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Linking climate change to population cycles of hares and lynx

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Abstract

The classic 10-year population cycle of snowshoe hares (*Lepus americanus*, Erxleben 1777) and Canada lynx (*Lynx canadensis*, Kerr 1792) in the boreal forests of North America has drawn much attention from both population and community ecologists worldwide; however, the ecological mechanisms driving the 10-year cyclic dynamic pattern are not fully revealed yet. In this study, by the use of historic fur harvest data, we constructed a series of generalized additive models to study the effects of density dependence, predation, and climate (both global climate indices of North Atlantic Oscillation index (NAO), Southern Oscillation index (SOI) and northern hemispheric temperature (NHT) and local weather data including temperature, rainfall, and snow). We identified several key pathways from global and local climate to lynx with various time lags: rainfall shows a negative, and snow shows a positive effect on lynx; NHT and NAO negatively affect lynx through their positive effect on rainfall and negative effect on snow; SOI positively affects lynx through its negative effect on rainfall. Direct or delayed density dependency effects, the prey effect of hare on lynx and a 2-year delayed negative effect of lynx on hare (defined as asymmetric predation) were found. The simulated population dynamics is well fitted to the observed long-term fluctuations of hare and lynx populations. Through simulation, we find density dependency and asymmetric predation, only producing damped oscillation, are necessary but not sufficient factors in causing the observed 10-year cycles; while extrinsic climate factors are important in producing and modifying the sustained cycles. Two recent population declines of lynx (1940–1955 and after 1980) were likely caused by ongoing climate warming indirectly. Our results provide an alternative explanation to the mechanism of the 10-year cycles, and there is a need for further investigation on links between disappearance of population cycles and global warming in hare–lynx system.

Keywords: asymmetric predation, global warming, *Lepus americanus*, *Lynx canadensis*, North Atlantic Oscillation, population cycles, Southern Oscillation

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Introduction

Population cycles of animals in the Northern Hemisphere have long been a puzzle in population ecology (Elton & Nicholson, 1942; Krebs *et al.*, 2001; Myers 1988; Stenseth, 1999; Stenseth *et al.*, 1997). Determining the underlying mechanisms of this phenomenon is essential in understanding the population dynamics of species and its interactions with other species in a community or ecosystem.

Biotic and abiotic causes have been proposed to explain the observed population cycles. Theoretical modeling studies have shown that density dependence with appropriate time lags can result in regular oscillations (May *et al.*, 1974) and this effect has been used to explain many cyclic population changes including those in voles and lemmings (Hornfeldt, 1994; Stenseth, 1999), forest insects (Turchin *et al.*, 1999), and large mammals (Post *et al.*, 2002). The classic Lotka-Volterra equation and its derived predator–prey model can also produce periodic solutions (Beddington *et al.*, 1975; May & Mclean, 2007; Tyson *et al.*, 2010) and often fit well mostly in laboratory population cycles (Wangersky, 1978), but it is often insufficient when applied to realistic populations (Gilpin, 1973; Berryman, 1992). Other ecologists have emphasized cyclic exogenous factors like solar activity (Sinclair & Gosline, 1997), climate (Hunter & Price, 2000), and forest fires (Fox, 1978), but how these exogenous factors produce cycles has not been investigated or simulated.

The 10-year population cycle of snowshoe hare (*Lepus americanus*, Erxleben 1777) and Canada lynx (*Lynx canadensis*, Kerr 1792) in the boreal forests of North America has drawn high attention from ecologists worldwide for a long time. Recent sustained declines of

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lynx populations have drawn much public attention. These declines are partly due to direct human impacts (Poole, 2003); but global warming is one factor which needs further investigation. Biotic hypotheses explaining this cyclic pattern mainly fall into three groups: hare–lynx interaction, plant–hare interaction, and plant–hare–lynx interaction (Krebs *et al.*, 2001; Zhang *et al.*, 2007). The view of simple prey-predator oscillations has been challenged because of the poor fit of the Lotka-Volterra model (Gilpin, 1973). Recent research has tended to favor the three trophic level hypothesis (Stenseth *et al.*, 1997; King & Schaffer, 2001; Krebs *et al.*, 2001), but modeling such interactions is often difficult due to shortage of critical data of plants, hares, and lynx.

The potential effect of abiotic driving factors (e.g., sunspot and global climate indices) has also been proposed (Elton & Nicholson, 1942; Hone *et al.*, 2011; Lindström *et al.*, 1996; Selås, 2006; Stenseth *et al.*, 2004; Zhang *et al.*, 2007). However, it is still not clear how climate change affects the 10-year cycles of hare and lynx populations. The available studies provide important but incomplete information about potential factors affecting hare and lynx dynamics, and the key question of how the 10-year cyclic pattern is produced is still unsolved. At present, as far as we know, no model has been successfully constructed to have a good fit to the observed long-term data of the 10-year hare–lynx cycles. There is a need to integrate the potential biotic and abiotic factors in modeling the hare–lynx dynamics.

The purpose of this study was to identify the effects and pathways of climate (by the use of both global climatic indices and local weather), prey-predation, and density dependence on the rates of population change in snowshoe hares and Canada lynx by using the historical fur harvest data (Fig. 1), and their roles in determining the observed 10-year hare–lynx cycle through model fitting and simulation. The construction of such models would help us to reveal the roles of climate change in the cyclic dynamics of snowshoe hares and Canada lynx, to explore the reasons of recent population declines, and to provide useful cues for future studies.

Materials and methods

Hare and lynx data

Odum's hare and lynx data. Maclulich (1937) first published both lynx and hare population data from 1845 to 1937. The data were compiled mainly from historic fur-trading records of Canada lynx and snowshoe hares recorded by the Hudson Bay Company. The hare data presented by MacLulich as one time series came from different sources. Data before 1903 represent fur records, whereas data after 1903 were derived from questionnaires. The hare–lynx data were reedited by Odum based on MacLulich's data (Odum, 1959). We used the Odum data for analyses (Fig. 1a, digitalized by using Engauge Digitizer 4.1, http://digitizer.sourceforge.net/).

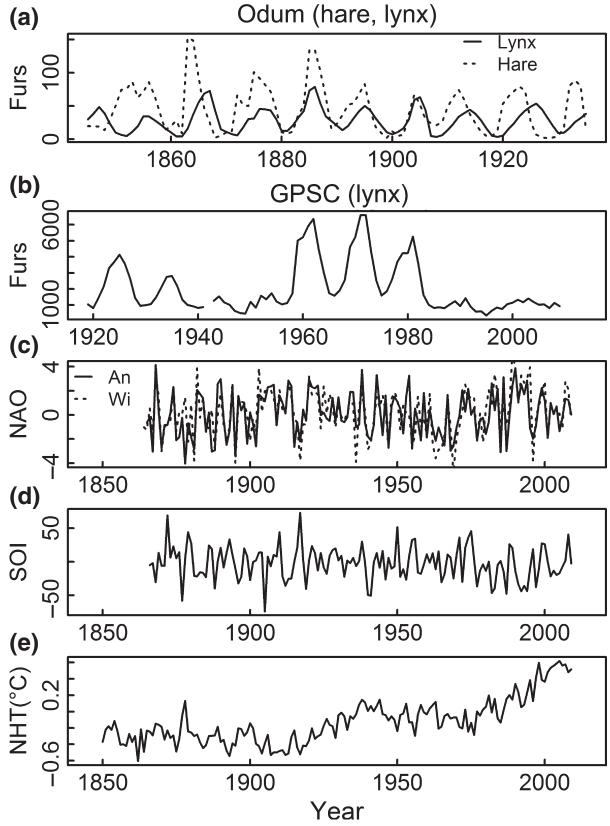

Fig. 1 The original data used in this study. (a) Odum's hare and lynx data represented by fur records (number in thousands), (b) GPSC lynx fur records, (c) North Atlantic Oscillation index (NAO); Wi: winter; An: annual, (d) Southern Oscillation index (SOI), (e) northern hemispheric temperature (NHT, °C).

GPSC lynx data. The lynx data represented by the pelt records from 1919 to 2009 come from Global Population Dynamics Database (NERC Centre for Population Biology, Imperial College, 2010) and Statistics Canada (http://www.statcan.gc.ca). The data used for local population analyses include pelt records of eight jurisdictions: Alberta (AB), British Columbia (BC), Manitoba (MB), Ontario (ON), Quebec (QC), Saskatchewan (SK), Northwest Territories (NT), and Yukon (YT). The data from the eight jurisdictions were averaged to get the regional lynx population fluctuation of Canada (Fig. 1b, referred as GPSC data hereafter). The pooled data by merging Odum and GPSC data were also analyzed (see Appendix S1).

Climate data

We used three global climate indices (i.e. North Atlantic Oscillation index (NAO), Southern Oscillation index (SOI) and the northern hemispheric temperature (NHT), shown in Fig. 1c–e) and local weather of each of the eight jurisdictions. The global climate indices are often taken as a package of weather (Stenseth & Mysterud, 2005). All of them were found to influence the climate within the geographic range of hares and lynx (Stenseth *et al*., 2004; Zhang *et al*., 2007; Hone *et al*., 2011) (see Appendix S2), but no integrative quantitative analyses have been conducted.

Global climate indices. In this study, the SOI data (1866–2009) were obtained from the National Center for Atmospheric Research (NCAR, USA, http://www.cgd.ucar.edu/cas/catalog/climind/soi.html). The NAO data (including winter and annual data, 1865–2011) were obtained from the Climate Analysis Section, NCAR, Boulder, USA (http://climatedataguide.ucar.edu). The NHT anomaly time series (1850–2010) was calculated by using the climatological stations data in northern hemisphere countries and was obtained from the Climatic Research Unit (CRU, UK, http://cdiac.ornl.gov) (Jones *et al*., 2011). For more detail, see Appendix S2.

Local weather. The local weather data (1919–2009) including temperature, rain, and snow in Canada were obtained from the Adjusted and Homogenized Canadian Climate Database of Environment Canada (http://www.ec.gc.ca). The local weather data for each jurisdiction in Canada used in the study were calculated by averaging the data of all stations (which have data from 1919 to 2009) in each jurisdiction. The regional weather data for overall Canada matching GPSC lynx data were calculated by averaging the data of all eight jurisdictions.

Population models

The annual per capita rate of population change in hares or lynx (R-function) at year t was defined as: $R_t = X_t - X_{t-1}$, where X_t is the natural logarithm transformed abundance of hare or lynx population at year t. Generally, we considered the effects of density dependence, prey-predation (if available), climate indices, and local weather (if available) on the population change in lynx or hares in the following models. In the following models, the smoothed functions (f_i, h_i and g_i) were implemented by the use of natural cubic spline functions, with a maximum of four knots. We defined the parameters a_0 as intercepts, and ε_t as a normally distributed stochastic perturbation.

For the Odum data, the effects of density dependence, predation and climate with time lag (k) were considered (Eqns 1 and 2). We assumed the rate of annual population change in lynx ($R_{L,\,t}$) at year t is determined by its own past abundance (L_{t-k}), the past abundance of hares (H_{t-k}), the past values of SOI, NAO, and NHT, similarly for hare ($R_{H,\,t}$).

$$\begin{aligned} R_{L,t} &= L_t - L_{t-1} \\ &= a_0 + g(L_{t-k}) + f(H_{t-k}) + h(\mathrm{NHT}_{t-k}) + h(\mathrm{NAO}_{t-k}) \\ &\quad + h(\mathrm{SOI}_{t-k}) + \varepsilon_t \end{aligned} \tag{1}$$

$$\begin{aligned} R_{H,t} &= H_t - H_{t-1} \\ &= a_0 + f(H_{t-k}) + g(L_{t-k}) + h(\mathrm{NHT}_{t-k}) + h(\mathrm{NAO}_{t-k}) \\ &\quad + h(\mathrm{SOI}_{t-k}) + \varepsilon_t \end{aligned} \tag{2}$$

For the GPSC data, because the hare data are not available, we considered the past abundance of lynx and global climate indices given above with time lags (Eqn 3); furthermore, available regional weather data on temperature (Temp_{t-k}), rainfall (Rain_{t-k}) and snowfall (Snow_{t-k}) were also considered in a separate model (Eqn 4). The same analyses were performed for the local population of each jurisdiction with corresponding data (Eqns 3 and 4).

$$\begin{aligned} R_{L,t} = L_t - L_{t-1} &= a_0 + g(L_{t-k}) + h(\mathrm{NHT}_{t-k}) \\ &\quad + h(\mathrm{NAO}_{t-k}) + h(\mathrm{SOI}_{t-k}) + \varepsilon_t \end{aligned} \tag{3}$$

$$\begin{aligned} R_{L,t} = L_t - L_{t-1} &= a_0 + g(L_{t-k}) + h(\mathrm{Temp}_{t-k}) \\ &\quad + h(\mathrm{Rain}_{t-k}) + h(\mathrm{Snow}_{t-k}) + \varepsilon_t \end{aligned} \tag{4}$$

By considering the results of previous studies (Arditi, 1979), the number of interacting levels (climate index→ local weather→ plant→ hare→ lynx) and the 10-year period of hare–lynx abundance, we set the maximum time lag at 5 years for all exploratory variables (only one time lag is selected for each variable).

Statistical modeling

We used generalized additive models (GAM) to fit the above models to the data (Hastie & Tibshirani, 1990). All analyses were carried out in R version 2.15.2 using the *mgcv* package version 1.7–22 (Wood, 2006; R Development Core Team, 2010). The optimal roughness of the smoothing terms was determined by minimizing the generalized cross-validation value (GCV) (Xu *et al*., 2011). The GCV of a model is an index for the model's out-of-sample predictive mean squared error (Cox *et al*., 1981) and was also used to compare alternative model formulations. A model with lower GCV has more explanatory power and was hence preferred to models with higher GCV. The best-fitting models were selected by minimizing the GCV from plenty of candidate models. The residual autocorrelations of models were checked for model diagnostics.

Model simulation

Deterministic stepwise predictions (i.e. $\varepsilon_t = 0$) of the best-fitting models were performed to see the behavior and fit of different models. The simulations were divided into four parts: first, for the models with climate effects, the simulations started using the initial observed abundance data of hare and/or lynx, and the original data of climatic variables as inputs to the simulation models; second, the simulations were performed in the models without climate effects similarly; third, as a comparison, we used randomly produced signals as input of external disturbances to R-functions in the models without climate effects, and also tested the effects of the randomly produced climate signals in the models with climate effects (Appendix S3); fourth, we tested the effects of cyclic signals such as about 11-year cyclic sunspot time series during the study period on simulation behaviors of the models without climate effects at the lag of 0–5 years (Appendix S3). For the Odum data, population dynamics of both hares and lynx were simulated, while for the GPSC data, only lynx population dynamics was simulated.

Pathway analysis

To understand the effects of global climate on lynx population through regional climate, pathway analyses (only for the GPSC data which have the corresponding local weather data) were applied to identify the direct and indirect effects of global climate through local weather on lynx population dynamics. The effects of global climate on the local weather were also analyzed by GAMs to select the candidate variables in the pathway structure. The pathway analysis was conducted in SPSS AMOS 17.0 (Amos Development Corp., Crawfordville, FL, USA). We note that pathway analysis reveals only the linear effects of variables.

Results

Factors affecting regional populations

As shown in Table 1, in the best-fitting models of the Odum data, the rate of population change in hares showed a first-order negative feedback association with density ($F_{2.2,\ 55.5} = 10.9$, $P < 0.001$), a 2-year delayed nonlinear negative association with lynx ($F_{3,\ 55.5} = 12.2$, $P < 0.001$), a 1-year delayed '~'-shaped association with NHT ($F_{3,\ 55.5} = 6.2$, $P < 0.01$) and a 5-year delayed negative association with annual NAO ($F_{1,\ 55.5} = 16.02$, $P < 0.001$); the rate of population change in lynx showed a second-order negative feedback association with density ($F_{1,\ 53.2} = 85.7$, $P < 0.001$), a 1-year delayed positive association with hare ($F_{2.5,\ 53.2} = 13.5$, $P < 0.001$), a 2-year delayed dome-shaped association with NHT ($F_{2.4,\ 53.2} = 3.2$, $P < 0.05$), a 5-year delayed dome-shaped association with winter NAO ($F_{2.9,\ 53.2} = 4.2$, $p<0.05$), and a 2-year delayed dome-shaped association with SOI ($F_{3,\ 53.2} = 4$, $p<0.001$) (Table 1, also see Appendix S4-Table S4.1 and Fig. S4.1).

In the best-fitting model of the GPSC data and global climate data, the rate of population change in lynx showed a third-order negative feedback association with density ($F_{1.5,\ 64.5} = 28$, $P < 0.001$), a 3-year delayed negative association with NHT ($F_{1,\ 64.5} = 7.8$, $P < 0.01$), a 3-year delayed negative association with winter NAO ($F_{1,\ 64.5} = 16.8$, $P < 0.001$) and a 4-year delayed 'U'-shaped association with SOI ($F_{2.6,\ 64.5} = 3.7$, $P < 0.05$). For the GPSC data and regional weather data, the rate of population change in lynx showed a third-order negative feedback association with density ($F_{1,\ 66.1} = 29.7$, $P < 0.001$), a 2-year delayed negative association with rainfall ($F_{2.3,\ 66.1} = 6.3$, $P < 0.01$) and a 5-year delayed positive association with snow ($F_{1,\ 66.1} = 4.4$, $P < 0.05$) (Table 1, also see Appendix S4-Table S4.1 and Fig. S4.2). When merging the Odum and GPSC data, we got similar results (Appendix S1).

Simulation analysis of regional populations

Simulation results of above models with global climate indices all showed persistent cycles, but those without

Table 1 Summary of the effects of global climate indices and local weather on lynx and hare populations in GAMs

	Lynx*	Hare	Temperature	Rain	Snow	NHT	NAO yr/wi	SOI
Odum hare	2(↓)	1(↓)				1s	5(↓)/	
Odum lynx	2(↓)	1(↑)				2n	/5n	2n
GPSC lynx	3(↓)			2(↓)	5(↑)	3(↓)	/3(↓)	4u
Pooled lynx	3(↓)					3n	/3(↓)	4u
Local lynx 1919–2009								
BC	1(↓)			2(↓)		5(↓)	4(↓)/	1(↓)
YT	2(↓)			4(↓)		4(↓)		1(↓)
NT	2(↓)					3(↓)	/3(↓)	4(↓)
AB	3(↓)		5(↑)		5(↑)	3(↓)	1(↓)/	
SK	2(↓)			5(↑)	2(↑)		/3(↓)	
MB	3(↓)				5s	2s	1(↓)/	4u
ON	2(↓)†, 3(↓)‡				5(↑)		/3(↓)	2(↑)
QC	2(↓)			2(↓)			/3(↓)	4(↑)

The numbers are the time lags. '↓': negative effect; '↑': positive effect; 'n': dome-shaped effect; 'u': U-shaped effect; 's': '~' -shaped effect; 'NAO yr/wi': annual NAO/winter NAO.

*All lynx populations have the same feedback effects in both models with local weather and global climate indices except for ON.

†For the model with local weather.

‡For the model with global climate indices.

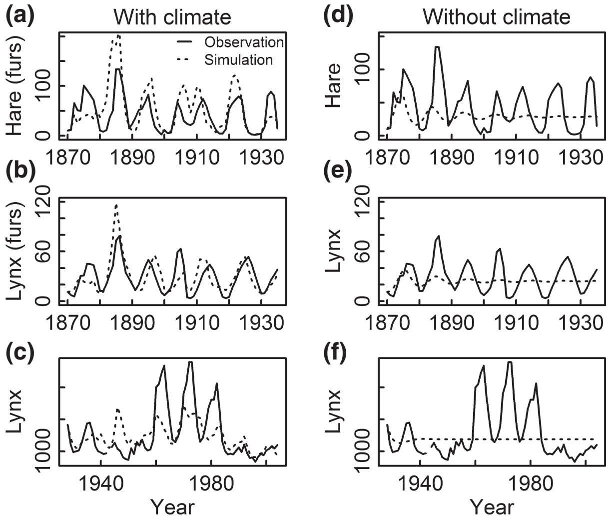

Fig. 2 The model simulation results (dashed, simulated value; solid, observed value). (a, b) and (d, e) the Odum hare and lynx data; (c, f) the GPSC lynx data. Left side: simulations with climate effects; right side: simulations without climate effects.

climate indices all produced damped oscillations or monotonic damping (Fig. 2 and, Appendix S1-Fig. S1.2). Simulations adding random signals to the R-functions and those using random climate signals can all produce cyclic patterns, but the fit was very poor compared to the model simulations with original climate indices (see Appendix S3-Fig. S3.1–S3.3). The simulations adding sunspot time series produced stable cycles with about 10-year period, but the simulated cyclic populations stayed considerably out of phase with the original data at all the time lags we used (Appendix S3-Fig. S3.4).

Factors affecting local populations

The associations of global climate and local weather with the rate of population change in lynx (1919–2009) were analyzed for eight jurisdictions, respectively. As shown in Table 1 and Supporting Information, Appendix S4-Table S4.2, both global climate and local weather showed variations in affecting the lynx population across Canada. NHT showed consistent negative associations with four populations (NT, AB, YT, and BC) with lags of 3–5 years and a '~'-shaped association with one population (MB) with a 2-year lag. The annual NAO showed consistent negative associations with three populations (AB, MB and BC) with a lag of 1 or 4 years; winter NAO showed consistent negative associations with four populations (NT, SK, ON, and QC) with a lag of 3 years. SOI showed negative associations with three populations (BC, YT, and NT) with a lag of 1 or 4 years, positive associations with two populations (ON, QC) with a lag of 2 or 4 years, and a 'U'-shaped association with one population (MB) with a lag of 4 years.

As shown in Table 1 and Appendix S4-Table S4.2, local temperature showed a positive association with only one population (BC) with a lag of 5 years. Rainfall showed consistent negative associations with three populations (BC, QC and YT) with a lag of 2 or 4 years and a positive association with one population (SK) with a lag of 5 years. Snow showed consistent positive associations with three populations (AB, ON and SK) with a lag of 2 or 5 years and a '~'-shaped association with one population (MB) with a lag of 5 years.

Pathway analysis on regional population

To determine the pathways from global climate→ regional climate→ regional lynx populations, we analyzed the effects of global climate on regional climate by GAMs in the corresponding period of the GPSC lynx model (Appendix S4-Table S4.3). On the basis of the GAM results, we constructed a preliminary pathway diagram from global climate, to regional climate and then the rate of population change in lynx (Fig. 3). After model selection by abandoning the insignificant coefficients ($P < 0.05$), the performance of the final pathway is adequate (CFI = 0.979, RMSEA = 0.037) (Byrne, 2009). The results suggest that the global climate of NHT (negative effect) and SOI (positive effect) can affect the lynx through the regional rainfall, and the global climate of winter NAO can negatively affect lynx directly or through regional snow with different time lags (Fig. 3).

Discussion

Effect of predation

Both theoretical (Hanski & Korpimäki, 1995) and empirical (Krebs *et al.*, 1995) studies have stressed the essential role of predation in generating cycles of small mammals in the northern hemisphere. In spite of the poor fit of the Lotka-Volterra model (Gilpin, 1973), some studies have pointed out the necessary role of the predator–prey interaction in causing the 10-year cycle of hare–lynx cycle (Krebs *et al.*, 1995, 2001; Stenseth *et al.*, 1997; King & Schaffer, 2001). In this study using the Odum data, the direct positive prey effect of hares on lynx was detected; but a direct negative predator effect on hares was not found. Instead, we found a 2-year delayed negative effect of lynx on hares, revealing the asymmetric predation effect in the hare–lynx system. Our observation of the delayed predation effect of predator on prey is inconsistent with the concept in the traditional prey–predator models (e.g. Lotka-Volterra model). The Canada lynx is a specialist predator of

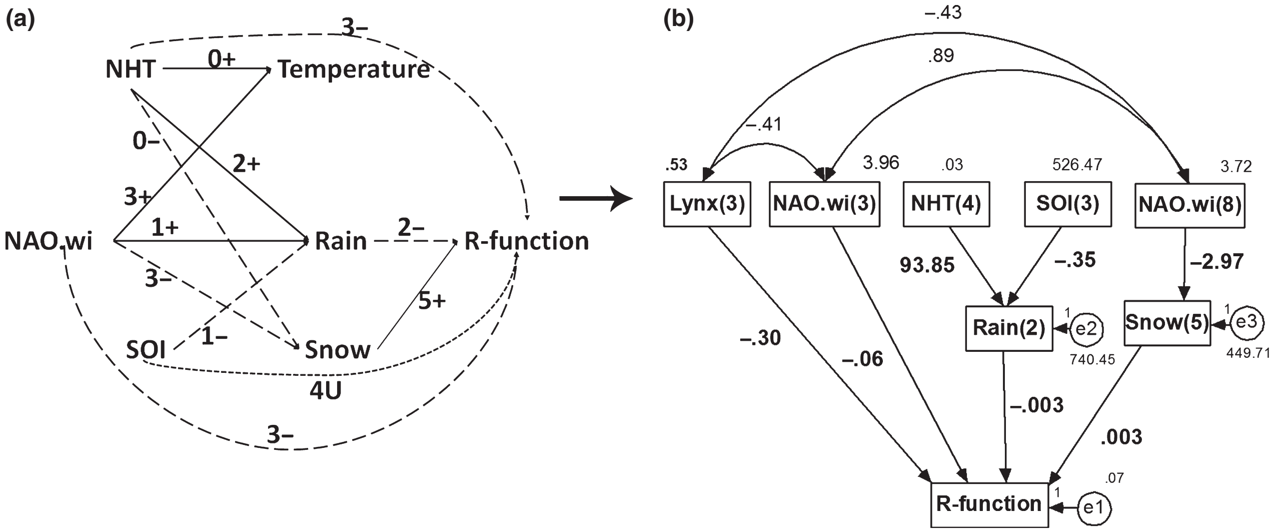

Fig. 3 (a) Preliminary pathway diagram based on generalized additive models (GAM) results and (b) the result of pathway analysis from global climate indices, local weather to R-function of lynx population with only significant effects ($P < 0.05$). In the preliminary pathway diagram, '–' indicates negative effect; '+' indicates positive effect; 'U' indicates the 'U'-shaped relation; the number indicates the time lag (years). In the pathway analysis, the value beside arrow line indicates estimates of regression weight; the value beside double headed arrow line indicates estimate of covariance; the value beside rectangle indicates estimate of variance; the value in the brackets indicates time lag (years) with respect to the R-function.

snowshoe hares and the annual productivity of lynx is directly related to the hare abundance (Nellis *et al.*, 1972). While the predation effect on hares comes from various predators including lynx, coyotes, and avian predators (O'donoghue *et al.*, 1997). This may result in the asymmetric predation in the hare–lynx system. Previous studies suggest that predators can impose chronic stress on hares and then negative effects on both their physiology and reproduction, which might cause the time lag in hare's response (Boonstra *et al.*, 1998; Sheriff *et al.*, 2010, 2011). In addition, the time lag in response of hares to lynx was probably caused by surplus killing from lynx or other predators in the decline phase of a hare cycle (Krebs *et al.*, 2001).

However, the models with predation but without climate forcing can produce only damped oscillations, while the models with climate forcing as well as random or cyclic sunspot signals can produce stable cycles. These results suggest that predation is necessary but not sufficient for the appearance of 10-year cycles in the hare–lynx system. By integrating the effects of density dependence, climate, predation, and time lag, we have succeeded in constructing a model which fits the observed data of the classic 10-year hare–lynx dynamics very well, in terms of both amplitude and interval of cycles.

Effect of climate

Large-scale climate phenomena such as NHT, NAO, and El Niño–Southern Oscillation, can strongly impact local weather around the world (Trenberth *et al.*, 2007), and then influence population dynamics of small mammals (Stenseth *et al.*, 2002; Zhang *et al.*, 2003; Hornfeldt *et al.*, 2005; Kausrud *et al.*, 2008) and many other species (Millar *et al.*, 2012; Li *et al.*, 2013). Although previous studies have reported the links of global climate indices or local climate with hare or lynx population (Stenseth *et al.*, 1999, 2004; Hone *et al.*, 2011), the pathways from global climate to hares or lynx through local climate have not been investigated. In the study, we identified several major pathways of global climate on lynx through rainfall and snow, and found that this external climatic forcing is an important condition for the appearance of the about 10-year cycles in the hare and lynx system (see below).

The global and local climate showed significant effects with various time lags (1–5 years), suggesting a cascade bottom-up effect: global climate→ local climate→ plant→ hare→ lynx (also see below). Previous study reported there were time lags of up to 4 years between the weather factors and lynx fur harvest changes (Arditi, 1979). In addition, hares and lynx may produce time lags themselves through maternal effects because they both have long life spans in the wild: snowshoe hares, 2–5 years (Saunders, 1988); Canada lynx, 14–15 years (Mowat & Slough, 1998).

Stenseth *et al.* (1996) suggest that dampened oscillations will be sustained in the presence of environmental stochasticity. This study showed that input of random signal or climatic stochastic signals to the damped oscillation models indeed produced cyclic patterns; but the fit of these models was very poor, reflected by many cases in which observed and simulated populations were out of phase (Appendix S3-Fig. S3.1–S3.3). Thus, stochastic climate signals or random signals are not sufficient to explain the observed 10-year cycles of hares and lynx. We also found models adding the cyclic signals (e.g., about 11-year cyclic sunspot time series) can produce cyclic patterns, but the fit was also very poor due to a mismatch of cycles between observed and simulated populations. Models with original climate indices not only produced 10-year cycles but also fitted the observed data of hares and lynx dynamics very well. These results suggest that climate forcing is not only essential in producing sustained cycles but also essential in modifying the cycle intervals; this resulted in good match of cycles between simulated and observed populations in the models with climate forcing.

North Atlantic Oscillation index has been suggested to affect the lynx population across Canada through temperature-induced change in snow condition (Stenseth *et al.*, 1999) or in an interactive manner (Hone *et al.*, 2011). In this study, we found that NAO showed a negative association with lynx populations, which is consistent with a previous study that high NAO can lead to lower lynx abundance with a 1-year lag through altering the effects of hare abundance (estimated by snow tracking counts), although the mechanism is not clear (Hone *et al.*, 2011). Our GAM analysis reveals a potential pathway from NAO to lynx through rainfall because the total time lag (3 years) of this pathway matches well with the time lag between NAO and lynx (Fig. 3). The pathway analysis confirmed the pathway from NAO to lynx through snow, but the total time lag (8 years) seems to be too long to be explained (Fig. 3). In contrast with previous literatures (Ottersen *et al.*, 2001), we found that positive NAO tended to increase temperature (3-year lag) and rainfall (1-year lag), but reduce winter snow (3-year lag) in Canada with time lag of 1 or 3 years over all the eight jurisdictions (Fig. 3). Thus, we argue that the delayed effects of NAO may be stronger than its direct effects on regional or local climate in the current year. The most likely pathway of the 3-year delayed negative effect of NAO on lynx over Canada is through its 1-year delayed positive effect on rainfall and through the negative effect of 2-year delayed rainfall on lynx. Indeed, rainfall is found to negatively affect hares' second-litter survival (Meslow & Keith, 1971).

In this study, we found SOI was negatively associated with overall regional rainfall in Canada at a 1-year time lag, and with lynx population, supporting the previous observation by Zhang *et al.* (2007). The impact of SOI on the climate varies across regions in Canada (Shabbar *et al.*, 1997), and thus the associations of lynx population in eight jurisdictions of Canada with SOI were also different, which resulted in the observed nonmonotonic nonlinear effects of SOI in the regional models (i.e. the dome- or 'U'-shaped effects, see Appendix S5). Our GAM analyses reveal a pathway from SOI to lynx through rainfall over Canada, and this is confirmed by pathway analysis, suggesting that there is a positive effect of SOI on lynx through its 1-year delayed negative effect on rainfall which has a 2-year delayed negative effect on lynx (Fig. 3).

Previous literature reviewing lynx fluctuations in Canada suggested the two collapses in the number of furs harvested during the 1950s and subsequent to the 1980s, probably came from over trapping, forest harvest, and restrictive trapping policies (Poole, 2003). By looking at the GPSC data, the two collapses of lynx fur harvesting correspond well to the increase in NHT (Appendix S6-Fig. S6.1), suggesting the declines might be linked to global warming. In case there was an influence of trapping effort during the last dozen years on the fur harvest, the GPSC fur data after 1993 were removed and then the GPSC data were reanalyzed, and the results are similar (Appendix S6-Data quality). The negative effects of NHT were also seen in many of the eight jurisdictions of Canada (Table 1), confirming the negative effects of global warming on lynx dynamics. The results provide first evidence on links between global warming and disappearance of the hare–lynx cycles, and it is worth further investigation in future studies because climate warming has been suggested to cause the disappearance of the lemming cycles (e.g., Kausrud *et al.*, 2008).

Interestingly, we found local temperature (positively associated with NHT) had no direct influence on lynx populations; instead, the negative effect of high NHT on lynx has two pathways: through its negative influence on winter snow (NHT → snow → lynx) and positive influence on rainfall (NHT → rainfall → lynx) (Fig. 3). The total time lags of the two pathways are 4 years and 5 years, respectively, slightly larger than that (3 years) between NHT and lynx (Fig. 3). Previous study warm temperature showed positive effect on adult and first litter young hares but high rainfall showed negative effect on second litter hares (Meslow & Keith, 1971). Our results suggest that the negative effect of rainfall induced by high NHT might exceed its positive effect on hares and finally on lynx.

Previous literature suggested that deeper snow conditions might lower the hunting efficiency of lynx (Stenseth *et al.*, 2004), and reduce the amount of browse available to hares for overwintering (Keith, 1983) and their survival (Meslow & Keith, 1971). Our observation on the pathway of NHT → snow → lynx suggests that the direct effect of snow may be less significant than its delayed effect. The temperature linked 5-year delayed positive effect of snow on lynx in this study might be caused through several trophic levels as predicted by the three-trophic-level hypothesis (Stenseth *et al*., 1997; Krebs *et al*., 2001); deeper snow may benefit plant growth in following years (Wipf *et al*., 2009; Peng *et al*., 2010). Therefore, global warming may negatively affect lynx by increasing rainfall and decreasing snow in Canada.

In addition, our jurisdiction models with local weather had a much poorer fit than those with global climate indices, as measured by GCV and explained deviance (Appendix S4-Table S4.2), supporting the view that large climate indices have better predictive power than local weather (Stenseth & Mysterud, 2005). This is probably because the variations of local population and climate are often larger than regional population and global climate index.

Density dependence

Density dependence has been widely recognized in natural animal populations (Lima *et al*., 2006). In this study, direct density dependence (DD) was found in hare population and 2–3 years delayed DD was found in lynx populations (Table 1). DD is mainly caused by intraspecific competitions for resources, and if introduced into the Lotka-Volterra models, it produces damped oscillations (Weisberg & Reisman, 2008). Delayed DD in lynx population might be caused by maternal effects or time of development. Lynx have a long life span (Saunders, 1988; Mowat & Slough, 1998) and young lynx need approximately 10 months' parental care and 2 years to attain adult size (Sunquist & Sunquist, 2002); thus the observed 2- or 3-year delayed DD effects are probably due to the necessary response time for lynx's reproduction and maturity. Direct DD is an important stabilizing force (Weisberg & Reisman, 2008) but delayed DD contributes to population oscillations (May *et al*., 1974; Hornfeldt, 1994).

Our results clearly indicate that the observed 10-year cycle is the result of joint forces of both intrinsic and external factors. Asymmetric predation, density dependence, and time lag play key roles in producing the damped oscillations, while the external climatic factors are essential in the appearances and intervals of sustained cycles of the hare and lynx system in Canada. Our results revealed the pathways from global climate to lynx populations through local climate, and highlighted the significance of delayed effects of climate factors on hare and lynx populations. Future studies should focus on investigating the underlying mechanism of the observed pathways and the population declines of lynx caused by climate warming. In addition, the observed nonmonotonic nonlinear effects (i.e. dome, 'U' or '~'-shaped effects) of climate are worthy of further investigation.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Analyses of pooled lynx data.
Appendix S2. Additional description of global climate indices.
Appendix S3. Simulations using random and sunspot signals.
Appendix S4. Tables and figures for the results of the best-fitting models of hares and lynx.
Appendix S5. Supplementary discussion for non-monotonic nonlinearity.
Appendix S6. Figure showing the association of NHT and lynx, plus discussion about data quality and supplementary analyses of GPSC data before 1993.