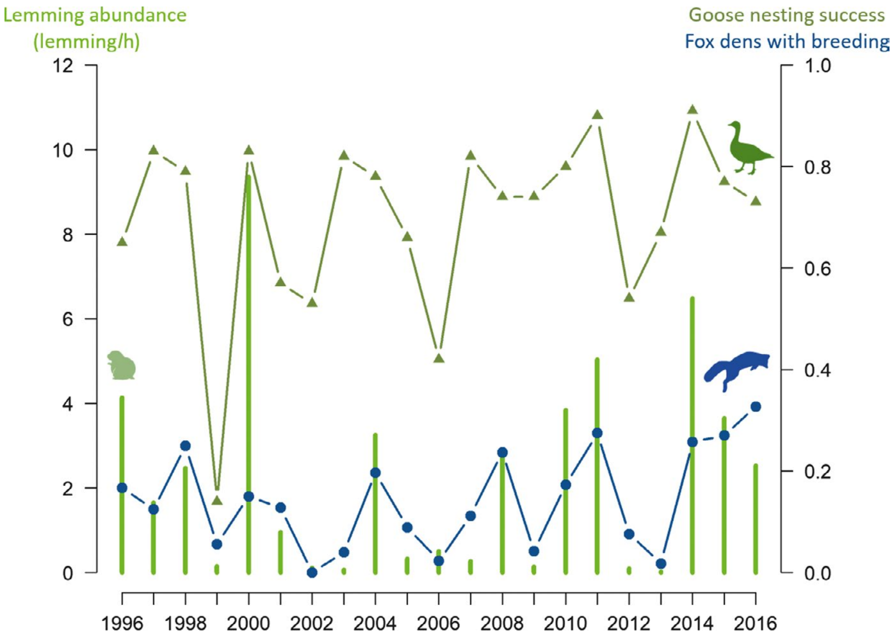

FIGURE 2 Variation of lemming abundance (green bars), greater snow goose nesting success (triangle dots) and proportion of the Arctic fox dens with breeding (circle dots) between 1996 and 2016, Bylot Island, Nunavut, Canada

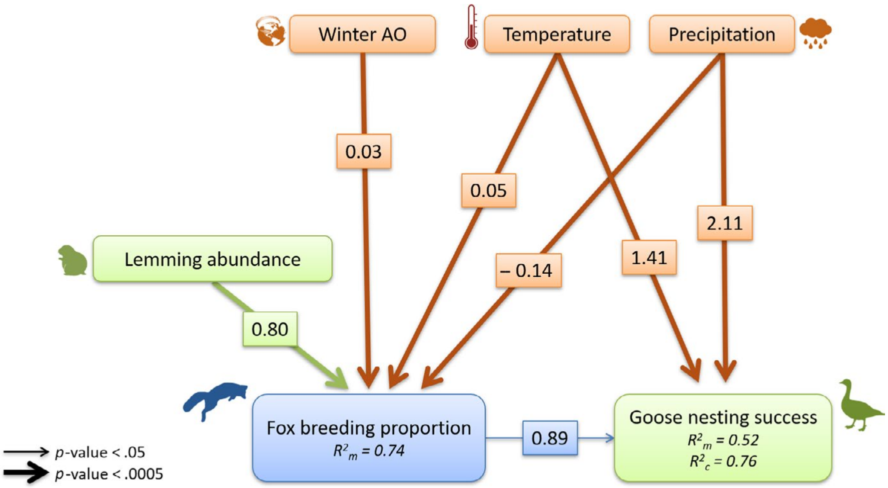

FIGURE 3 Path diagram with model-averaged estimates showing the significant direct and indirect links between regional and local climate variables and the reproduction of prey (lemming and snow goose), and their predator (Arctic fox). Arrows represent the direction of causal links. Each value on top of the arrows displays the path coefficients, which represent the strength (value) and the effect (positive/negative) of the causal link. The thickness of arrows depends on the significance level of this path coefficient (thick: $p < .0005$; thin: $p < .05$). R_c^2 and R_m^2 are the explained variances with and without random effects, respectively (R_c^2 is lacking in fox box because we did not use random effects in the model to explain the variability of the proportion of fox dens with breeding)

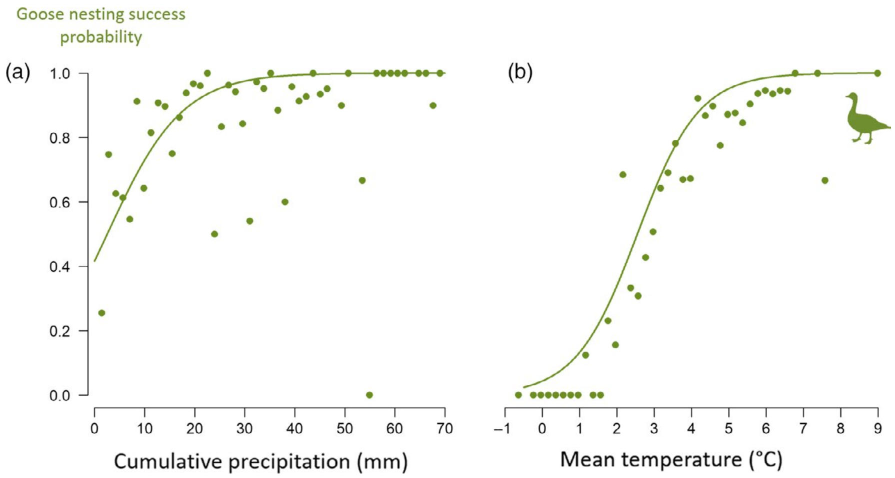

FIGURE 4 Relationship between goose nesting success probability, cumulative precipitation (*prec*; a), and mean air temperature (*temp*; b) during the nesting period of each nest (mean number of monitored nests across years = 192, range number of monitored nests across years = [42; 315]), between 1996 and 2016, Bylot Island, Nunavut, Canada. Local climate displays a key role in the variation of goose nesting success (Figure 3). Even though analyses were performed on individual data points (see 'Materials and Methods'), for sake of clarity the proportion of successful nests observed for 50 evenly spaced bins along the x-axis is presented for cumulative precipitation (a) and mean air temperature (b)

goose nesting success ($PC_{\text{fox-goose}} = 0.89 \pm 0.39$; Figure 4). We did not find any evidence for a link between spring AO and goose nesting success. Contrary to our expectations, summer AO was not linked to local climate (i.e. temperature and precipitation) during the goose nesting period.

Lemming abundance, local and regional climatic factors were all related to the proportion of fox dens with breeding and explained 74% of its variation. However, lemming abundance was the principal driver of fox breeding with a positive causal link at least 5 times stronger than any other causal links (Figure 5; $PC_{\text{lmg-fox}} = 0.80 \pm 0.01$; $PC_{\text{temp-fox}} = 0.05 \pm 0.01$; $PC_{\text{prec-fox}} = -0.14 \pm 0.01$; $PC_{\text{winAO-fox}} = 0.03 \pm 0.002$; Figure 3). Local temperature and precipitation during the goose nesting period had a contrasted influence on the proportion of fox dens with breeding, which increased with high temperature but decreased with high precipitation, with a stronger effect of the latter variable ($PC_{\text{prec-fox}}$ was 2 times stronger than the $PC_{\text{temp-fox}}$). The stronger wind, lesser precipitation and warmer temperature associated with an increasing winter AO positively influenced the reproduction of foxes. However, its influence was weak ($PC_{\text{winAO-fox}} = 0.03 \pm 0.002$). Contrary to our original hypotheses, we

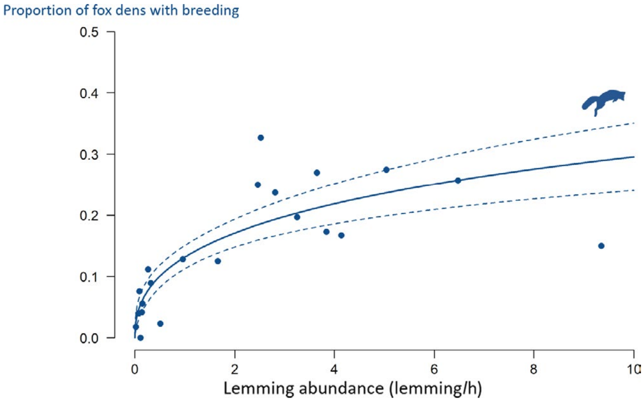

FIGURE 5 Relationship between the proportion of fox dens with breeding (*fox*) and lemming abundance (*lmg*) during the summer season, between 1996 and 2016, Bylot Island, Nunavut, Canada. Lemming abundance is the critical causal variable explaining variation in proportion of fox dens with breeding in our path model (Figure 3). The solid and dashed lines represent predicted values and confidence interval, respectively

found no link between winter AO and lemming abundance. Finally, goose nesting success displayed indirect causal paths with all of climate variables ($PC_{\text{winAO–fox–goose}} = 0.03$; $PC_{\text{temp–fox–goose}} = 0.04$, $PC_{\text{prec–fox–goose}} = -0.12$; Figure 3), the strongest one linking precipitation and goose nesting success, through the proportion of fox dens with breeding. We found no indirect causal path linking fox breeding and the regional and local climate indices. Our a-posteriori analysis allowed us to explore further the causal link between the proportion of fox dens with breeding and goose nesting success. This analysis supported our hypothesis that these two observed variables are linked via two latent variables, the consumption rates of lemmings and goose eggs by foxes. These two variables are themselves subject to an influence of local climate (see details in Figure S3). This provides a mechanistic explanation for the causal link between the proportion of fox dens with breeding and goose nesting success in Figure 3.

4 | DISCUSSION

While the body of evidence showing the potential impacts of climate change on trophic interactions is expanding (Renner & Zohner, 2018), it is still unclear whether predator–prey systems will be more affected by direct or indirect climate-driven processes, even in simple food webs. Here, we found that both regional (winter AO) and local climate could both directly affect the breeding success of an Arctic herbivore, the snow geese, and indirectly through effects on its main predator, the Arctic fox. Our path analyses suggested that goose reproduction is mainly driven by direct local climate effects since precipitation and air temperature were twice as strong as a climate effect mediated through the reproductive activity of foxes on goose nesting success. Contrary to our expectations, we found no relationship between either regional or local climate and summer lemming abundance, although lemmings still played an important role in this system by their strong, positive effect on fox breeding activity.

4.1 | Predator–prey interactions

Several studies demonstrated the key role of lemming population cycles on the tundra food web dynamics (e.g. Ims & Fuglei, 2005; Schmidt et al., 2012). While our study further illustrates that role, our analyses allowed us to quantify the relative strengths of predator–prey links between the Arctic fox and its two major prey. Latent variables helped to illustrate the hypothesized mechanisms (8 & 9 in Table 1) driving the almost equally strong and positive causal links between (a) lemming abundance → proportion of fox dens with breeding and (b) proportion of fox dens with breeding → goose nesting success (Figure S3). We hypothesized that the link between lemmings and fox breeding is due to an increase in lemming consumption rate by foxes (latent variable) in years of high lemming abundance, which leads to a strong numerical response of breeding foxes. This numerical response has also been documented by previous studies across the range of Arctic foxes (Angerbjörn, Tannerfeldt, & Erlinge, 1999; Braestrup, 1941). The positive link between fox breeding and goose nesting success is the consequence of another hypothesized latent variable, the rate of consumption of goose eggs by foxes. When lemming abundance increases, goose egg consumption decreases due to the functional response of foxes. The type of indirect interactions between lemmings and geese can vary between apparent mutualism and apparent competition as a result of the strongly fluctuating abundance of lemmings between years (Bêty et al., 2002). The link between lemming abundance and goose nesting success through fox predation behaviour, a latent variable, can be viewed as a form of apparent mutualism (see Abrams, Holt, & Roth, 1998; Bêty et al., 2002).

Few studies have measured both the causal links and strength of relationships in a food web (but see Antiqueira et al., 2018; Ogilvie et al., 2017). Here, we did so by linking numerical and functional responses of a predator and indirect interactions between its prey. Our study, based on long-term data series, improves our understanding of a simplified Arctic food web and helps quantify apparent interactions between two prey species sharing a common predator.

4.2 | Climate and goose nesting success

While most climate change-related studies primarily focus on measuring the response of organisms to temperature increase, we are only starting to examine the consequences of changes in rainfall on vital rates of animals. Most results point to negative effects of rainfall on reproduction via increased risks of young mortality and foraging cost for parents (Lamarre et al., 2018; Öberg et al., 2015).

An increase in summer temperatures and precipitations may positively influence goose nesting success through an increase in resource accessibility (e.g. greater access to food resources with earlier snow melt; unlimited access to surface drinking water after rainfall, Lecomte et al., 2009). In addition to confirming impacts of air temperature, our results showed the crucial role of rainfall in our system being the most influential climate parameter on goose nesting success (Figure 3).

Temperature and precipitation both can have bottom-up effects in many system (Holmgren et al., 2006; Ogutu, Piepho, Dublin, Bhola, & Reid, 2008). Here, we argue that the difference in strength of these effects can be the result of water access not just being a resource (e.g. to alleviate the fasting cost during incubation; Le Maho et al., 1981) but especially by being a driver of the risk of predation on goose nests resulting in a top-down process. The surge in water accessibility created by temporary water holes after rainfall reduces the distance travelled by females to drink during an incubation recess and thereby decreases both predation opportunity and success by foxes (i.e. goose egg consumption rate; Lecomte et al., 2009). By altering the predator–prey interactions between foxes and geese, increased water access via rainfall positively affects goose nesting success. Hence, our study illustrates novel pathways by which local climate conditions can induce cumulative indirect and direct effects on species and their trophic interactions.

4.3 | Climate and fox breeding

Because individual species often present an unique response to climate variability, climate impacts on trophic interactions are complex to unravel. Depending on the species, variation in air temperature or rainfall may improve predator efficiency (Creel et al., 2016; Grigaltchik et al., 2012) or favour prey survival and/or reproduction (Lecomte et al., 2009; Mysterud, 2016). Compared to geese, fox breeding displayed weaker and more ambivalent links with local climate (i.e. positive effect of both temperature and precipitation on goose nesting success vs. opposite effects of these variables on the proportion of fox dens with breeding). To a lesser extent, our study showed that conditions during winter and early summer could partially determine the proportion of breeding fox dens due to the ability of foxes to quickly respond to increasing food availability (lemming abundance; presence of geese in spring and summer; Hall, 1989; Hersteinsson, 1984). We suggest that the regional winter climate can directly affect fox breeding through carry-over effects on their body condition and stress level at the start of the breeding season. Local climate during late spring/early summer can also indirectly drive fox breeding through an alteration in predator–prey interactions by modifying the availability of one of the food resources (goose eggs).

Climate effects may occur throughout the life cycle of a species. Cumulative impacts during wintering and breeding seasons may exacerbate the effect of climate variation on species dynamics (Pomara & Zuckerberg, 2017; Williams et al., 2015). For instance, the resilience of species to energetic stress in winter and during the subsequent breeding season can be determined by climatic conditions during winter and during post-winter resource acquisition (Breed, Stichter, & Crone, 2013; Irwin & Lee, 2003). Our results illustrate the successive impact of winter regional and summer local climate on Arctic fox breeding activity. Although we did not have data on fox body condition, we suggest the following potential mechanism. Harsh conditions during winter, associated with a negative AO index in our area, can increase thermoregulation costs and decrease body condition, food availability and predation opportunities (Williams et al., 2015). This may lead to poor female body condition, small litter size, reduced birthweight and consequently low pup survival (Angerbjörn, Arvidson, Norén, & Strömgren, 1991). These mechanisms suggest a delayed effect of specific winter conditions on fox reproduction, with eventual detrimental consequences on breeding propensity and pup survival.

During the goose nesting period, precipitation had a weak negative effect on fox breeding. We suggest this causal link may be partly mediated through predator–prey interactions between geese and foxes (i.e. rate of goose eggs consumption). Arctic foxes are characterized by high behavioural flexibility, which allows for an important variation in their feeding niche. Tarroux et al. (2012) showed that in the presence of a large goose colony, Arctic foxes are more versatile and behave more as a generalist forager than a specialist one. During spring and summer, goose eggs are always part of the fox diet regardless of the variability in lemming abundance between years (Careau et al., 2008). If high precipitation increases the ability of geese to defend their nest from fox attacks as we argued above, this could reduce egg consumption rate by foxes. This change in fox resource acquisition could reduce their reproductive success and explain the negative link detected between precipitation and the proportion of fox dens with breeding.

4.4 | Climate and lemming abundance

Although winter AO index is a proxy for air temperature and precipitation in the Arctic, we detected no causal relationship between winter AO and summer lemming abundance. This may be because winter AO is too much of a coarse-grain climate index for lemmings, which may be sensitive to climate conditions at much smaller spatial and temporal scales. Indeed, several studies have shown the importance of snow properties in the subnivean space for lemmings (Berteaux et al., 2017; Ims et al., 2008). In particular, subnivean conditions with a dry snowpack and a soft basal depth hoar without wetting/refreezing events (Berteaux et al., 2017) may enhance lemming survival and improve reproduction during the winter via increased thermal insulation, food access and predator protection (Korslund & Steen, 2006; Lindström & Hörnfeldt, 1994). Dominé et al. (2018) also showed that the physical properties of the subnivean space may be determined during a short time window at the onset of the winter, when the snow cover gets established.

5 | CONCLUSIONS

The contrasting response of one prey (snow goose) and its predator (Arctic fox) to temperature and precipitation variations suggests that predator–prey relationships are modulated by multiple climate interactions. This potential climate-based decoupling between species adds another layer of complexity in our understanding of food web response to a changing climate. Moreover, recent reviews (Cahill et al., 2012; Ockendon et al., 2014) highlighted our limited understanding of climate change impacts on food webs. While most studies only focus on the climatic tolerance of species (Mitchell et al., 2018) or alterations on direct trophic interactions (Creel et al., 2016; Legagneux et al., 2014), little is known about the indirect climate effects on species and trophic interactions. Our study integrated the combined effects of regional and local climate as well as direct and indirect trophic interactions into a single analytical framework based on long-term data series. Doing so, we quantified the mechanisms underlying the multiple pathways through which climate can affect species reproduction including via trophic interactions and demonstrated that prey reproduction can be mainly driven by local climate effects, while its predator reproduction is subject to both regional and local climate impacts. Improving our understanding of the relationships between regional climate indices like the AO and local climate variables, and climate effects on all parts of a species life cycle is necessary to enhance our capacity to anticipate direct and indirect climate impacts on food web dynamics.

ACKNOWLEDGEMENTS

The research relied on the logistic assistance of the Polar Continental Shelf Program (Natural Resources Canada). The study was funded by the Canada Foundation for Innovation (Grant to NL), Canada Research Chairs (Grant to NL), Natural Sciences and Engineering Research Council of Canada (Grant to NL and GG), the Canadian Network of Centres of Excellence ArcticNet (Grant to NL and GG), Université de Moncton and the Canadian Wildlife Service (Grant to GG). This work is part of an PhD project in the Canada Research Chair in Polar and Boreal Ecology at Université de Moncton, which benefited from early comments by J. Bêty. We acknowledge the support from the Centre d'Étude Nordiques. We thank Frédéric Letourneux and Mathieu Manuel for their help with the fieldwork. We also thank all the Bylot Island field team for their assistance in this project, especially members of the fox team. Thanks to J. Bêty for his advices on the design of the project and D. Berteaux for exciting discussions about Arctic foxes. We thank François Rousseu for his constructive comments on a previous version of this manuscript.

AUTHORS' CONTRIBUTIONS

N.L. and G.G. conceived the study. C.-C.J., N.L., G.G., and D.B. collected data. C.-C.J. and B.S. performed the analyses. All authors participated in the writing.

DATA AVAILABILITY STATEMENT

The data and our code are available through the Figshare Repository: https://doi.org/10.6084/m9.figshare.7674206 (Juhasz, Shipley, Gauthier, & Lecomte, 2019).

ORCID

Claire-Cécile Juhasz https://orcid.org/0000-0001-7326-8444

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SUPPORTING INFORMATION

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

How to cite this article: Juhasz C-C, Shipley B, Gauthier G, Berteaux D, Lecomte N. Direct and indirect effects of regional and local climatic factors on trophic interactions in the Arctic tundra. *J Anim Ecol*. 2020;89:704–715. https://doi.org/10.1111/1365-2656.13104