

# The subtle role of climate change on population genetic structure in Canada lynx

JEFFREY R. ROW<sup>1</sup>, PAUL J. WILSON<sup>2</sup>, CELINE GOMEZ<sup>1</sup>, ERIN L. KOEN<sup>2</sup>, JEFF BOWMAN<sup>3</sup>, DANIEL THORNTON<sup>1,4</sup> and DENNIS L. MURRAY<sup>1</sup>

<sup>1</sup>Department of Biology, Trent University, Peterborough, Ontario K9J 7B8, Canada, <sup>2</sup>Environmental and Life Sciences, Trent University, Peterborough, Ontario K9J 7B8, Canada, <sup>3</sup>Wildlife Research and Development Section, Ontario Ministry of Natural Resources, Trent University DNA Building, 2140 East Bank Drive, Peterborough, Ontario K9J 7B8, Canada, <sup>4</sup>Panthera, 8 West 40th Street, 18th Floor, New York, NY 10018, USA

## Abstract

Anthropogenically driven climatic change is expected to reshape global patterns of species distribution and abundance. Given recent links between genetic variation and environmental patterns, climate change may similarly impact genetic population structure, but we lack information on the spatial and mechanistic underpinnings of genetic–climate associations. Here, we show that current genetic variability of Canada lynx (*Lynx canadensis*) is strongly correlated with a winter climate gradient (i.e. increasing snow depth and winter precipitation from west-to-east) across the Pacific-North American (PNO) to North Atlantic Oscillation (NAO) climatic systems. This relationship was stronger than isolation by distance and not explained by landscape variables or changes in abundance. Thus, these patterns suggest that individuals restricted dispersal across the climate boundary, likely in the absence of changes in habitat quality. We propose habitat imprinting on snow conditions as one possible explanation for this unusual phenomenon. Coupling historical climate data with future projections, we also found increasingly diverging snow conditions between the two climate systems. Based on genetic simulations using projected climate data (2041–2070), we predicted that this divergence could lead to a threefold increase in genetic differentiation, potentially leading to isolated east–west populations of lynx in North America. Our results imply that subtle genetic structure can be governed by current climate and that substantive genetic differentiation and related ecological divergence may arise from changing climate patterns.

**Keywords:** climate gradient, habitat imprinting, isolation by resistance, landscape genetics, principal components analysis, snow conditions

Received 18 June 2013 and accepted 4 December 2013

## Introduction

Large-scale climate patterns are consistently one of the strongest global predictors of species diversity and abundance (Thuiller *et al.*, 2004; Luoto *et al.*, 2006). Given the extent that anthropogenic factors are projected to modify climate patterns, a major research focus has centered on quantifying the species-level impacts of climate change, with much of this work pointing to widespread changes in global biodiversity (Burns *et al.*, 2003; Parmesan & Yohe, 2003; Root *et al.*, 2003; Thomas *et al.*, 2004; Thuiller *et al.*, 2005; Hoegh-Guldberg & Bruno, 2010). More recently, evidence has emerged linking dispersal with environmental and climatic boundaries (Geffen *et al.*, 2004; Sacks *et al.*, 2004; Stenseth *et al.*, 2004; Garroway *et al.*, 2008; Muñoz-Fuentes *et al.*, 2009), suggesting that changes in climate may similarly reshape within-species variation for

widespread species. However, aside from the few examples of demonstrated correlation between large-scale genetic structure and climate conditions, the underlying spatial patterns associated with climate change are not fully articulated. This leaves us with limited understanding of the mechanisms underlying genetic–climate associations and places us in a poor position to predict these potentially more subtle consequences of climate change.

Restricted dispersal between different ecotypes or across climate boundaries could be the result of a variety of factors related to habitat quality or the behavior of individuals. One possible explanation for restricted dispersal across a transition zone is deterioration of habitat quality within the transition zone or a particular ecotype. This would lead to a lower number of individuals moving through or into the undesirable habitat and result in increased genetic differentiation. Recently, some have suggested these patterns could also arise through habitat imprinting, where individuals are more

Correspondence: Jeffrey R. Row, tel. +1 705 748 1011 X6148, fax +1 705 748 1003, e-mail: jeff.row@me.com

likely to choose habitats where conditions are similar to those in which they were reared (Geffen *et al.*, 2004; Stenseth *et al.*, 2004; Muñoz-Fuentes *et al.*, 2009). Although imprinting to natal habitat conditions has been shown experimentally for a variety of species (Thorpe, 1945; Wecker, 1963; Teuschl *et al.*, 1998; Vogel *et al.*, 2002), there is less direct evidence found across natural populations (but see: Olson & Horne, 1998). However, the role of natal habitat imprinting in generating genetic boundaries for wide-ranging species, was supported through radio-telemetry data, where individual coyotes were found less likely to disperse across an ecological boundary (Sacks *et al.*, 2005) likely leading to an identified genetic barrier (Sacks *et al.*, 2004). Regardless of the underlying mechanism, if dispersal patterns are related to climatic conditions, then regional variation in climate change could modify or displace transition zones and have genetic implications for the species that span them.

Two prevailing climate trends in North America, the Pacific-North American (PNO) and North Atlantic Oscillation (NAO), converge in eastern North America, causing a cline of differential snow conditions (Hurrell, 1996). Given the ecological importance of snow conditions for temperate species (Telfer & Kelsall, 1984; Campbell *et al.*, 2005), there is strong potential for these differential conditions to cause increased genetic structure for the terrestrial animals across this region (Stenseth, 1999; Rueness *et al.*, 2003). This appears to be the case for the Canada lynx (*Lynx canadensis*), whose range extends across the northern half of North America and across the PNO-NAO climate boundary. Overall genetic differentiation across the range of lynx is low, with several studies finding little or no differentiation across large geographic scales (Schwartz *et al.*, 2002; Rueness *et al.*, 2003; Strobeck, 2006; Row *et al.*, 2012), which is likely related to the long-distance dispersal patterns of lynx (Slough & Mowat, 1996; Poole, 1997). Studies that have compared range-wide genetic variation in lynx, however, showed differentiation to be greater across the PNO-NAO climate boundary compared to other parts of their range, including populations distributed on either side of the Rocky Mountains (Rueness *et al.*, 2003; Row *et al.*, 2012). Given the influence of snow hardness on lynx capture success of their primary prey, snowshoe hare (*Lepus americanus*), some have suggested this pattern may be driven by differential snow conditions within the PNO and NAO (Rueness *et al.*, 2003; Stenseth *et al.*, 2004). Yet, despite this observation there is a paucity of information on the spatially explicit distribution of individuals and genetic variation throughout this region.

In this study, we carried out a test of the spatial relationship between lynx genetic structure and

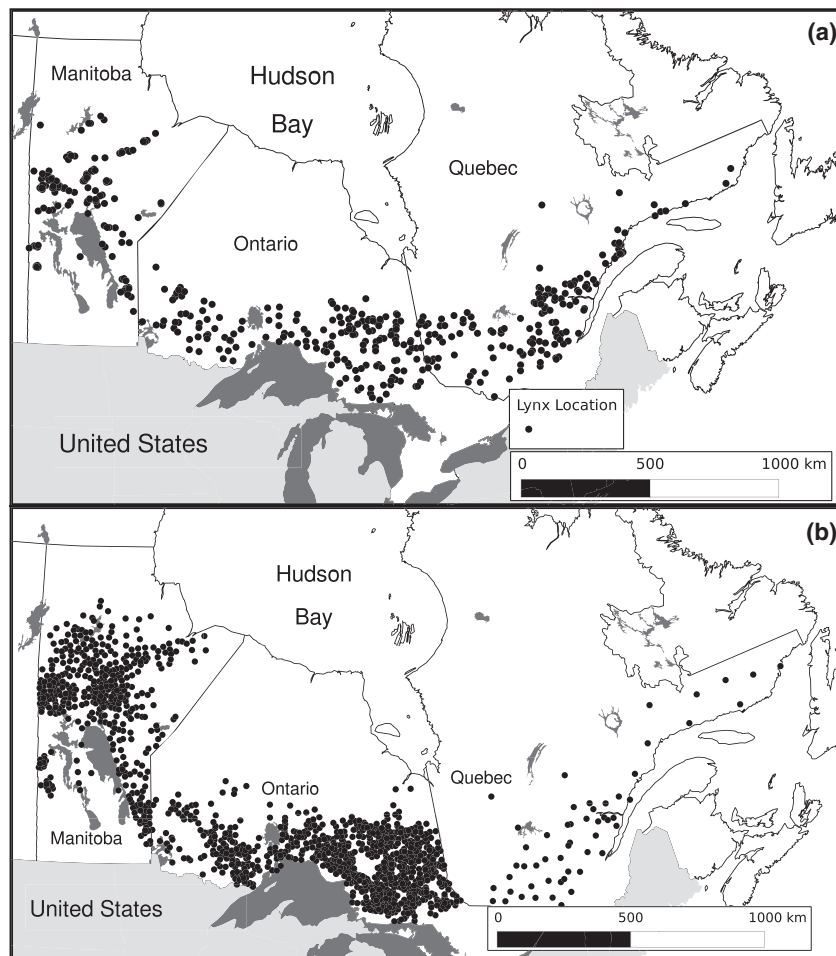
abundance relative to climatic variation, using samples and harvest records collected from eastern Canada, and across the PNO and NAO climate systems. We controlled and tested for the possible effects of distance and other ecological variables (density of forest, anthropogenic disturbance) on genetic structure, which could lead to a spurious correlation between climate and genetic patterns. Secondly, we used an isolation by resistance analysis (McRae, 2006) and abundance data to compare the likelihood of three different potential isolating mechanisms: (i) limited dispersal across a climatic transition zone, perhaps through habitat imprinting or other behavioral syndromes; (ii) a single climatic zone providing more favorable conditions, leading to restricted and asymmetric dispersal across climate boundaries; or (iii) unfavorable habitat conditions within the transition zone itself. If habitat imprinting or other behavioral response is responsible for restricted gene flow, we predicted that the transition zone will provide a higher cost to dispersal without a gap in distribution or drop in abundance.

Although the region examined here represents a continent-wide climatic transition zone, we have very little information on how climate change may be impacting snow conditions across the PNO-to-NAO climatic zones. Thus, in addition to quantifying the genetic implications of climatic patterns for lynx across this region, we use historical (1958–2008) climate data and future projections (2041–2100) to determine the effects of climate change on this transition zone. We used genetic simulations to quantify the possible effects of any documented changes in snow conditions on lynx population structure.

## Materials and methods

### Genetic sampling and abundance

From fur auction houses, we collected tissue samples from the hide of legally trapped (2009–2011) lynx ( $N = 499$ ) distributed from Manitoba to Quebec, Canada (Fig. 1a). We extracted DNA and genotyped individuals for 14 microsatellite loci (Lc111, Fca441, Lc118, Fca096, Fca035, Lc109, Fca559, Lc106, Lc110, Fca031, Fca043, Fca077, Fca090, and Fca391) following the methods outlined in Row *et al.* (2012). We generated random locations within each trapline or management unit to use as the lynx sampling locations because we did not know the exact harvest location. Across the same region (Fig. 1b), we derived a proxy for recent lynx abundance by finding the maximum number of harvested lynx per trapline or management unit over the last 10 years (1997–2007) and dividing this by the area of the management unit or trapline. We omitted traplines where no individual lynx was trapped over the 10-year period.



**Fig. 1** Distribution of Canada lynx (*Lynx canadensis*) genetic samples and harvest data collected from Manitoba to Quebec, Canada. (a) Genetic sampling locations were derived by randomly generating locations within each trapline or management unit. (b) Centroids of trapline or management units for which harvest records were used to quantify lynx abundance.

### *Climate and ecological variation*

We determined winter climate values using North American climate grids (~10 km<sup>2</sup> resolution; McKenney *et al.*, 2006) and calculated average, contemporary (2000–2010) winter (October–April) climate conditions [minimum and maximum temperature, snow depth (2000–2008 only), amount of winter precipitation, and the difference between minimum and maximum temperature] at each lynx sampling location. We summarized the climate patterns using a Principal Components Analysis (PCA) with the first principal component (hereafter CV1) explaining the majority (92%) of the climate variation across this region (Figure S1). Snow conditions were the strongest contributor to this axis, with low values of CV1 representing lower winter precipitation (loading = 0.96) and less snow depth (loading = 0.23); temperature variables were only minor contributors to the axis (loadings < 0.08). We multiplied the axis loadings by raw climate values to derive CV1 climate grids used in the analyses described below.

To quantify ecological variation, we calculated the density of four different forest variables: open needle-leaved

coniferous forest (15–40% canopy cover), open broad-leaved deciduous forest (15–40% canopy cover), closed needle-leaved coniferous forest (>40% canopy), and closed broad-leaved deciduous forest (>40% canopy cover) at each lynx sampling location. To derive the percent coverage within 10 km<sup>2</sup> grid cells, we resampled raw data from Globecover 2009 landcover maps (300 m<sup>2</sup> resolution) (Sophie *et al.*, 2010). We also used the Global Human Influence Index grid (Sanderson *et al.*, 2002), resampled to 10 km<sup>2</sup>, to derive a human influence score. Again, we summarized ecological variation across our study area using a PCA. The first two PCA axes explained >83% of the variation (Figure S1), with the first axis (EV1) distinguishing between open and closed forest (loadings: open needle-leaved = −0.83; closed broad-leaved = 0.35; closed needle-leaved = 0.43) and the second axis (EV2) separating needle-leaved from broad-leaved forest and increased human influence (loadings: closed broad-leaved = −0.11; human = −0.11; open needle-leaved = 0.41; and closed needle-leaved = 0.90). We retained these two axes and used their loadings to derive two ecological grids used in the analysis below.

### Genetic variation

We first quantified genetic variation across our study region using spatial Bayesian clustering as implemented in TESS 2.3.1 (Chen *et al.*, 2007). We followed the users manual and used a nonadmixture analysis to estimate the number of genetic clusters ( $k$ ). In total, we ran 10 replicates of 100 000 MCMC iterations (50 000 burn-in) for values of  $k$  between 1 and 5. We chose the most likely number of clusters according to when the mean Deviance Information Criterion (DIC) values from the 10 replicate runs reached a plateau and/or the Q-matrix of assignment probabilities stabilized.

Spatial Bayesian clustering assumes individuals can be placed in discrete clusters and thus previous studies have identified an inability of this approach to correctly distinguish clinal (Frantz *et al.*, 2009) or low levels of (Latch *et al.*, 2006) genetic structure. Thus, we further quantified genetic structure using a spatial Principal Components Analysis (sPCA) using the *adeget* package (Jombart, 2008) in R (R Development Core Team, 2012). sPCA is a modification of PCA analysis that simultaneously maximizes the genetic variance between individuals and spatial autocorrelation in the principle axes. In the sPCA, the proximity of individuals was defined using a Gabriel graph connection network (Gabriel & Sokal, 1969) and following Jombart (2008), we tested for significant, geographically correlated genetic structure in the principle axis using a global randomization test. If significant genetic structure was found, we visualized the extent and spatial distribution of genetic structure using scree plots and displaying retained axes geographically. Each axis represents differentiation along a given axis with most extreme values being most differentiated.

### Genetic–climate associations

We tested for significant associations between retained sPCA axes (i.e. genetic variation) and environmental [i.e. Climate (CV1) and Ecological (EV1 & EV2)] Variation by first testing for spatial autocorrelation in the residuals of a linear regression using a Lagrange Multiplier test (Anselin *et al.*, 1996). If significant spatial autocorrelation was present, we used a Generalized Least-Squared (GLS) regression, which assumes spatial autocorrelation within a sphere, with a set maximum distance (range) and baseline autocorrelation ( $y$ -intercept; nugget). This method compares favorably to other spatial regression methods (Beale *et al.*, 2010). The range and nugget were first selected by optimizing the root mean square error and then conducting the same analysis with a fixed range of 500 km (distance of positive spatial autocorrelation in allele frequencies; Figure S2) and 1000 km (approximate maximum dispersal distance by lynx; Poole, 1997) and a fixed nugget set to the mean value selected by the optimized models. We compared all univariate and multivariate models with the retained PCA components and selected the best model using AIC<sub>c</sub>. Results were consistent for all values of the range and nugget and thus only the results with a fixed nugget and range (500 km) are reported.

Only winter climate conditions (CV1) showed a significant correlation with genetic variation (see results). Alternative explanations for the correlation are (i) isolation by distance between individuals (IBD); (ii) resistance to dispersal within and into the PNO (low CV1 values) or NAO (high CV1 values) climate systems; or (iii) from restricted dispersal across the transition zone due to changing climate conditions. We tested among these possible scenarios by comparing individual pairwise genetic distance (proportion of shared alleles;  $D_{PS}$ ; Bowcock *et al.*, 1994) to pairwise resistance distances (McRae, 2006) derived from cost surfaces using CIRCUITSCAPE 3.5.7. Cost surfaces were derived from the CV1 climate grids to represent each of the three dispersal scenarios. In the first, resistance values ranged between 1 and 115 and were consistent (same distribution and range) with the CV1 grid values, but rescaled to positive values greater than one. Thus, in this scenario resistance to dispersal was higher for the NAO climate system and represented less gene flow from west-to-east. PCArev was the reverse of the PCA grid [Max(PCA) – PCA value] and represented a high cost to dispersing from east-to-west. Lastly, we derived transition zone cost surfaces representing the highest costs to dispersal in the transition zone (center of CV1) using a slight modification of the equation provided by Shirk *et al.* (2010):

$$R_i = R_{max} * e^{-\frac{(PCA_i - MaxCost)^2}{Stp.(SD(PCA))^2}} \quad (1)$$

Here,  $R_i$  is the final cost for a given grid cell, PCA is the vector of all PCA scores, and  $PCA_i$  is the PCA score for the given grid cell, which will be transformed.  $R_{max}$  is the maximum resistance value, which was set to the range of PCA values, so that the resulting values would range between one and the absolute range. Thus, when there was a greater difference between climate conditions (i.e. range of PCA scores), there would be a greater cost to traversing the transition zone in either direction. MaxCost is the PCA value that will have the highest associated cost, which was set to the median value of the PCA axis values for the given cost grid and Stp controls the level of steepness (scaled by the standard deviation) as one moves away from MaxCost. We used four different values for Stp (1 SD, 0.5 SD, 0.1 SD, 0.01 SD) resulting in four transition zone cost grids. We determined if resistance was reflective of dispersal patterns over-and-above straight-line distance (resistance derived from an undifferentiated landscape) using a partial mantel's test (999 permutations) as implemented in the *ecodist* package (Goslee & Urban, 2007) in R. For all significant results, we also tested the correlation between genetic distance and straight-line distance, while controlling for resistance, which should be nonsignificant (Cushman *et al.*, 2006) and was reported if otherwise.

### Changes in climate across transition zone

We determined if there were changes in winter climate patterns across this region by first multiplying loadings of the CV1 axis by the raw yearly winter climate data from 1958–2008 (McKenney *et al.*, 2006) and conducting a per-cell linear



stacked regression to establish the spatial trends through time. In addition, we visually compared climate grids and cost surfaces derived by multiplying CV1 loadings by mean winter climate conditions for the time periods of 1960–1970, 2000–2010, 2041–2070, and 2071–2100. Future climate data were generated under the Canadian General Climate model with an A2 scenario (McKenney *et al.*, 2011a). The A2 scenario assumes rapid population growth, deforestation, and increasing GHG emissions (Nakicenovic & Swart, 2000), and provides somewhat more liberal, but qualitatively consistent, projections of future emissions. It is notable that the A2 scenario is used extensively as basis for climate-change projections in biology (La Sorte & Jetz, 2010; Lehoudey *et al.*, 2010; McKenney *et al.*, 2011b) and some evidence has suggested other more conservative scenarios are no longer valid given the current emission rates (Raupach *et al.*, 2007; Beaumont *et al.*, 2008).

Future snow depth was not calculated using the climate change models and so we built a predictive model for snow depth using the contemporary (2000–2008) environmental data where we had snow depth estimates. We derived the model with the highest predictive power by testing seven different models (Table S1) and determined the model with the lowest AIC<sub>c</sub> and highest explained variation in snow depth ( $R^2$ ). Based on preliminary tests, the relationship between predicted snow depth and modeled snow depth appeared nonlinear and thus we included polynomial terms in our models. The model with all polynomial terms and an interaction between minimum temperature and precipitation had the highest  $R^2$  (0.89) and lowest AIC<sub>c</sub>. We validated the predictive power of this model using historical (1960–1970) climate data, for which we have all climatic variables (snow depth, min and max temperature, and precipitation). Although there were some differences between modeled and predicted snow depth for high values, a linear model demonstrated a relatively high predictive power ( $R^2 = 0.88$ ). Maps of predicted and modeled snow depth were also very similar. Thus, we used this model to predict snow depth for the two future time periods (2041–2070 and 2071–2100).

#### *Predicted effects of climate change on genetic variation*

Because of the close relationship between climate and genetic structure (see results), we predicted the effects of future climate projections using individual-based genetic simulations in CDPOP v 1.2.08 (Landguth & Cushman, 2010). CDPOP simulates genetic exchange across a set of  $N$  individuals based on their life history characteristics and movement parameters (mate searching and dispersal distances). Individual locations for the simulations were set up by generating a regular  $20 \times 20$  km grid of individuals within a polygon that buffered lynx sample locations by 150 km and removed locations in open water (3676 total individuals, Figure S3).

We simplified the simulations by forcing nonoverlapping generations; within each time-step (generation), individuals would search for a mating partner and the resulting offspring would disperse to fill each grid location. Mate searching and dispersal distances were based on an inverse-square probability function (Cushman & Landguth, 2010) with a set maxi-

mum resistance. We selected the most appropriate maximum dispersal parameters by replicate simulations and comparing mean simulated to observed values for four genetic summary statistics: (i) genetic differentiation ( $F_{ST}$ ) between the western region (West) and in the transition zone (Middle); (ii)  $F_{ST}$  between the eastern region (East) and Middle; (iii)  $F_{ST}$  between East and West; and (iv) the correlation between the first genetic axis in an sPCA with CV1 values. To keep sample sizes consistent between simulated and observed data, we subsampled the full grid and all resistances were based on current climate cost grids, which show the greatest correlation with genetic distance.

We quantified the effect of climate divergence on genetic differentiation by calculating new resistance values from projected climate data (2041–2070) and running five replicate simulations with the dispersal parameters set using the current correlation between climate and genetic structure. For each set of parameter and resistance values, we quantified the expected increase in genetic differentiation by comparing  $F_{ST}$  between east and west regions.

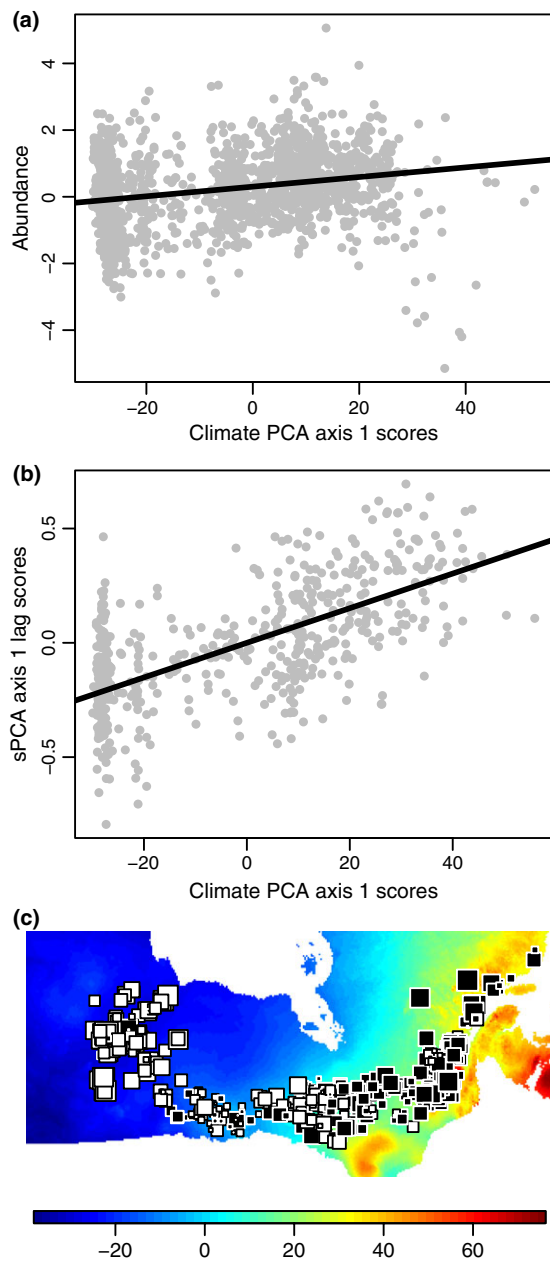
## **Results**

### *Genetic variation*

Neither DIC values nor the Q-matrix significantly changed with increasing values of  $k$  in the spatial Bayesian clustering. This suggested that there was only one single genetic cluster and weak genetic structure across this region. In contrast with these results, (sPCA) on individual genotypes revealed significant, geographically correlated genetic structure [ $n_{per} = 999$ ,  $\max(t) = 0.005$ ,  $P = 0.001$ ]. Eigenvalue plots further indicated spatial genetic structure in the principal axis, which had more extreme values of explained variation and spatial autocorrelation (hereafter sPCA1; see Figure S4). Along the first principle axis, individuals within the PNO and NAO were the most differentiated (i.e. positive and negative PCA values), with individuals in the middle having less extreme values. We interpret this finding as evidence of a west–east genetic cline (Fig. 2; Figure S4).

### *Genetic–climate associations*

Climate grids derived from winter snow conditions (CV1) displayed strikingly similar geographic variation as our genetic patterns (Fig. 2b and c). The Lagrange Multiplier test revealed significant spatial correlation within the OLS residuals ( $LM_{err} = 27.31$ ,  $P < 0.001$ ) of a linear regression between genetic variation and both climate and ecological PCA axes (sPCA1  $\sim$  CV1 + EV1 + EV2). Thus, we used a GLS regression to control for the spatial autocorrelation. A comparison between models found the exclusion of CV1 led to a large drop in



**Fig. 2** Correlation between winter climate variation and (a) log (maximum harvest), and (b) genetic variation across the Pacific-North American (PNO) to North Atlantic Oscillation (NAO) climatic systems, for the Canada lynx (*Lynx canadensis*). Genetic variation was represented by lag scores (each value replaced by mean of its neighbors) of the first component of a spatial Principal Component Analysis (sPCA1) on lynx genotypes. Current winter climate conditions were summarized using a PCA with the first component Climate Variation (CV1) shown, (c) A geographic representation of sPCA1 ranging from small (large white squares) to large (large black squares) values, overlaid on a climate grid derived from multiplying CV1 loadings by raw climate data. Low values (blue) represent low winter precipitation and snow depth and high values (red) represent high winter precipitation and snow depth.

AIC<sub>c</sub>, while the inclusion of basic ecological variables (EV1 & EV2) led to little improvement in model fit, suggesting that they had negligible influence on genetic variation across this region (Table 1). Although there appeared to be a slight increase in lynx abundance from west-to-east, there was no apparent reduction in abundance (Fig. 2a) through the transition zone.

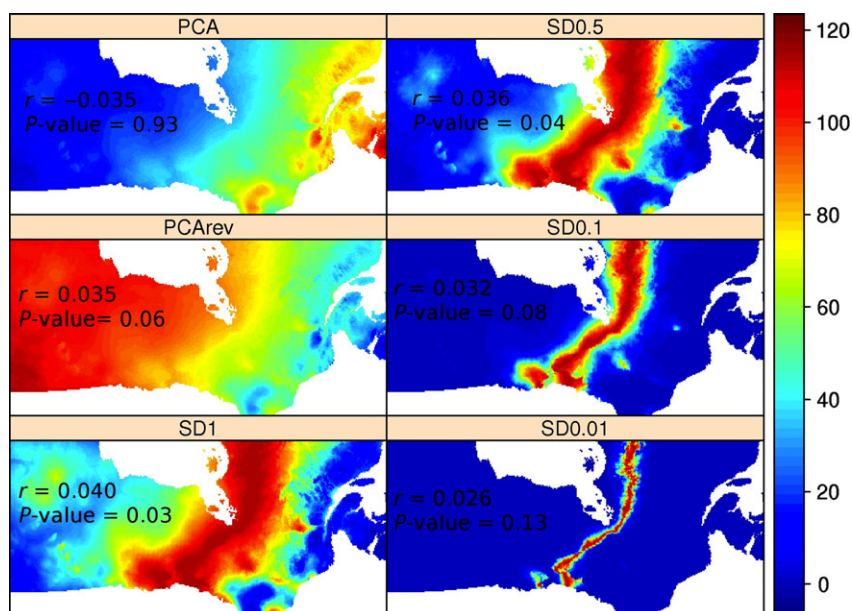
Using IBR analysis, we found that only pairwise resistance derived from a cost surface in which we assigned higher costs to dispersal across the center of the climatic transition zone (i.e. restricted dispersal from west-to-east and east-to-west) led to a significant correlation with individual pairwise genetic distance while controlling for distance (Fig. 3). Correlation coefficients between genetic distance and resistance decreased as the steepness of the decline in cost away from the middle of the transition zone increased (Fig. 3); this further supported an environmental gradient subtly influencing genetic patterns rather than an actual dispersal barrier. Although the correlation coefficient for PCAre<sub>v</sub> (increased resistance to gene flow within the PNO) was lower and nonsignificant, correlation coefficients were close and had overlapping confidence intervals. Thus, we could not rule out asymmetric gene flow with lower dispersal from east-to-west.

#### Changes in climate across the transition zone

Regression coefficients from a per-cell linear regression using climate grids derived from the loadings of CV1 (1958–2008), revealed positive and negative regression coefficients east and west of the center of the transition zone, respectively (Figure S5). This implies a decrease in winter precipitation and snow depth in the PNO climate system and the opposite within the NAO climate system. Comparing mean CV1 PCA climate and cost grids from data in four different time periods further

**Table 1** Model selection results for a Generalized Least-Squared (GLS) regression showing correlation between genetic variation spatial Principal Components Analysis (sPCA) and both current winter Climate Variation (CV1) and Ecological Variables (EV1 & EV2)

| Model                  | AIC <sub>c</sub> | Delta AIC | Log-Likelihood |
|------------------------|------------------|-----------|----------------|
| sPCA ~ CV1 + EV1       | 327.80           | 0.00      | –159.86        |
| sPCA ~ CV1             | 328.43           | 0.63      | –161.19        |
| sPCA ~ CV1 + EV1 + EV2 | 328.77           | 0.97      | –159.32        |
| sPCA ~ CV1 + EV2       | 329.63           | 1.82      | –160.77        |
| sPCA ~ EV1             | 337.90           | 10.10     | –165.93        |
| sPCA ~ EV2             | 339.11           | 11.30     | –166.53        |



**Fig. 3** Partial mantel's correlation coefficients and *P*-values for the correlation between individual pairwise genetic distance ( $D_{PS}$ ) and resistance, while controlling for distance. Resistance was calculated from six cost grids derived from the loadings of the first principal axis of a PCA summarizing current winter climate variation (CV1). The first two cost surfaces assign high costs to dispersal for high (PCA) and low (PCArev: reverse of PCA values) PCA values. The last four cost surfaces – (SD1, SD0.5, SD0.1, and SD0.01) – were transformed using Eqn (1) to represent the center of PCA distribution providing the highest cost to dispersal with varying levels of steepness away from the center. In all cases, red colors represent high resistance with blue representing low resistance.

supported diverging climate patterns, mainly through an increase in CV1 values (increased winter precipitation and snow depth) within the NAO climate system (Fig. 4; see Figure S6).

#### *Predicted effects of climate change on genetic variation*

Resistances used from genetic simulations were calculated from the SD1 cost surface grid (Fig. 3) because these resistance values had the greatest correlation with genetic variation. We originally ran nine different combinations of maximum dispersal and mate search distances (Table S2) and chose three combinations where simulated and observed statistics were most similar (15 max & 60 max; 10 max & 65 max; 10 max & 70 max) (Figure S7). Using these three sets of dispersal distances with resistances derived from future climate projections (2041–2070), we found an increase in genetic divergence between east and west regions that was 2–3 times larger, with nonoverlapping confidence intervals for all but one parameter set (Fig. 4; Figure S8).

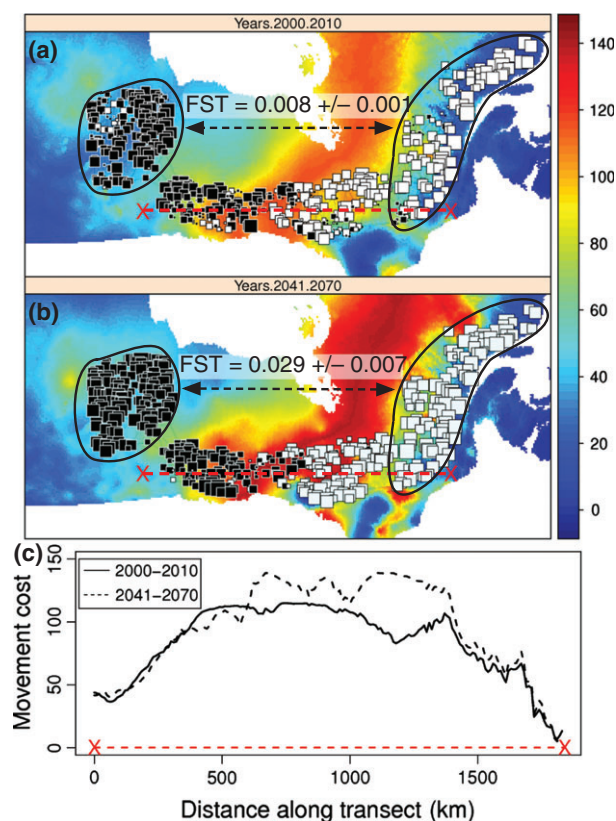
#### **Discussion**

The presence of clinal genetic differentiation and a lack of correlation with ecological variables point to nonrandom lynx dispersal due to differential snow conditions

across eastern North America. Previous studies have similarly found that genetic differentiation between populations in the PNO and NAO climate systems was greater than between populations in other areas of their range (Rueness *et al.*, 2003; Row *et al.*, 2012). Here, however, we combined evenly distributed genetic sampling with abundance and climate data to show that this increased differentiation is not likely due to a distribution gap or differences in habitat quality, but more likely from a reduced flow of dispersing individuals across the climatic transition zone. Given the extent and speed with which climate patterns are expected to change across this region, the spatial link between climate and dispersal found here could have strong implications for lynx and other species ranging across ecological boundaries.

The association between winter climate conditions and genetic variation is perhaps not surprising for lynx. Lynx have a propensity to disperse in the winter months during population crashes (Poole, 1997) and snow conditions can play a role in the capture rate of their main prey, snowshoe hare (Murray & Boutin, 1991). Lynx also have morphological adaptations that afford them advantages over their competitors in deep snow conditions (Murray & Boutin, 1991). Thus, it seems likely the propensity for individuals to disperse into areas with familiar snow conditions could have





**Fig. 4** Climate projections and genetic simulations suggest climate change will lead to a divergence in winter climate conditions and increase genetic differentiation across the Pacific-North American (PNO) to North Atlantic Oscillation (NAO) climatic systems. Current (a) and future (b) winter climate cost grids used in genetic simulations and resulting genetic variation [lag scores of first spatial Principal Components Analysis (sPCA) axis] and differentiation (mean  $F_{ST}$  ( $\pm$ SD) between East and West region using five replicates) from simulations are shown. Cost grids represent low (blue) to high (red) resistance to gene flow. For all simulations, maximum mate searching and dispersal distances were set to 54.82 and 237.58 cost units respectively. (c) A transect through the transition zone demonstrates an increased dispersal cost due to diverging climate conditions within climate each system.

strong implications for disperser survival rate. Despite this association, current genetic differentiation between the climatic regions is low, which is consistent with previous studies on lynx population structure (Schwartz *et al.*, 2002; Rueness *et al.*, 2003; Strobeck, 2006; Row *et al.*, 2012). These previous studies, however, did not explicitly include environmental variables and have generally only tested for increasing differentiation with geographic distance. Surely snow conditions are likely to vary in other parts of the lynx distribution and it would be interesting to determine the extent of this variation and whether similar associations emerge.

In addition to their effects on lynx dispersal and population dynamics, snow conditions have a strong influence on the ecology of other northern temperate species (Sweeney & Sweeney, 1984; Telfer & Kelsall, 1984; McKelvey *et al.*, 2011). For example, on a smaller scale than that examined here, Garroway *et al.* (2008), similarly, found that snow conditions influenced dispersal patterns of fisher (*Pekania pennanti*): individuals dispersed away from regions with deep snow. Due to the continental scale of the snow transition zone examined here, it is thus likely that this climatic transition zone will have similar relationships for other species across this region. For species with shorter dispersal distances than lynx, it may be difficult to disentangle the role of this large-scale gradient from more local effects such as habitat fragmentation, roads and other small-scale dispersal barriers.

Other studies across North America have found similar associations between large-scale ecological boundaries and genetic structure, with many suggesting that these patterns are related to habitat imprinting (Geffen *et al.*, 2004; Sacks *et al.*, 2004; Muñoz-Fuentes *et al.*, 2009). Since the term was introduced by Lorenz (1937), there have been both experimental and behavioral evidence suggesting that mammals will imprint upon, and subsequently choose, habitats similar to those in which they were reared (Wecker, 1963; Olson & Horne, 1998; Sacks *et al.*, 2005). Here, our evidence goes beyond simple correlation between genetic variation and snow conditions, we also excluded other landscape variables or differences in habitat quality throughout the transition zone, as driving this pattern. Based on our results, it appears that individuals are less likely to disperse to areas with unfamiliar snow conditions, which is consistent with the habitat imprinting hypothesis. However, other possibilities, such as a direct restriction in gene flow into the PNO climate system, could not be entirely ruled out. It follows that behavioral studies conducted on individuals across this region would be beneficial in further testing the hypothesis.

In addition to impacting dispersal, the strong gradient in snow conditions and the ecological importance of these conditions are likely to result in local adaptation to snow conditions for lynx populations within the PNO and NAO climate systems. In fact, there has been an increasing amount of both theoretical and empirical research that supports ecological and climatic gradients in generating diversity and even speciation events through divergent selection (Doebeli & Dieckmann, 2003; Grahame *et al.*, 2006). Restricted dispersal, however, is often not considered in models exploring selection gradients (e.g., Doebeli & Dieckmann, 2003) across transition zones. Given our results and other recent studies (Sacks *et al.*, 2005), there could be additive



effects of restricted dispersal and local adaptation on genetic variation. Increasingly enhanced genomic tools (Shendure & Ji, 2008) allow for the generation of large amounts of neutral and adaptive genetic data, which could be used to test the prevalence and potential additive effects of restricted dispersal and selection across climatic transition zones.

Most climate change research examining the ecological effects of changing climate patterns have centered on quantifying expected changes in species diversity, distribution, and abundance (Burns *et al.*, 2003; Thomas *et al.*, 2004; Hoegh-Guldberg & Bruno, 2010). However, the global effects of climate change are expected to vary geographically (Stott *et al.*, 2010) and through this variation there is likely to be changes in the extent and geographic location of climatic boundaries (e.g., Rosenfeld & Givati, 2013). Indeed, we found snow conditions within the PNO and NAO climate systems to diverge with climate projections, suggesting greater winter precipitation in the NAO climate system; in contrast, historical data suggested the opposite within the PNO, which will promote drier winter conditions. It is also noteworthy that although we used a single climate model for our projections, studies using multiple models or ensemble approaches have similarly projected that precipitation within the PNO will remain stable or decrease less than within the NAO (Elía & Côté, 2010; McKenney *et al.*, 2011b). Our genetic simulations suggest that this climate divergence may dramatically increase genetic differentiation for lynx without any physical changes on the landscape. Thus, in addition to examining how climate change will shift patterns of species diversity, more research should focus on establishing its more subtle effects on climatic boundaries, and quantifying the ecological and evolutionary consequences for species that span such boundaries.

## Acknowledgments

We thank North American Fur Auction and Fur Harvesters Auction Inc. for facilitating sample collection, C. Parsons, J. Paul, S. Simpkins, and K. Smith for laboratory assistance, volunteers for assistance with sample collection, and D. Berezanski, H. Golden, and T. Jung for identifying lynx harvest locations. We also thank D. McKenney and P. Papadopol at the Canadian Forest Service for supplying climate data. Funding was provided by NSERC (Strategic grant to DLM, JB and PJW, and a scholarship to ELK) Genetic simulations were made possible by the facilities of the Shared Hierarchical Academic Research Computing Network (SHARCNET:www.sharcnet.ca) and Compute/Calcul Canada.

## References

Anselin L, Bera A, Florax R, Yoon M (1996) Simple diagnostic tests for spatial dependence. *Regional Science and Urban Economics*, **26**, 77–104.

- Beale CM, Lennon JJ, Yearsley JM, Brewer MJ, Elston DA (2010) Regression analysis of spatial data. *Ecology Letters*, **13**, 246–264.
- Beaumont LJ, Hughes L, Pitman AJ (2008) Why is the choice of future climate scenarios for species distribution modelling important? *Ecology Letters*, **11**, 1135–1146.
- Bowcock A, Ruiz-Linares A, Tomfohrde J, Minch E, Kidd J, Cavalli-Sforza LL (1994) High resolution of human evolutionary trees with polymorphic microsatellites. *Nature*, **368**, 455–457.
- Burns CE, Johnston KM, Schmitz OJ (2003) Global climate change and mammalian species diversity in U.S. national parks. *Proceedings of the National Academy of Sciences of the United States of America*, **100**, 11474–11477.
- Campbell J, Mitchell M, Groffman P, Christenson L, Hardy J (2005) Winter in north-eastern North America: a critical period for ecological processes. *Frontiers in Ecology and the Environment*, **3**, 314–322.
- Chen C, Durand E, Forbes F, François O (2007) Bayesian clustering algorithms ascertaining spatial population structure: a new computer program and a comparison study. *Molecular Ecology Notes*, **7**, 747–756.
- Cushman SA, Landguth EL (2010) Spurious correlations and inference in landscape genetics. *Molecular Ecology*, **19**, 3592–3602.
- Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. *American Naturalist*, **168**, 486–499.
- Doebeli M, Dieckmann U (2003) Speciation along environmental gradients. *Nature*, **421**, 259–264.
- Elía R, Côté H (2010) Climate and climate change sensitivity to model configuration in the Canadian RCM over North America. *Meteorologische Zeitschrift*, **19**, 325–339.
- Frantz AC, Cellina S, Krier A, Schley L, Burke T (2009) Using spatial Bayesian methods to determine the genetic structure of a continuously distributed population: clusters or isolation by distance? *Journal of Applied Ecology*, **46**, 493–505.
- Gabriel KR, Sokal RR (1969) A new statistical approach to geographic variation analysis. *Systematic Zoology*, **18**, 259.
- Garraway CJ, Bowman J, Carr D, Wilson PJ (2008) Applications of graph theory to landscape genetics. *Evolutionary Applications*, **1**, 620–630.
- Geffen E, Anderson MJ, Wayne RK (2004) Climate and habitat barriers to dispersal in the highly mobile grey wolf. *Molecular Ecology*, **13**, 2481–2490.
- Goslee S, Urban D (2007) The ecodist package for dissimilarity-based analysis of ecological data. *Journal of Statistical Software*, **22**, 1–19.
- Grahame JW, Wilding CS, Butlin RK (2006) Adaptation to a steep environmental gradient and an associated barrier to gene exchange in *Littorina saxatilis*. *Evolution*, **60**, 268–278.
- Hoegh-Guldberg O, Bruno JF (2010) The impact of climate change on the world's marine ecosystems. *Science*, **328**, 1523–1528.
- Hurrell J (1996) Influence of variations in extratropical wintertime teleconnections on Northern Hemisphere temperature. *Geophysical Research Letters*, **23**, 665–668.
- Jombart T (2008) Adegenet: a R package for the multivariate analysis of genetic markers. *Bioinformatics*, **24**, 1403–1405.
- La Sorte FA, Jetz W (2010) Projected range contractions of montane biodiversity under global warming. *Proceedings of the Royal Society B: Biological Sciences*, **277**, 3401–3410.
- Landguth EL, Cushman SA (2010) CDPOP: a spatially explicit cost distance population genetics program. *Molecular Ecology Resources*, **10**, 156–161.
- Latch EK, Dharmarajan G, Glaubitz JC, Rhodes OE (2006) Relative performance of Bayesian clustering software for inferring population substructure and individual assignment at low levels of population differentiation. *Conservation Genetics*, **7**, 295–302.
- Lehodey P, Senina I, Sibert J, Bopp L, Calmettes B, Hampton J, Murtugudde R (2010) Preliminary forecasts of Pacific bigeye tuna population trends under the A2 IPCC scenario. *Progress in Oceanography*, **86**, 302–315.
- Lorenz K (1937) The companion in the bird's world. *The Auk*, **54**, 245–273.
- Luoto M, Heikkinen RK, Pöyry J, Saarinen K (2006) Determinants of the biogeographical distribution of butterflies in boreal regions. *Journal of Biogeography*, **33**, 1764–1778.
- McKelvey K, Copeland J, Schwartz M *et al.* (2011) Climate change predicted to shift wolverine distributions, connectivity, and dispersal corridors. *Ecological Applications*, **21**, 2882–2897.
- McKenney DW, Pedlar JH, Papadopol P, Hutchinson MF (2006) The development of 1901–2000 historical monthly climate models for Canada and the United States. *Agricultural and Forest Meteorology*, **138**, 69–81.
- McKenney D, Hutchinson M, Papadopol P *et al.* (2011a) Customized spatial climate models for North America. *American Meteorological Society*, **92**, 1611–1622.

- McKenney DW, Pedlar JH, Rood RB, Price D (2011b) Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. *Global Change Biology*, **17**, 2720–2730.
- McRae B (2006) Isolation by resistance. *Evolution*, **60**, 1551–1561.
- Muñoz-Fuentes V, Darimont CT, Wayne RK, Paquet PC, Leonard JA (2009) Ecological factors drive differentiation in wolves from British Columbia. *Journal of Biogeography*, **36**, 1516–1531.
- Murray D, Boutin S (1991) The influence of snow on lynx and coyote movements : does morphology affect behavior? *Oecologia*, **88**, 463–469.
- Nakicenovic N, Swart R (eds.) (2000) *Special Report on Emissions Scenarios*. University Press, Cambridge, UK.
- Olson G, Horne B (1998) Dispersal patterns of juvenile townsend's ground squirrels in southwestern Idaho. *Canadian Journal of Zoology*, **76**, 2084–2089.
- Parnesan C, Yohe G (2003) A globally coherent fingerprint of climate change impacts across natural systems. *Nature*, **421**, 37–42.
- Poole K (1997) Dispersal patterns of lynx in the Northwest Territories. *The Journal of Wildlife Management*, **61**, 497–505.
- R Development Core Team (2012) *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, Available at: <http://www.R-project.org/> (accessed 30 January 2014).
- Raupach MR, Marland G, Ciais P, Le Quéré C, Canadell JG, Klepper G, Field CB (2007) Global and regional drivers of accelerating CO<sub>2</sub> emissions. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 10288–10293.
- Root T, Price J, Hall K, Schneider S, Rosenzweig C, Pounds A (2003) Fingerprints of global warming on wild animals and plants. *Nature*, **421**, 57–60.
- Rosenfeld D, Givati A (2013) The Artic oscillation, climate change and the effects on precipitation in Israel. *Atmospheric Research*, **132–133**, 114–124.
- Row JR, Gomez C, Koen EL, Bowman J, Murray DL, Wilson PJ (2012) Dispersal promotes high gene flow among Canada lynx populations across mainland North America. *Conservation Genetics*, **13**, 1259–1268.
- Rueness EK, Stenseth NC, O'Donoghue M, Boutin S, Ellegren H, Jakobsen KS (2003) Ecological and genetic spatial structuring in the Canadian lynx. *Nature*, **425**, 69–72.
- Sacks BN, Brown SK, Ernest HB (2004) Population structure of California coyotes corresponds to habitat-specific breaks and illuminates species history. *Molecular Ecology*, **13**, 1265–1275.
- Sacks BN, Mitchell BR, Williams CL, Ernest HB (2005) Coyote movements and social structure along a cryptic population genetic subdivision. *Molecular Ecology*, **14**, 1241–1249.
- Sanderson E, Malanding J, Levy M, Redford K, Wannebo A, Woolmer G (2002) The human footprint and the last of the wild. *BioScience*, **52**, 891–904.
- Schwartz MK, Mills LS, McKelvey KS, Ruggiero LF, Allendorf FW (2002) DNA reveals high dispersal synchronizing the population dynamics of Canada lynx. *Nature*, **415**, 520–522.
- Shendure J, Ji H (2008) Next-generation DNA sequencing. *Nature biotechnology*, **26**, 1135–1145.
- Shirk AJ, Wallin DO, Cushman SA, Rice CG, Warheit KI (2010) Inferring landscape effects on gene flow: a new model selection framework. *Molecular Ecology*, **19**, 3603–3619.
- Slough B, Mowat G (1996) Lynx population dynamics in an untrapped refugium. *The Journal of Wildlife Management*, **60**, 946–961.
- Sophie B, Pierre D, Eric VB (2010) *GLOBCOVER 2009 - Products Description and Validation Report*. European Space Agency, Paris, France.
- Stenseth NC (1999) Common dynamic structure of Canada lynx populations within three climatic regions. *Science*, **285**, 1071–1073.
- Stenseth NC, Shabbar A, Chan KS *et al.* (2004) Snow conditions may create an invisible barrier for lynx. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 10632–10634.
- Stott PA, Gillett NP, Hegerl GC, Karoly DJ, Stone DA, Zhang Zwiers F, X, Zwiers F (2010) Detection and attribution of climate change: a regional perspective. *Wiley Interdisciplinary Reviews: Climate Change*, **1**, 192–211.
- Strobeck C (2006) Fine-scale genetic structure and dispersal in Canada lynx (*Lynx canadensis*) within Alberta, Canada. *Canadian Journal of Zoology*, **84**, 1112–1119.
- Sweeney J, Sweeney J (1984) Snow depths influencing winter movements of Elk. *Journal of Mammalogy*, **65**, 524–526.
- Telfer E, Kelsall J (1984) Adaptation of some large North American mammals for survival in snow. *Ecology*, **65**, 1828–1834.
- Teuschl Y, Taborsky B, Taborsky M (1998) How do cuckoos find their hosts? The role of habitat imprinting. *Animal Behaviour*, **56**, 1425–1433.
- Thomas CD, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Nature*, **427**, 145–148.
- Thorpe W (1945) The evolutionary significance of habitat selection. *The Journal of Animal Ecology*, **14**, 67–70.
- Thuiller W, Araujo M, Lavorel S (2004) Do we need land-cover data to model species distributions in Europe? *Journal of Biogeography*, **31**, 353–361.
- Thuiller W, Lavorel S, Araújo MB, Sykes MT, Prentice IC (2005) Climate change threats to plant diversity in Europe. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 8245–8250.
- Vogel W, Taborsky M, Taborsky B, Teuschl Y, Honza M (2002) Cuckoo females preferentially use specific habitats when searching for host nests. *Animal Behaviour*, **64**, 843–850.
- Wecker S (1963) The role of early experience in habitat selection by the prairie deer mouse, *Peromyscus maniculatus bairdi*. *Ecological Monographs*, **33**, 307–325.

## Supporting Information

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

**Figure S1.** Proportion of explained variation for Principal Component Analysis (PCA) axes using current (2000–2010) winter (October–April) climate variables and ecological variables [open (15–40% canopy cover) needle-leaved coniferous forest & broad-leaved deciduous forest; closed (>40% canopy cover) needle-leaved coniferous forest & broad-leaved deciduous forest, anthropogenic habitat disturbance] at lynx sampling locations. (a) Loadings for the first principal component of the climate PCA suggest the axis separated low winter precipitation (loading = 0.96) and less snow depth (loading = 0.23) from high winter precipitation and deep snow; temperature variables were only minor contributors to the axis (loadings < 0.08). (b) Loadings for the first principal component of the ecological variables distinguished between open and closed forest (loadings: open needle-leaved = −0.83; closed broad-leaved = 0.35; closed needle-leaved = 0.43), while the second axis separated between needle-leaved and broad-leaved forest and human influence (loadings: closed broad-leaved = −0.11; human = −0.11; open needle-leaved = 0.41; closed needle-leaved = 0.90).

**Figure S2.** Spatial autocorrelation correlogram for the correlation between allele frequencies (Moran's *I* for 14 microsatellite loci) of Canada lynx distributed from Manitoba to Quebec in eastern North America (see Fig. 1). Twenty distance classes were derived to retain an equal number of pairwise comparisons within each distance class and dotted lines show mean permuted values for 999 permutations of individuals randomly shuffled among the 20 distance classes. Observed values and permutations were calculated using SPAGeDI v1.3.

**Figure S3.** Grid of individuals used in CDPOP genetic simulations (black) and the subset of individuals used in the calculation of genetic summary statistics (red). Subset locations were randomly chosen within each region to represent the same sample size of the observed data.

**Figure S4.** Results of spatial Principal Components Analysis (sPCA) on Canada lynx (*Lynx canadensis*) genotypes distributed across Manitoba to Quebec. (a) Bar chart representing positive and negative eigenvalues, (b) scree plots for sPCA axis showing the spatial autocorrelation of each PCA axis, and (c) spatial representation of principal axis scores. A permutation test on the individual components found significant, geographically correlated genetic structure ( $n_{per} = 999$ ,  $\max(t) = 0.005$ ,  $P = 0.001$ ).

**Figure S5.** (a) Regression coefficients from per-cell linear regressions for overlaid Principal Component Analysis (PCA) climate grids from 1958–2008. Temporal climate grids were derived by multiplying the loadings of climate variation (CV1) (Figure S3) by the raw climate data in each successive year. (b) Significance levels for per-cell regressions with negative significant change in climate over time in blue, positive significant change in red, and no significant change in gray. Sample locations are indicated with 'x'.

**Figure S6.** (a) Climate grids summarizing the temporal change in winter climate conditions across the Pacific-North American (PNO) to North Atlantic Oscillation (NAO) climatic systems. Grids were derived by multiplying the loadings from CV1 (Figure S3) by the climate data in each time period. (b) Temporal climate grids were transformed to cost grids using Eqn (1) with a standard deviation of one. Overall patterns suggest that climate conditions are diverging across the PNO-to-NAO transition zone.

**Figure S7.** Mean ( $\pm$ SD) simulated genetic summary statistics for five replicate simulations with differing maximum mate searching (legend) and dispersal distance (*x*-axis). Resistance values used in simulations were calculated using CIRCUITSCAPE with SD1 cost grid (Fig. 2). Observed genetic summary statistics ( $F_{ST}$ ) calculated from Canada lynx subpopulations are shown in red and are generally within the range of values produced by the simulations.

**Figure S8.** Mean ( $\pm$ SD) simulated genetic summary statistics for five replicate simulations calculated using current (squares, 2000–2010) and future (circles, 2041–2071) climate cost grids (see: Figure S5b). Three different maximum mate searching and dispersal distance combinations are shown with all but one (mate searching 15 of the MaxCost; dispersal 70 of MaxCost) showing a large increase in differentiation.

**Table S1.** Model selection and results for snow depth prediction using contemporary (2000–2010) winter (October–April) climate variables.

**Table S2.** Mate searching and dispersal distance parameters for genetic simulations used in CDPOP. Distances were entered as resistances derived from a cost surface with an increased cost to dispersing across a climatic transition zone (Fig. 2; SD1). The percentage of maximum resistance, the actual resistance value, and the resulting average dispersal distance in km are shown.