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Disentangling the relative influences of global drivers of change in biodiversity: A study of the twentieth-century red fox expansion into the Canadian Arctic

Daniel Gallant[1,2] | Nicolas Lecomte[2] | Dominique Berteaux[1]

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

[2]Chaire de recherche du Canada en écologie polaire et boréale and Centre d'Études Nordiques, Université de Moncton, Moncton, NB, Canada

Correspondence
Daniel Gallant
Email: daniel.gallant@canada.ca

Present address
Daniel Gallant, Kouchibouguac National Park of Canada, Kouchibouguac, NB, Canada

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Abstract

1. The poleward range shift of the red fox (*Vulpes vulpes*) > 1,700 km into the Arctic is one of the most remarkable distribution changes of the early twentieth century. While this expansion threatens a smaller arctic ecological equivalent, the arctic fox (*Vulpes lagopus*), the case became a textbook example of climate-driven range shifts.
2. We tested this classical climate change hypothesis linked to an important range shift which has attracted little research thus far.
3. We analysed Canadian fur harvest data from the Hudson's Bay Company Archives (14 trading posts; 1926–1950), testing hypotheses based on changes in summer and winter climates. Summer warming might have triggered a bottom-up increase in ecosystem productivity, while winter warming might have lowered thermal stress, both favouring red fox expansion. Additionally, we evaluated the hypothesis that red fox expansion was driven by the appearance of human sedentary sites (n = 110) likely bringing food subsidies into the unproductive tundra.
4. Analysis of red fox expansion chronologies showed that expansion speed was higher during warmer winters. However, the expansions occurred under both cooling and warming trends, being faster during cooler summers in the Baffin Island region. The increasing proportion of red fox in fox fur harvests was best explained by human activity, while generalized linear mixed models also revealed a marginal effect of warmer winters. Generalized additive models confirmed human presence as the most important factor explaining rates of change in the proportion of red fox in fox fur harvests.
5. Using historical ecology, we disentangled the relative influences of climate change and anthropogenic habitat change, two global drivers that transformed arctic biodiversity during the last century and will likely continue to do so during this century. Anthropogenic food subsidies, which constitute stable food sources, facilitated the invasion of the tundra biome by a new mammalian predator and competitor, with long-term consequences that still remain to be understood.

KEYWORDS
anthropocene, biogeography, climate change, distribution, food subsidies, fur trade, human activity, *Vulpes vulpes*

1 | INTRODUCTION

Changes in the twentieth-century phenology and distribution of a large number of plant and animal species are consistent with those expected from climate warming (Chen, Hill, Ohlemüller, Roy, & Thomas, 2011; Lenoir, Gegout, Marquet, de Ruffray, & Brisse, 2008; Parmesan & Yohe, 2003). Yet the steps leading from detection of ecological changes to their attribution to climate warming are challenging, as correlations do not always indicate causal relationships (Berteaux et al., 2006). In addition to climate warming, habitat change, exploitation of species, pollution and introductions of new species have largely contributed to global biodiversity changes. Disentangling the possible drivers of ecological change is critical to inform management and conservation policy (Rudd et al., 2011).

Predators have special relevance among species undergoing changes because they strongly influence the structure and function of some ecosystems, such as the arctic tundra (Legagneux et al., 2012; Legagneux et al., 2014). One of the most remarkable range expansions in recent history is the poleward range shift of the red fox (*Vulpes vulpes*) > 1,700 km into the arctic tundra (Chirkova, 1968; Macpherson, 1964; Marsh, 1938; Skrobov, 1960). Hersteinsson and Macdonald (1992) identified climate warming as the potential driving force behind this change, which became an often-cited example of current climate-driven range shifts (Angerbjörn et al., 2013; Anisimov et al., 2007; Parmesan & Yohe, 2003; Post et al., 2009; Walther et al., 2002).

The red fox expansion encroached on habitats occupied by the arctic fox (*Vulpes lagopus*), a key tundra predator. When in sympatry, these two species compete for food (Elmhagen, Tannerfeldt, & Angerbjörn, 2002; Hersteinsson & Macdonald, 1982) and shelter (Gallant, Reid, Slough, & Berteaux, 2014; Rodnikova et al., 2011). Interference competition through aggression by the larger red fox also occurs (Frafjord, Becker, & Angerbjörn, 1989; Pamperin, Follmann, & Petersen, 2006). Although coexistence of the two species was observed in the western American Arctic (Eberhardt, 1977; Gallant, Slough, Reid, & Berteaux, 2012), the fate of the arctic fox probably depends on whether red fox presence continues to increase in the Arctic. This calls for a better understanding of the causes of large-scale change in red fox distribution.

We explore the expansion of the red fox through the analysis of historic fur harvest records. We set our approach in the context of two major, large-scale changes impacting the Canadian Arctic during the twentieth century, climate change influenced by anthropogenic aerosol emissions (Lashof & Ahuja, 1990; Rahmstorf et al., 2007) and increased economic activity driven in large part by the fur trade (Damas, 2002; Usher, 1973). Hersteinsson and Macdonald (1992) postulated that the northern limit of red fox distribution in North America is defined by ecosystem productivity. They hypothesized that climate warming, and especially warmer and longer summers, triggered a bottom-up increase in productivity, which increased food availability and allowed red foxes to colonize the tundra (hereafter, the summer productivity hypothesis). Recent climate-driven increases in productivity are indeed particularly evident from marked vegetation changes in the Arctic due to a warmer and longer growing season (Anisimov et al., 2007; Elmendorf et al., 2012). The notion that ecosystem productivity in the Arctic may have limited the red fox but not the ecologically similar arctic fox is supported by the larger body size of the former, which implies higher caloric needs (Carbone, Teacher, & Rowcliffe, 2007). The summer productivity hypothesis generates three predictions: (1a) The speed of red fox expansion is positively correlated with summer temperatures, (1b) summer temperature was the most important factor explaining temporal trends in the proportion of red fox in fur harvests, and (1c) sites with the largest increase in the proportion of red fox correspond to those where summer temperature warming was most intense.

Cold winter temperatures exacerbate energy requirements of homeotherms (Fuglei & Øritsland, 1999; Irving, Krog, & Monson, 1955) at a time when, for predators, important parts of the prey base migrated south or are protected by snow cover (Jędrzejewski & Jędrzejewska, 1992). Arctic foxes are highly adapted to live under cold conditions (Audet, Robbins, & Larivière, 2002; Scholander, Walters, Hock, & Irving, 1950) and can even lower their basal metabolic rate (Fuglei & Øritsland, 1999). They are also adapted to starvation conditions (Fuglei & Øritsland, 1999; Prestrud & Nilssen, 1992). Winter conditions in the Arctic could have limited the distribution of the red fox because of its higher energy burden compared to its congener. Bartoń and Zalewski (2007) found that winter severity (i.e. cold temperature, deep and long snow cover) was more important than summer temperature or primary production in describing spatial variation of red fox density in Eurasia. Therefore, warming winter temperatures could have enabled the red fox to expand northward by reducing thermal stress, whereas shallower snow cover can facilitate locomotion and access to prey (hereafter, the winter stress hypothesis). The winter stress hypothesis generates three predictions: (2a) the speed of red fox expansion is positively correlated with winter temperatures, (2b) winter temperature and/or winter precipitation was the most important factor explaining temporal trends in the proportion of red fox in fur harvests, and (2c) sites with the largest increase in the proportion of red fox correspond to those where winter temperature warming was most intense and/or those with the most pronounced diminution in winter precipitation.

While range shifts are recognized as a common response of species to climate change, other congruent perturbations may be at play. The impact of food subsidies created by human activities is not always considered in studies on population dynamics of arctic vertebrates (but see Gilg et al., 2012; Giroux et al., 2012; Henden, Stien, Bårdsen, Yoccoz, & Ims, 2014; Killengreen et al., 2011), and it should be given proper consideration in the case of the red fox expansion in North America. During the twentieth century, the appearance of sedentary human communities in the Canadian North was a key step in the long history of Inuit use of the land (Gagnon & Berneaux, 2009) and led to the production of garbage dumps, which contained discarded food and other organic waste (Cockburn, 1986; Gagnon, 1999; Qikiqtani Inuit Association, 2013). Foxes are known to exploit anthropogenic food sources in the Arctic (Eberhardt, 1977; Savory, Hunter, Woodler, & O'Brien, 2014), and records of foxes attracted to human activities in the Arctic go back to the nineteenth century (Ross & Ross, 1835; Simmonds, 1860). Sedentary human communities in the Canadian Arctic thus created conditions with stable and predictable food subsidies for generalist predators such as red foxes and could have caused their expansion by lifting the productivity barrier (hereafter, the food subsidies hypothesis). The food subsidies hypothesis generates three predictions: (3a) sedentary human communities were established before the expansion of the red fox into new regions of the tundra, (3b) human presence is the most important factor explaining temporal trends in the proportion of red fox in fur harvests, and (3c) sites with the largest increase in the proportion of red fox correspond to those where human activity was the most intense.

In this research, we explore how the twentieth-century red fox range expansion into the Canadian Arctic relates to (1) the summer productivity, (2) the winter stress and (3) the food subsidies hypotheses, in an attempt to disentangle the relative influence of climate change and the appearance of sedentary communities as major drivers of change in the Arctic. This is also an effort to use historical ecology as a way to answer some of the pressing questions related to ecological change in the Arctic.

2 | MATERIALS AND METHODS

2.1 | Historical data on the red fox expansion

A general chronology of the red fox expansion into the Canadian Arctic, starting in 1918 and ending in 1962 when red fox reached Ellesmere Island (Macpherson, 1964), was established from available literature. Red and arctic fox fur harvest data were retrieved from the Hudson's Bay Company Archives in Winnipeg (Manitoba) in order to obtain a spatially explicit description of the red fox expansion by computing fur harvest data from 1926 to 1950 for 14 northern Canadian fur trading posts (Figure 1). These trading posts were active for most of 1926–1950, and this covers the main period of red fox expansion in the Canadian Arctic Archipelago (Macpherson, 1964) and on the mainland, west of the Hudson Bay (Marsh, 1938).

2.2 | Historical data on climate

July and February mean monthly temperatures were used to represent summer and winter climate. Vascular plant growth is correlated with summer temperatures in the Arctic (Buchwal, Rachlewicz, Fonti, Cherubini, & Gärtner, 2013; Jonasson, Michelsen, Schmidt, & Nielsen, 1999), and July is the warmest month (Rigor, Colony, & Martin, 2000; Woo & Ohmura, 1997). February is the coldest month at high latitudes in North America (Laidler et al., 2009; Woo & Ohmura, 1997). Total snow precipitation in February was also considered, because snow depth reduces prey accessibility to predators (Jędrzejewski & Jędrzejewska, 1992). Environment Canada's climate database was searched for weather stations having the most complete records from 1926 to 1950 in northern Canada. There were 22 and 23 such weather stations identified for July and February, respectively (Figure 1). Missing data in these time series were estimated through interpolation (Appendix S1). Nine and eight of the 14 trading posts targeted for analyses did not coincide with locations where weather

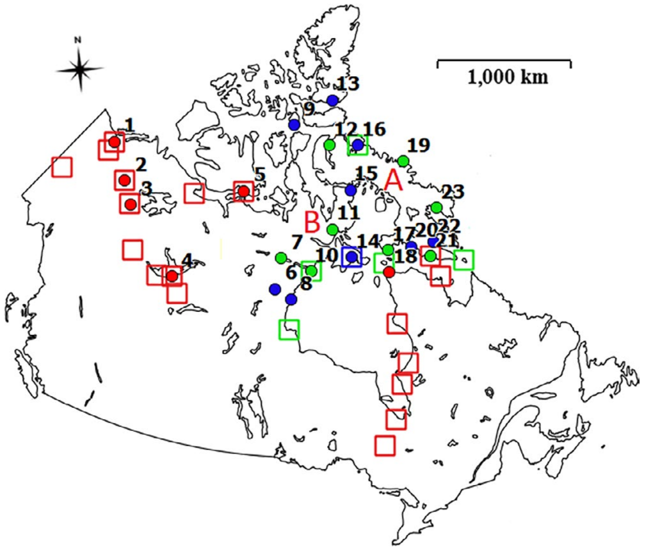

FIGURE 1 Geographical origin of data from northern Canada used in this study. Filled circles indicate the 23 locations with available data on red fox first detections and fur harvest time series. Open squares indicate the 24 locations with climate data from weather stations, of which 22 and 23 had near complete climate records for July and February, respectively. Blue symbols indicate locations used in the study of red fox expansion chronologies (step 1 of data analyses), red symbols indicate locations with time series analysed in generalized linear models (step 2) and generalized additive models (step 3), and green symbols indicate locations used in all data analyses. There were thus 17 locations used in establishing chronologies, and 14 locations used in analyses of time series. Locations with red fox data are labelled by numbers, as follows: Aklavik (1), Fort Good Hope (2), Fort Norman (3), Fort Resolution (4), Cambridge Bay (5), Padley (6), Baker Lake (7), Eskimo Point [present day Arviat] (8), Resolute Bay (9), Chesterfield Inlet (10), Repulse Bay (11), Arctic Bay (12), Grise Fiord (13), Coral Harbour (14), Igloolik (15), Pond Inlet (16), Cape Dorset (17), Wolstenholme (18), Clyde River (19), Amadjuak (20), Lake Harbour (21), Frobisher Bay [present day Iqaluit] (22) and Pangnirtung (23). Letters show the two regions where red fox expanded its distribution from the 1920s to the 1960s, namely Baffin Island (A) and continental Nunavut (B)

stations recorded July and February temperatures, respectively (Figure 1). Climate data for these sites were estimated through spatial interpolations based on data from the 22 and 23 weather stations with records for July and February temperatures, respectively (Appendix S1).

2.3 | Historical data on human presence

Anthropogenic food subsidies are difficult to quantify, because both data on food wasted by humans and on the accessibility of that food to other species are often lacking (Parfitt, Barthel, & Macnaughton, 2010). Sedentarization of human populations in the Canadian Arctic mainly occurred in the early twentieth century and was driven by the rapid growth of the arctic fox fur trade, as most settlement locations started with the foundation of a fur-trading post (Appendix S2). Presence of sedentary sites in a given region was used as an indicator of anthropogenic food subsidies available to foxes. Cockburn (1986), Gagnon (1999) and Qikiqtani Inuit Association (2013) support our premise that the appearance of focal points of human activity in northern Canada resulted in the creation of garbage dumps, which are often used by predators (Eberhardt, 1977; Savory et al., 2014).

Foundation dates of sedentary sites found on the Northern Settlements Map of the National Atlas of Canada (Fremlin, 1974) were used to represent the intensity of regional human presence. There were 110 sedentary sites (or settlements) established north of 60° N before 1951. To obtain cumulative counts of human communities around trading posts, each human community was associated to the closest studied trading posts. The smallest, average and largest distances between settlements and their closest trading post were 20 km, 286 km and 1,164 km, respectively (*n* = 110). Human influence contributed by each settlement was estimated by dividing 1,164 by its distance to the closest trading post, thus obtaining a distance-based weighted score ranging from 1.0 to 58.2. These scores were summed up annually until 1950 for each settlement, starting the year it was founded. For each trading post, a proxy for anthropogenic food subsidies was thus obtained, integrating the number of settlements in its vicinity, the distance of those settlements and the amount of time each settlement was active.

2.4 | Testing predictions

All analyses were made in R version 2.15.2 (R Development Core Team, 2014), except when stated otherwise. We worked through

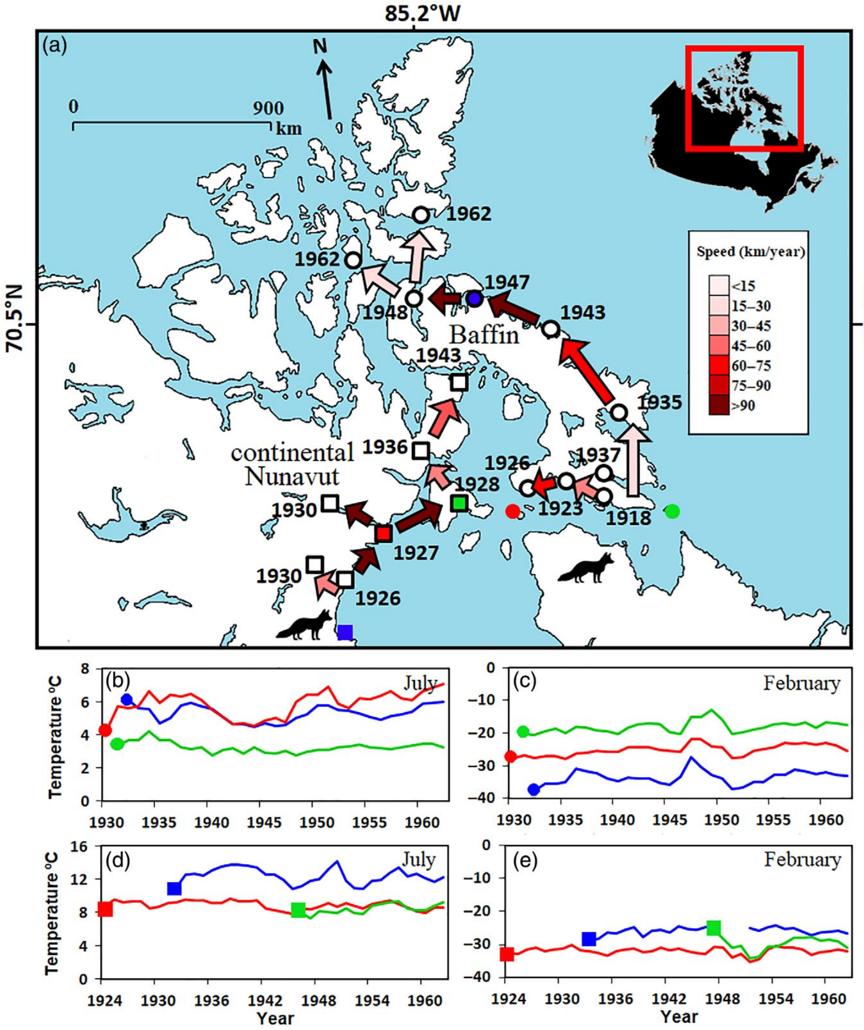

FIGURE 2 (a) Red fox expansion in the Baffin (open black circles) and continental Nunavut (open black squares) regions of the Canadian Arctic during the first half of the twentieth century, as reconstructed from first detections at various locations (see text for details). Arrow colours show speed of red fox expansions. Also shown are four-year moving averages of (b) July and (c) February temperatures (°C) from weather stations at Nottingham Island (red circle), Pond Inlet (blue circle) and Resolution Island (green circle) in the Baffin region, as well as for (d) July and (e) February temperatures (°C) from weather stations at Chesterfield Inlet (red square), Churchill (blue square) and Coral Harbour (green square) in the continental Nunavut region

three steps to test predictions about the causality of red fox northward expansion.

Step 1: The chronology of red fox first detections was studied at various trading posts and human communities to determine whether the progression of the expansion was correlated with climate (predictions 1a and 2a) or followed human sedentarization (prediction 3a). Analysis of the published literature and of fur harvest records from the Hudson's Bay Company Archives allowed us to revise the chronology of the red fox expansion from Lake Harbour to Grise Fiord, in the eastern Canadian Arctic Archipelago (Figure 2a). Using the same approach, the chronology of the red fox expansion was determined from Eskimo Point (present-day Arviat) to Igloolik in continental Nunavut, along the western coast of the Hudson Bay (Figure 2a).

To determine whether red fox expansion speed was correlated with changes in climate, the speed (km/year) of the successive appearances of red fox for each segment of its expansion was calculated in both regions (Figure 2a). Due to temporal autocorrelation, repeated-measures correlation was computed with mean monthly temperature data from the warmest (July) and the coldest (February) months of the year. The two regions where red fox expanded were treated as replicates. Resolute Bay and Grise Fiord (founded in 1947 and 1956, respectively) were excluded from correlations because they originated from recent relocations of humans (Royal Commission on Aboriginal Peoples, 1994). Repeated-measures correlation, applied using the 'RMCORR' package version 0.3.0 in R version 3.2.3, integrated paired observations that were recorded multiple times on replicates (Bakdash & Marusich, 2017). Data from the weather stations with the most complete time series where red fox expanded were used, that is three stations for the Baffin region (Resolution Island, Pond Inlet and Nottingham Island) and three stations for continental Nunavut (Churchill, Coral Harbour and Chesterfield Inlet). For each region, 4-year moving averages were calculated from normalized temperature time series (i.e. each dataset divided by its respective global mean), using the proper time span for each segment of the expansion to match it with its calculated speed. This gave us a measure of mean temperature change for each segment of the expansion in each region. Next, the chronology of the two red fox expansions was compared with that of human sedentarization patterns by plotting foundation dates of sites according to their latitude. To determine whether the foundation dates of trading posts influenced the red fox expansion chronologies, a repeated-measures correlation (Bakdash & Marusich, 2017) was computed ('RMCORR' package) between the number of years elapsed between the foundation of anthropogenic sites and their respective first red fox detections, and site latitude. A positive correlation would indicate that human sedentarization occurred prior to the red fox expansions and that dates of first red fox detection reflect red fox arrivals and are not an artefact of the chronology of human sedentarization at these localities.

Step 2: The explanatory power of various climatic and human variables was analysed using generalized linear mixed models (GLMMs) to test predictions 1b, 2b and 3b. These models offer a wide array of error distributions to choose from and can thus better fit our data structure than linear models. Because fur harvest levels relative to the two species were poorly reflected by trends in fur prices, unaltered fur harvest data were used in analyses in a context where red foxes were gradually appearing for the first time further north, while overall arctic fox fur harvests, although cyclic, remained stationary from the late 1920s to the mid-1950s (Appendix S2). The proportion of red fox furs in yearly fox fur harvests was the response variable in GLMMs, hence representing changes in the relative abundance of red fox furs in the harvests, with arctic fox furs coded as '0' and red fox furs as '1'.

Generalized linear mixed models with a zero-inflated negative binomial distribution model were used to analyse the fur harvest data. The total number of fox furs was used as an offset, and trading posts were treated as a random factor in the models. The 'GLMMADMB' package version 0.8.3.2 (Fournier et al., 2012) in R version 3.1.2 was used to fit the models. The time series were screened for unit root problems and were found to be exempt from such issues (Appendix S1).

The built models included one or more of the four predictors (i.e. July and February mean temperature [°C], index of human presence [log-transformed for linearity] and February snow precipitation [cm]). The variables were rescaled so that estimated regression parameters within models could be compared to each other. The effect of climate change on species can be time-lagged (Menéndez et al., 2006; Thompson & Ollason, 2001), especially for plants (Chapin, Shaver, Giblin, Nadelhoffer, & Laundre, 1995); therefore, lag effects of one to five and also ten years were tested for all climate variables. The Akaike information criterion corrected for small sample size (AIC_c) was used to compare the performance of various models (Burnham & Anderson, 2002). The performance of single-variable models was first compared to identify the variable that performed best at explaining trends in the data. Because the tested predictions were not mutually exclusive and >one factor could drive the red fox expansion, these first models were further compared to multivariate models by adding variables to the best univariate model and retaining them if they lowered the AIC score, until the best model was found. The full model and models built exclusively from climate variables were also considered in our model comparisons.

Step 3: Generalized additive models (GAMs) were used to describe sitewise differences in the rate of change (linear slopes from 1926 to 1950) of the proportion of red fox furs in harvests, using the four predictor variables described above (predictions 1c, 2c and 3c). The smoothing terms of GAMs allow better model fit to describe complex relationships between factors for our data covering a large geographical area, likely resulting in statistical noise in our predictor variables. There were 13 trading posts included in this analysis (Figure 1). Aklavik was excluded because it was a clear outlier in exploratory analyses (this settlement was a transportation hub and was probably drawing considerable amounts of furs from both the taiga and the tundra).

The 'MGCV' package version 1.7-27 in R version 3.2.3 (Wood, 2001) was used to conduct additive nonparametric regression models with

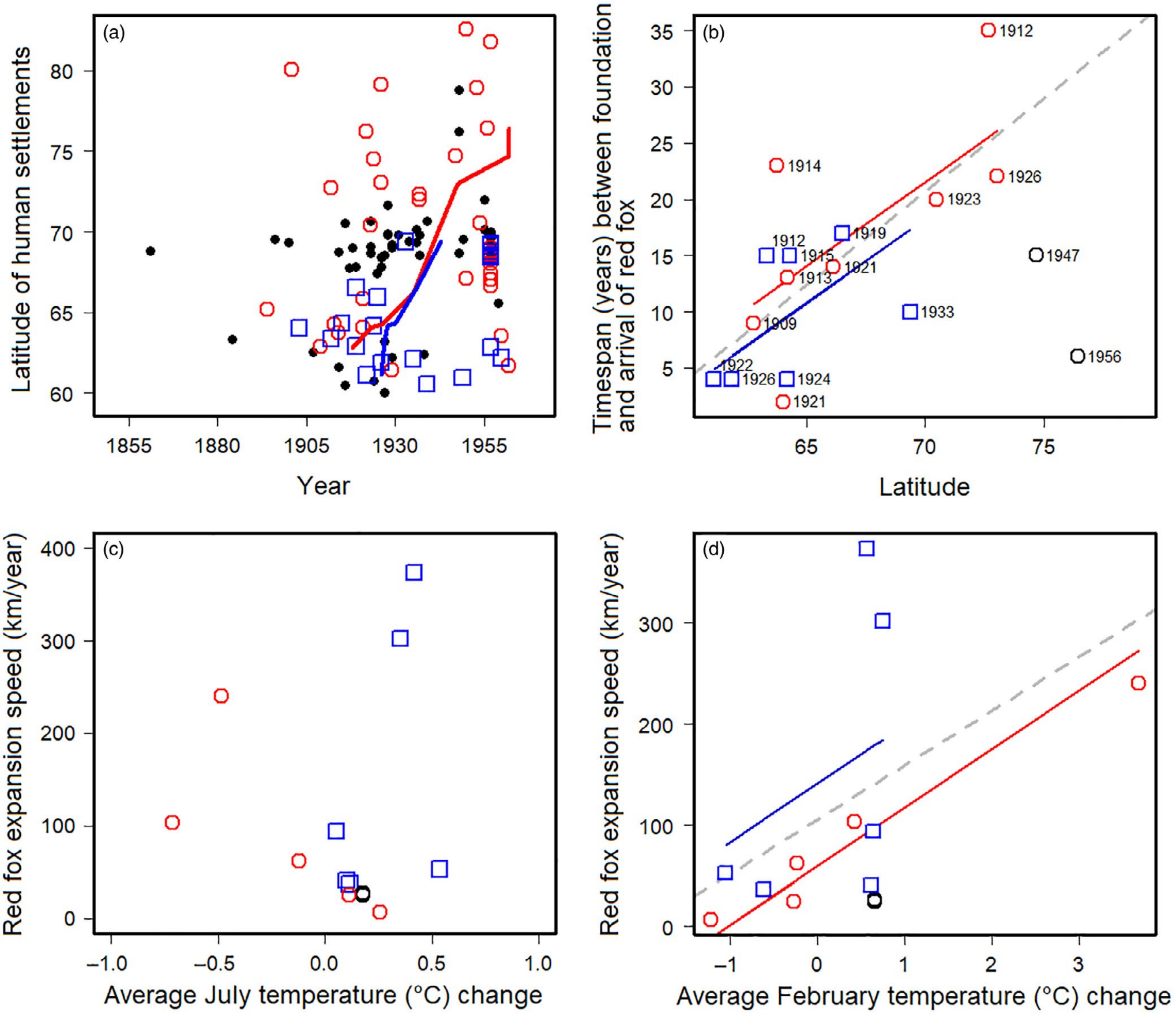

FIGURE 3 (a) Relation between the year of foundation and the latitude of human settlements in the Canadian arctic regions of Baffin (open red circles) and continental Nunavut (open blue squares). Coloured lines represent red fox expansions for respective regions, and black dots represent human settlements in other parts of the Canadian Arctic. (b) Relation between latitude and delay (years) between the foundation of 17 human settlements and the first red fox detection at these settlements for the Baffin (open red circles) and the continental Nunavut (open blue squares) regions (repeated measures correlation $r_{12} = 0.654$, $p = .011$), with year of foundation of settlements indicated. Open black circles here and for subsequent panels represent Resolute Bay (1947) and Grise Fiord (1956), two locations excluded from correlations (see text for details). (c) Expansion speed (km/year) of red fox between pairs of locations as a function of mean annual change in July temperature (°C) for the Baffin (open red circles) and the continental Nunavut (open blue squares) regions ($r_8 = -0.119$, $p = .744$). (d) Expansion speed (km/year) of red fox between pairs of locations as a function of mean annual change in February temperature (°C) for the Baffin (open red circles) and the continental Nunavut (open blue squares) regions ($r_8 = 0.632$, $p = .050$)

the family distribution set to 'quasi', and with an identity link function and constant variance. Restricted maximum likelihood (REML) was set as the smoothing parameter estimation method (McCullagh & Nelder, 1989). Parameters for each predictor variable were estimated with a smoothing spline using the 'gam' function of the MGCV package (Wood, 2001). Because GAM models were fitted using REML and the compared models involved different random effects and no fixed effects, model performance was compared with the help of REML scores, R^2 and percentage of explained deviance.

3 | RESULTS

3.1 | Description and speed of red fox expansion

Our review of the presence of red fox in the Canadian Arctic led to the revision of two distinct expansion chronologies (Appendix S3). These revised chronologies indicate that red fox expanded simultaneously in Baffin Island (and nearby islands) and in the continental part of present-day Nunavut (Figure 2a). The Baffin expansion

TABLE 1 Comparison of models describing the proportion of red fox furs found in fox fur harvests at 14 trading posts in northern Canada from 1926 to 1950

Model[a]	−2 (log likelihood)	Number of parameters (K)[b]	AIC_c	ΔAIC_c (Δ_i)	Akaike weight (w_i)
Index of human presence + Winter temperature	2,461.62	6	2,473.87	0.00	0.30
Index of human presence + Winter temperature + Snow	2,459.94	7	2,474.27	0.40	0.24
Index of human presence	2,465.30	5	2,475.47	1.61	0.13
Index of human presence + Winter temperature + Summer temperature	2,461.60	7	2,475.93	2.06	0.11
Index of human presence + Winter temperature + Summer temperature + Snow	2,459.86	8	2,476.28	2.42	0.09
Index of human presence + Snow	2,464.30	6	2,476.55	2.68	0.08
Index of human presence + Summer temperature	2,465.18	6	2,477.43	3.56	0.05
Snow + Winter temperature	2,473.50	6	2,485.75	11.88	<0.01
Snow	2,477.10	5	2,487.27	13.41	<0.01
Winter temperature	2,477.42	5	2,487.59	13.73	<0.01
Snow + Summer temperature	2,476.56	6	2,488.85	14.98	<0.01
Winter temperature + Summer temperature	2,477.22	6	2,489.45	15.58	<0.01
Summer temperature	2,479.54	5	2,489.71	15.85	<0.01

[a] Spearman's rho correlation values between predictors are 0.235 for human presence and winter temperature, 0.602 for human presence and summer temperature, 0.026 for human presence and snow, 0.056 for winter and summer temperatures, 0.292 between winter temperature and snow, and 0.013 between summer temperature and snow.

[b] Includes the intercept, the dispersion parameter associated with the negative binomial distribution, the zero-inflation parameter, as well as the random factor (trading post).

started from the Ungava Peninsula in northern Quebec, where red fox has a historic presence (Gordon, 1887; Province of Quebec, 1913), whereas the continental expansion started from the tree line north-west of Churchill, Manitoba (Figure 2a). These two large-scale replicates give strength to our causal interpretations.

Overall, red fox expanded northward at a rate of 67 and 52 km/year during 1926–1950 for Baffin and continental Nunavut, respectively. Expansion speed was positively correlated with February temperature change (r_8 = 0.632, 95% CI −0.131 to 0.925, *p* = .050), but not with July temperature change (r_8 = −0.119, 95% CI −0.760 to 0.639, *p* = .744). The expansion patterns were consistent between Baffin and continental Nunavut for February temperatures (Figure 3d), but not for July temperatures (Figure 3c). In both regions, red fox expanded even during cooling trends for both July and February temperatures (Figures 2a-e and 3c-d). In the Baffin region, red fox expanded most rapidly when temperatures were cooling in July (Figure 3c).

The settlement of arctic communities and their associated societal changes (Appendix S2) occurred mostly between 1910 and 1940 (Figure 3a), when most sedentary sites in the Canadian Arctic were founded. The average delay between the foundation of a given settlement and its first red fox detection was 16 ± 3 years (*n* = 10) and 10 ± 2 years (*n* = 7) for Baffin and continental Nunavut, respectively (Figure 3b). The average delay between the foundation of a given settlement and the first red fox detection increased by 2.5 ± 2 years (*n* = 7) and 2 ± 1 years (*n* = 6) per degree of latitude for Baffin and continental Nunavut, respectively (Figure 3b, r_{12} = 0.654, 95% CI 0.128 to 0.893, *p* = .011).

3.2 | Drivers of red fox expansion

Comparisons of model performance confirm that human presence was the single most important factor describing trends in the abundance of red fox furs in the harvests, as the univariate model with the human variable had the largest Akaike weight among univariate models (Table 1). The exploration of the impact of time lags (1–5 and 10 years) confirmed human presence as the overall most important explanatory factor. Comparisons of univariate models showed that climate models had larger AIC_c values relative to the human model for all lag scenarios ($5.2 \le \Delta AIC_c \ge 13.2$). The top three models could not be distinguished from each other, because $\Delta AIC_c \le 2$ (see Burnham & Anderson, 2002). Climate variables performed poorly, and their contribution to model performance was negligible (Table 1). The best model included human presence and changes in winter temperature, but the human variable's estimated coefficient was over five times larger than the winter temperature coefficient (Table 2). This model was only marginally better than the univariate model with the human variable (Table 1), so winter temperature explained a negligible amount of additional variability in the proportion of red fox in fox fur harvests.

TABLE 2 Regression results of a generalized linear mixed model showing the effect of human presence and winter temperature on the proportion of red fox furs found in fox fur harvests at 14 trading posts in northern Canada from 1926 to 1950

Coefficient	Coefficient estimate	Standard error	Z	p
Intercept	−5.47	0.72	−7.55	4.40E−14
Index of human presence	0.07	0.02	4.04	5.30E−05
Winter temperature	0.01	0.01	1.91	0.06

Note: Variance and standard deviation for the random factor (study site) was 4.51 ± 2.12, respectively. Estimates and standard errors for the negative binomial dispersion parameter and the zero-inflation parameter were 0.89 ± 0.14 and 0.11 ± 0.04, respectively.

The index of human presence, and to a lesser degree, change in mean July temperature, best explained differences in temporal changes in the proportion of red fox at trading posts (Table 3). Trading posts with more and older settlements nearby had the largest increase in the proportion of red fox, reaching a plateau at mid-range values (Figure 4). Red foxes expanded as summer temperatures were on a cooling trend but the increase in the proportion of red fox in harvests was smaller at sites with the largest cooling trends (Figure 4).

4 | DISCUSSION

There was no support for a climate-driven red fox expansion in arctic North America based on changes in the relative abundance of red fox in harvest data, although the speed of their expansion was higher during warmer winters, and increases of red fox furs in harvests were smaller for sites with the most pronounced summer cooling. Although climate change was not found to be a driver of the red fox expansion, the results suggest that thermal stress brought by harsh winter temperatures influenced the speed of the expansion. Most importantly, this study gives strength to the food subsidy hypothesis. This fits archaeological and historical evidence suggesting that red foxes were able to withstand the harsh climatic conditions of the eastern Canadian Arctic well before their northward spread during the twentieth century. They were indeed present in the western Canadian Arctic during past centuries (Hooper, 1853; Nagy, 1988; Ross, 1861), when temperatures in the northern hemisphere were cooler than they were during the twentieth century (Fischer et al., 1998; Mann, 2002). Red foxes were also historically present in the Ungava peninsula of northern Quebec (Gordon, 1887; Province of Quebec, 1913), even in winter (Gordon, 1887; Mair & MacFarlane, 1908). These observations suggest that prior to the twentieth century, some parts of the cooler Arctic had sufficient resources, either natural or anthropogenic, to sustain the larger red fox, while this was not the case for the northernmost parts of the Canadian Arctic. As our results show, human sedentarization progressed northward at a faster pace than red foxes did. The observation that settlements existed years before trappers reported their first red fox shows that the studied red fox expansions are not artificial distribution shifts created by the northward spread of detection capabilities. Our data rather do track the leading edge of an expanding species.

Overall, our results agree with studies performed in Fennoscandia, where human activity favoured red fox colonization and survival (Elmhagen & Rushton, 2007; Killengreen et al., 2011; Selås, Johnsen, & Eide, 2010; Selås & Vik, 2007). In the boreal zone, the expansion of agriculture across Sweden during the nineteenth century, which increased resource availability, favoured the northward expansion of the red fox by influencing the strength of the release effect caused by the extinction of top predators like wolves *Canis lupus* (Elmhagen & Rushton, 2007). Wolf presence and distribution are not well documented to this day in the North American Arctic, so it is unknown whether a similar release effect was at play during the North American

TABLE 3 Comparison of two-factor and single-factor additive nonparametric regression models of change in the proportion of red fox in fox fur harvests between 1926 and 1950 at 13 trading posts in northern Canada

Comparison group	Factors in model	R^2	Explained deviance (%)	REML score
2 factors	Index of human presence + Change in mean July temperature[a]	0.49	65.70	−27.85
	Index of human presence + Change in mean February temperature	0.12	26.70	−26.71
	Change in mean July temperature + Change in mean February temperature	0.08	22.90	−26.53
1 factor	Index of human presence	0.20	26.60	−30.35
	Change in mean July temperature	0.10	17.20	−29.70
	Change in mean February temperature	−0.09	0.39	−28.68

Note: Factors are index of human presence, change in mean July temperature (°C) and change in mean February temperature (°C).

[a] Parametric coefficient values for the best model: intercept estimate = 0.06 ± 0.01; equivalent degree of freedom = 1.95 for index of human presence and 1.97 for change in mean July temperature; reference degree of freedom = 2.25 for index of human presence and 2.44 for change in mean July temperature.

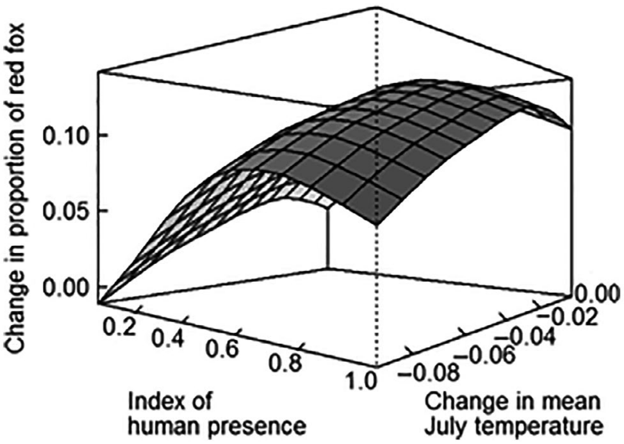

FIGURE 4 Fitted surface for additive nonparametric regressions of change in the proportion of red fox in fox fur harvests during 1926–1950 at 13 fur-trading posts in northern Canada. Predictor variables are index of human presence (rescaled from 0 to 1) and change in mean July temperature

red fox expansion. In the low arctic tundra of northern Norway, a key mechanism at play was the subsidies generated by semi-domesticated reindeer (*Rangifer tarandus*) herds that grew larger due to changes in husbandry (Forbes et al., 2009; Moen & Danell, 2003). In that case, subsidies were formed by reindeer carcasses, which constituted a critical part of red fox diet in winter and during years of low arvicoline density (Killengreen et al., 2011). Our study, which spans bioclimatic zones ranging from the low to the high Arctic and covers hundreds of thousands of square kilometres, further supports the hypothesis that the poleward expansion of boreal predators such as the red fox is linked to various human activities in the North, which can range from agriculture and husbandry to human settlements.

Alongside anthropogenic food subsidies, our results suggest that climate warming can also influence changes in the biogeography of predators, indicating that the North American Arctic could incur cumulative effects from multiple anthropic drivers of change. This is similar to recent changes in the biogeography of foxes in Fennoscandia (Elmhagen & Rushton, 2007). Our modelling suggested that the increasing presence of red fox in the Canadian Arctic may have been slowed by cooling temperatures at some sites. This suggests a flexible response to climatic trends. Unexpectedly, red fox progressed northward faster when summers were cooling in the Baffin region. While environmental conditions are harsher under cooler climates and could lower reproductive success and increase mortality, animals may be able to expand farther due to the longer persistence of seasonal sea ice. Foxes can travel long distance on sea ice (Pamperin, Follmann, & Person, 2008; Tarroux, Berteaux, & Bêty, 2010), and genetic analyses have shown that sea ice connects arctic fox populations on a large spatial scale (Mellows et al., 2012; Norén et al., 2011).

Although we made considerable efforts to retrieve historical information from multiple sources in order to test our research hypotheses, to our knowledge, data on abundance and changes in food subsidies across the Canadian Arctic during the first half of the twentieth century do not exist and thus could not be included quantitatively. We thus relied on an indirect index of human presence to address this variable. It could seem surprising at first that relatively few focal points of human-created food subsidies, spread across a vast Arctic region, may have caused a major change in the distribution of a predator. However, these subsidies occurred in an ecosystem where predators often face starvation (Macpherson, 1969; Prestrud & Nilssen, 1992). In addition, settlements were well within reach of each other for red foxes, given their dispersal abilities (Storm et al., 1976; Walton, Samelius, Odden, & Willebrand, 2018). Field studies showed that subsidies can influence resource selection by predators (Bino et al., 2010; Giroux et al., 2012; Savory et al., 2014) and increase their survival, fitness (Bino et al., 2010; Craighead, Sumner, & Mitchell, 1995; Pons & Migot, 1995) and abundance (Montagano, Leroux, Giroux, & Lecomte, 2018). However, we know little about the quantity of density-independent resources necessary to cause numerical responses in predators (but see Montagano et al., 2018; Persson, 2005). Understanding the link between food subsidies and the population responses of predators is essential to predict further expansions, as well as their ecosystem-wide consequences.

Our search of a climate-based explanation for the expansion of the red fox in the Canadian Arctic highlights the need to critically evaluate hypotheses based on climate change, even when the direction and timing of observed ecological changes appear consistent with climate trends. As mentioned by Parmesan and Yohe (2003), other human activities, like changes in land use, had a dominant influence on global biological changes during the twentieth century. The invasion of the Arctic by the red fox could now be considered as a compelling example of how anthropogenic ecological changes, even at low human population density, can translate into large-scale distribution shifts of predator species, likely having large consequences on the arctic terrestrial food web.

We are only starting to understand the magnitude of the impact that predictable anthropogenic food subsidies have on the structure and function of ecosystems (Oro, Genovart, Tavecchia, Fowler, & Martinez-Abrain, 2013). Anthropogenic food subsidies beneficial to predators may lead to deep ecological changes. Our study provides evidence that these food subsidies led to the appearance of a new predator in arctic terrestrial food webs over vast expanses of this biome, the ecosystem-wide consequences of which remain to be understood. In many parts of the Arctic, red fox do not yet dominate the arctic fox in abundance. Removal of anthropogenic waste is shown to be an effective way to reduce red fox populations associated with human settlements (Bino et al., 2010). Our results point to improvement of human waste management in arctic communities as a solution that could curtail the presence of red fox in arctic tundra landscapes.

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AUTHORS' CONTRIBUTIONS

D.B. conceived of the study, D.G. and D.B. designed the study, D.G. collected the data, D.G. and N.L. analysed the data, and D.G. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data files are available on figshare: https://doi.org/10.6084/m9.figshare.9122528.v1 (Gallant, Lecomte, & Berteaux, 2019).

ORCID

Daniel Gallant https://orcid.org/0000-0002-3170-0523
Nicolas Lecomte https://orcid.org/0000-0002-8473-5375
Dominique Berteaux https://orcid.org/0000-0003-2728-5985

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SUPPORTING INFORMATION

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

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