

Variation in abundance across a species' range predicts climate change responses in the range interior will exceed those at the edge: a case study with North American beaver

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Abstract

The absence of information about how abundance varies across species' ranges restricts most modeling and monitoring of climate change responses to the range edge. We examine spatial variation in abundance across the northeastern range of North American beaver (*Castor canadensis*), evaluate the extent to which climate and nonclimate variables explain this variation, and use a species–climate envelope model that includes spatial variation in abundance to predict beaver abundance responses to projected climate change. The density of beaver colonies across Québec follows a roughly logistic pattern, with high but variable density across the southern portion of the province, a sharp decline in density at about 49°N, and a long tail of low density extending as far as 58°N. Several climate and nonclimate variables were strong predictors of variation in beaver density, but 97% of the variation explained by nonclimate variables could be accounted for by climate variables. Because of the peak and tail density pattern, beaver climate sensitivity (change in density per unit change in climate) was greatest in the interior and lowest at the edge of the range. Combining our best density–climate models with projections from general circulation models (GCM) predicts a relatively modest expansion of the species' northern range limit by 2055, but density increases in the range interior that far exceed those at the range edge. Thus, some of the most dramatic responses to climate change may be occurring in the core of species' ranges, far away from the edge-of-the-range focus of most current modeling and monitoring efforts.

Keywords: abundant center hypothesis, climate change, climate envelope modeling, furbearer, mammal, quantile regression, relative abundance, rodent, spatial ecology, wildlife

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Introduction

Climate is a major determinant of the distribution and abundance of species (Andrewartha & Birch, 1954; Jeffree & Jeffree, 1994; Lomolino *et al.*, 2006). Global average surface temperatures have increased by 0.6 ± 0.2 °C since the late 19th century and are expected to rise from 1.4 to 5.8 °C over the next century (Houghton *et al.*, 2001). Thus, there is a need to develop models linking species distributions to climate change scenarios in order to anticipate the effects of global warming on

plant and animal populations (Ludwig *et al.*, 2001; Lawler *et al.*, 2006). Species–climate envelope approaches are being used extensively to predict how climate change will alter species distributions (Box, 1981; Sutherst & Maywald, 1985; Austin, 1992; Huntley *et al.*, 1995; Iversen & Prasad, 1998; Peterson *et al.*, 2002; Thuiller, 2003; Skov & Svenning, 2004; Thomas *et al.*, 2004; Araújo & Rahbek, 2006; Elith *et al.*, 2006; Botkin *et al.*, 2007). Essentially, this method attempts to relate current species distributions with current climatic conditions, then uses predicted future climate scenarios usually derived from general circulation models (GCM), to predict associated shifts in species' geographic distributions (Davis *et al.*, 1998; Lawler *et al.*, 2006).

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Species–climate envelope models rely on occurrence data to predict the impacts of climate change on species distributions and regional biodiversity (Erasmus *et al.*, 2002; Huntley *et al.*, 2004; Araújo *et al.*, 2005). Although presence/absence range maps provide a useful indication of the broad regional occurrence of a given species, they exclude information about how local abundance varies across the range. As a result, species–climate envelope approaches are capable of predicting range shifts, but not changes in abundance across the range. Although some climate envelope models assume a ramp of suitability or occurrence probability near the edge of the range, the absence of data regarding how abundance actually varies across the range limits predictions of species responses to climate change to the periphery of species range. Similarly, monitoring of species responses to recent climate change has primarily focused on species range expansions and contractions, with little attention paid to changes in abundance between range boundaries (Parmesan & Yohe, 2003; Root *et al.*, 2003; Martinez-Meyer *et al.*, 2004; Araújo *et al.*, 2005). Thus, at present, we have little idea whether climate change modeling and monitoring efforts focused on the periphery of species' ranges are over- or underestimating the impacts of climate change. Our ability to provide more sensitive and/or representative assessment of climate change impacts thus rests on our understanding of geographical abundance patterns.

Numerous ecological and evolutionary hypotheses are based on the assumption that the local abundance of a species is highest in the center of its geographical range, and declines gradually into a tail of low abundance as its range edge is approached (Andrewartha & Birch, 1954; Whittaker, 1956; Hengeveld & Haeck, 1982; Rapoport, 1982; Brown, 1984; Brussard, 1984; Gaston, 1990, 2003; Brown *et al.*, 1995). However, there is a paucity of rigorous empirical tests for this assumption and, among the few species that have been examined thoroughly, there is extensive variability in the location of peak abundance within the range (Sagarin & Gaines, 2002a, b; Sorte & Hofmann, 2004). This is particularly the case among mammals, where only a few studies have documented geographical abundance patterns across large spatial extents (Caughley *et al.*, 1988; Rodriguez & Delibes, 2002; Williams *et al.*, 2003). Hence, although data are sparse and support for population density peaking in the geographical center of the range is weak, there are theoretical and empirical reasons to expect that many species will be characterized by some pattern of systematic variation in local abundance across their range. This pattern will frequently include a tail of low abundance near the periphery of at least some portions of their range boundaries.

An important consequence of a tail of low abundance near a range edge is that the change in abundance per unit distance will tend to decrease as the range edge is approached. Because most climate variables will tend to vary more linearly across the same gradient, the change in abundance per unit change in climate (i.e., the species' local climate sensitivity) should decrease as the range edge is approached. Consequently, for species with a tail of low abundance at the periphery of their range, species–climate envelope models incorporating variation in abundance across the range should predict weak impacts of climate change at the edge of the range, and stronger impacts where the tail ramps upwards to higher abundance closer to the range interior. Predictions of climate change impacts focused on presence–absence data at the edge of species' ranges may therefore underestimate the magnitude of species' responses to climate change in the range interior.

In the present study, we incorporate spatial variation in relative abundance into a climate envelope model to test the hypothesis that predicted species responses to climate change will be larger near the interior of the range than at the edge of the range. We test this hypothesis using a unique, previously unpublished dataset involving 161 surveys of the regional abundance of North American beaver (*Castor canadensis*), covering 74% of their 1.1 million km² range in Québec, Canada. Beaver are well-suited to examining abundance patterns because their local abundance can be accurately assessed via aerial surveys of dams, lodges, and autumn food caches (Bergerud & Miller, 1977; Novak, 1987), their general habitat requirements (deciduous and shrubby vegetation along stable waterways; Slough & Sadleir, 1977; Allen, 1983; Howard & Larson, 1985) can be identified from land cover classifications, and they have been extensively surveyed in some regions. Despite better-than-typical survey efforts, equivalent estimates of local abundance are not available across their entire range, which encompasses most of North America. However, the volume and extent of the data available across Québec provides a unique opportunity to examine how beaver abundance varies across more than 1 million km² from the northeastern interior of their range to the northeastern edge of their range, and how this variation might influence predictions of climate change impacts on beaver density. The main objectives of this study were to (a) examine the spatial variation in beaver abundance across the northeastern portion of their range, (b) evaluate the extent to which climate and nonclimate variables predict this variation, and (c) use a species–climate envelope model that includes spatial variation in abundance to predict beaver density responses to projected climate change. We predicted that beaver abundance will decline in a

logistic fashion from the interior to the edge of their range and will be strongly correlated with climate variables that decline roughly linearly across the same gradient. Thus, we hypothesized that the beaver climate sensitivity (change in abundance per unit change in climate) will be highest in the midrange and lowest at the core and edge of the range.

Materials and methods

Beaver density surveys

Beaver density estimates were derived from reports obtained from the Direction de l'Aménagement de la Faune de l'Outaouais (Gatineau, Québec), the Direction de l'Aménagement de la Faune de Mauricie (Trois-Rivières, Québec), and documentation centers at the Québec Ministry of Environment (Québec, Québec) and at Hydro Québec (Montréal, Québec). Results from aerial surveys conducted in the far north of Québec by SIJ (see Jarema, 2006) were also included in the dataset. We included only helicopter surveys in our analysis because plane surveys can overlook a majority of beaver structures (correction factor up to 75%; Payne, 1981; Potvin & Breton, 1982). The majority of study areas were surveyed in autumn, after deciduous leaf fall and before waterway freeze up, when beavers were completing their food caches. Survey teams consisted of a pilot and a minimum of one observer/navigator in a helicopter flying at low altitude (<100 m) and speed (<140 km h⁻¹). Both active and abandoned sites were recorded, with three active categories: (1) lodge with fresh food cache, (2) fresh food cache without the presence of a lodge, and (3) other obvious signs of beaver presence (e.g., peeled sticks, well-maintained dams, runways and burrows, beaver).

Areas were surveyed using total coverage or subsampling. Total coverage was the methodology used for 77% of surveys included in our study and involves surveying all waterways within the study area. Subsampling was used for the remaining 23% and involved dividing the study zone into equally sized quadrats (4, 9, 25 or 50 km²), randomly selecting 9–23% of these quadrats, and surveying all the waterways within selected quadrats. Whether the entire study area was surveyed, or a subsample of quadrats was surveyed, the total number of active beaver colonies observed was divided by the total area surveyed, to yield the average number of beaver colonies per km². Survey years ranged from 1966 to 2004, but most surveys (80%) were initiated between 1980 and 1995. If a study region was surveyed in more than 1 year, and the survey coverage was within 20% of the maximum survey coverage, beaver densities were averaged. Otherwise, only the

beaver density estimated from the most extensive survey was included in the analysis.

To render beaver survey data compatible with GIS, we obtained the vector data for recreational and protected areas in Québec (e.g., controlled harvesting zones, wildlife reserves, outfitting operations, national parks, and ecological reserves) (Limites des territoires récréatifs et protégés 1:250 000) and used digital maps imported from Lafond *et al.* (2003). The area, perimeter, and midpoint coordinates were then calculated for each of the 161 study polygons included in our analysis.

Climate and nonclimate explanatory variables

Point estimates of trimonthly temperature minima and maxima, precipitation totals, and agroclimatic indices (Table 1) were obtained for each study polygon centroid from Selected Modeled Climate Data for Point Locations created by The Landscape Analysis and Application Section (LAAS), Great Lakes Forestry Centre (GLFC), Canadian Forest Service (CFS), and Natural Resources Canada (NRCan). The originators used a software package called ANUCLIM (Centre for Resource and Environment Studies, Canberra, Australia) to obtain estimates of monthly mean climate variables, bioclimatic parameters, and indices relating to crop growth (McKenney, 2006). For average trimonthly temperatures, we used the Canadian Gridded Climate Data (50 km grid; Hopkinson, 2001). Once the gridded values were imported into ARCVIEW 8.2 (ESRI, Redlands, CA, USA), they were projected to NAD 1983 Québec Lambert, interpolated to a raster image using Inverse Distance Weighted in 3D Analyst, reclassified at intervals of 1.0 °C, and finally converted from a raster image to a feature. The final product was intersected with all study area polygons.

Potential nonclimate predictors of beaver density were selected based on previous beaver habitat studies (reviewed in Jarema, 2006) and included the nature and extent of waterways, shorelines, vegetation cover, soil composition, slope, beaver harvest intensity, and predator abundance (Table 1). The length, area, and perimeter of waterways (rivers, lakes, and wetlands) within each study polygon were estimated from 92 National Topographic Digital maps (1:250 000). Buffers around all waterways, 200 m in width to include the maximum inland foraging distance of beaver (Allen, 1983; Müller-Schwarze & Sun, 2003), were constructed using BUFFERWIZARD in ARCVIEW 8.2 (ESRI). Land cover within the 200 m buffer zones was estimated, for study polygons north of the 52nd parallel, from the Mosaïque du Québec (Photocartotheque Québécoise, 1:250 000 scale, 15 land cover classes; see Jarema, 2006) and, for study polygons south of the 52nd parallel, from the Spatiocarte Portrait du Québec Forestier Méridional (Direction des Inventaires Forestiers, 1:1250 000

Table 1 Climate and nonclimate variables evaluated as potential predictors of beaver density across Québec

Climate variable	Definition	Nonclimate variable	Definition
PET	Potential evapotranspiration (mm) over growing season*	Smalllakes	Number of lakes <1 km ² within the polygon†
GDD	Growing degree days (°C days) above base temperature for the entire growing season*	Largelakes	Number of lakes >1 km ² within the polygon†
T_{avgann}	Average annual temperature (°C)‡	Rivershoreline	Proportion of total shoreline (rivers, lakes, wetlands) in the polygon that is along rivers†
T_{avgdjf}	Average December–January–February temperature (°C)§	Lakeshoreline	Proportion of total shoreline (rivers, lakes, wetlands) in the polygon that is along lakes†
T_{avgmam}	Average March–April–May temperature (°C)§	Wetlandshoreline	Proportion of total shoreline (rivers, lakes, wetlands) in the polygon that is along wetlands†
T_{avgjja}	Average June–July–August temperature (°C)§	Riverbuffer	Proportion of polygon area within 200 m buffers around all rivers†
T_{avgson}	Average September–October–November temperature (°C)§	Lakebuffer	Proportion of polygon area within 200 m buffers around all lakes†
T_{maxdjf}	Average maximum December–January–February temperature (°C)‡	Wetlandbuffer	Proportion of polygon area within 200 m buffers around all wetlands†
T_{maxmam}	Average maximum March–April–May temperature (°C)‡	CdecidB	Proportion of 200 m buffer around all rivers, lakes, and wetlands in polygon covered by deciduous forest (including deciduous regrowth)†
T_{maxjja}	Average maximum June–July–August temperature (°C)‡	CmixedB	Proportion of 200 m buffer around all rivers, lakes, and wetlands in polygon covered by mixed forest (including mixed regrowth, mixed dominated by young coniferous, and mixed dominated by young deciduous)†
T_{maxson}	Average maximum September–October–November temperature (°C)‡	CconiferB	Proportion of 200 m buffer around all rivers, lakes, and wetlands in polygon covered by coniferous forest (including coniferous regrowth)†
T_{mindjf}	Average minimum December–January–February temperature (°C)‡	CshrubB	Proportion of 200 m buffer around all rivers, lakes, and wetlands in polygon covered by shrubs and lichens or shrubs and mosses†
T_{minmam}	Average minimum March–April–May temperature (°C)‡	CmossrockB	Proportion of 200 m buffer around all rivers, lakes, and wetlands in polygon covered by moss and rock†
T_{minjja}	Average minimum June–July–August temperature (°C)‡	CrockB	Proportion of 200 m buffer around all rivers, lakes, and wetlands in polygon covered by rocks†
T_{minson}	Average minimum September–October–November temperature (°C)‡	CagricB	Proportion of 200 m buffer around all rivers, lakes, and wetlands in polygon used by agriculture†
T_{iso}	Mean diurnal temperature range divided by the annual temperature range‡	CurbanB	Proportion of 200 m buffer around all rivers, lakes, and wetlands in polygon occupied by populated areas†
T_{seas}	Temperature seasonality expressed as the coefficient of variation of monthly mean temperatures‡	CbuiltupB	Proportion of 200 m buffer around all rivers, lakes, and wetlands in polygon occupied by populated zones where buildings are so close together that, for cartographic purpose, they are represented by a built-up area outline†
P_{avgann}	Sum of all monthly average precipitation estimates (mm)‡	Slope<2°	Proportion of polygon area occupied by a slope <2°†
P_{avgdjf}	Average December–January–February precipitation (mm)‡	Slope<10°	Proportion of polygon area occupied by a slope <10°†
P_{avgmam}	Average March–April–May precipitation (mm)‡	Slope<30°	Proportion of polygon area occupied by a slope <30°†
P_{avgjja}	Average June–July–August precipitation (mm)‡	Slope>30°	Proportion of polygon area occupied by a slope >30°†
P_{avgson}		Slope<2°B	

Continued

Table 1 Continued

Climate variable	Definition	Nonclimate variable	Definition
P_{seas}	Average September–October–November precipitation (mm)‡		Proportion of 200 m buffer around all rivers, lakes, and wetlands occupied by a slope $<2^\circ$ †
	Precipitation seasonality expressed as the coefficient of variation of monthly average precipitation‡	Slope $<10^\circ$ B	Proportion of 200 m buffer around all rivers, lakes, and wetlands occupied by a slope $<10^\circ$ †
		Slope $<30^\circ$ B	Proportion of 200 m buffer around all rivers, lakes, and wetlands occupied by a slope $<30^\circ$ †
		Slope $>30^\circ$ B	Proportion of 200 m buffer around all rivers, lakes, and wetlands occupied by a slope $>30^\circ$ †
		Smineral	Proportion of polygon containing surface material made up of predominantly mineral particles containing $<30\%$ organic matter by weight¶
		Sorganic	Proportion of polygon containing surface material made up of $>30\%$ organic matter by weight¶
		Ssoftrock	Proportion of polygon containing surface material made up of rock that can be dug with a shovel (i.e., undifferentiated shales, upper Cretaceous and Tertiary materials)¶
		Sgranite	Proportion of polygon containing surface material made up of granite¶
		Slimestone	Proportion of polygon containing surface material made up of limestone¶
		Shardrock	Proportion of polygon containing surface material made up of hard rock of unspecified origin and undifferentiated properties¶
		Beaverharvest	Average beaver harvest per unit area for ‘Structured’ or ‘Free Zones’ in the Administrative Regions of Québec
		Beardensity	Estimated black bear density (individuals km^{-2}) by trapping zones**
		Wolfdensity	Estimated wolf density (individuals km^{-2}) in administrative regions or wildlife reserves††,‡‡
		Limitedroads	Kilometers of roads that vary seasonally in condition or to which public access is denied divided by polygon area†
		Roads	Kilometers of roads for the movement of motor vehicles divided by polygon area†

*Bootsma & McKenney (2005).

†Natural Resources Canada. 2006. Centre for Topographic Information: Glossary for NTBD data 1:250 000. http://www.cits.rncan.gc.ca/cit/servlet/CIT/site_id=01&page_id=1-002-001.html#b.

‡Landscape Analysis and Application Section (LAAS), Great Lakes Forestry Centre (GLFC), Canadian Forest Service (CFS), Natural Resources Canada (NRCAN). Resources Canada 2006. Selected Modeled Climate Data for Point Locations. Sault Ste. Marie. LAAS. §Hopkinson (2001).

¶Centre for Land and Biological Resources Research. 1996. Soil Landscapes of Canada, v.2.2, Research Branch, Agriculture and Agri-Food Canada. Ottawa.

||Pierre Canac-Marquis Coordonnateur Piégeage Faune et Parcs Québec.

**Jolicoeur (2006).

††Jolicoeur & Heneault (2002).

‡‡Lariviere *et al.* (1998).

scale, 22 land cover classes; see Jarema, 2006). Slopes within the 200 m buffer zones were calculated from the same National Topographic Digital Maps using ARCVIEW 8.2 (ESRI) 3D Analyst to create a TIN from contour lines and the SLOPE function in Surface Analysis to derive slopes in degrees. The image was then reclassified using the following defined intervals: 0–2.0°, 2.1–10.0°, 10.0–30.0°, >30.1°, which provided, for each polygon, the area within the 200 m buffer represented by the different slope categories. The dominant value for soil composition within each study polygon (KINDMAT field) was obtained from Canadian Soil Information (CanSIS) website. For each study polygon, the area covered by built-up regions (populated zones where buildings are so close together that, for cartographic purpose, they are represented by a built-up area outline) and the length of roads were derived again from the National Topographic Digital Maps. To incorporate the abundance of potential beaver predators in the analysis, wolf (*Canis lupus*) densities were calculated by dividing the estimated number of wolves in each administrative region by the area of that administrative region (Lariviere *et al.*, 1998; Jolicoeur & Heneault, 2002), whereas black bear (*Ursus americanus*) densities were calculated by dividing the estimated number of black bears within each trapping zone by the area of that trapping zone (Lamontagne *et al.*, 2006). The average number of beaver harvested per km² was calculated by dividing the average number of beaver harvested in regions referred to as 'libre' (private lands and certain crown lands where trapping is carried out with no particular constraints) and 'structurée' (crown lands subdivided into trapping territories where exclusive trapping rights are leased to certain trappers) by the area of these zones within each administrative region (P. Canac-Marquis, Coordinator, Société de la Faune et des Parcs Québec, personal communication 2004).

Model selection

Our modeling objective is to identify highly predictive but parsimonious models of beaver density based on variables that are commonly forecasted by GCM's. As a result, our model selection approach is biased towards climate over nonclimate variables, and univariate over multivariate models. However, in addition to identifying the strongest climate predictors of beaver density, we seek to quantify the opportunity cost of excluding nonclimate variables and multivariate climate models. Thus, we first compare the independent and combined explanatory power of climate vs. nonclimate variables, then examine the relative explanatory power of multivariate vs. univariate climate models, then focus on the strength and the form of the best univariate climate–density models.

The data were heteroscedastic and beaver density appeared to have a nonlinear relationship with most

variables. Accordingly, beaver density was square-root transformed, which is a commonly used transformation for abundance data that is similar in effect to the log transform but that works on zeros. All proportional explanatory variables were arcsine-transformed before the analysis.

The role of climate vs. nonclimate variables was evaluated using regression on principal components. Specifically, a principal component analysis (PCA) was calculated on all 24 climate variables and the scores of each site on the first two axes were retained. Similarly, a PCA was performed on all 36 nonclimate variables and the scores of each site on the first two axes were retained. A Borcard partition (partial regression analysis) was performed to evaluate the proportion of variance explained by the scores on first two principal components solely for climate, solely for nonclimate, and jointly for climate and nonclimate.

To compare multivariate species–climate envelope models with univariate models, we (1) performed a multivariate linear regression with all 24 climate variables, (2) used two common multivariate selection models (stepwise regression and regression trees) to identify how many variables would be chosen and the predictive power (r^2) of these sets of variables, and (3) examined the predictive power of each climate and nonclimate variable as a univariate predictor of beaver density. The top 10 univariate climate variables with the highest r^2 -values were selected to model their relationship with beaver density. The nontransformed data strongly suggested an envelope relationship rather than a simple curvilinear relationship so quantile regression was used (Cade & Noon, 2003). We examined the 10th, 50th, and 90th quantiles using linear, quadratic, and normal (Gaussian) curves,

Linear	Density = $a + b \times (z)$
Quadratic	Density = $a + b(z) + c \times (z)^2$
Normal	Density = $c \times e^{-(z-b)^2/a^2}$

where z is the best predictor, and a , b , and c are free parameters estimated using the interior point algorithm (Koenker & Park, 1996) adapted for MATLAB version 7.3 (Mathworks, Natick, MA, USA) by David Hunter (<http://www.stat.psu.edu/~dhunter/code/qmatlab/>). We compared distribution models using a quantile regression analog to the OLS coefficient of determination derived by Koenker & Machado (1999) that provides pseudo- r^2 for any quantile (traditional r^2 can be used on the 50th percentile, but not on other percentiles).

Climate sensitivity, climate change, and beaver density change

The top three univariate climate models for the 10th, 50th, and 90th percentiles were selected and used to

predict present and future beaver densities across Québec. Gridded climate data from 1961 to 1990 and scenarios from 2040 to 2069 were used, respectively, for present and future periods (Bootsma & McKenney, 2005). These present and future climate data included monthly maximum and minimum air temperature, average annual air temperature, precipitation, growing degree-days, and potential evapotranspiration (PET). The climate model and emission scenario (CGCM1 GA1) used to predict future climate were described by

Flato *et al.* (2000) and Boer *et al.* (2000a, b). To evaluate the generality of this model and scenario combination, we compared it with four other combinations involving two additional models with two emission scenarios each (CGCM2 A2, B2, Flato & Boer, 2001; HADCM3 A2, B2, Gordon *et al.*, 2000; Pope *et al.*, 2000). Climate sensitivity is expressed as the change in beaver density resulting from a 10% change in a given climate variable, calculated with parameters from the best-fit climate-density model. Similarly, beaver density change was

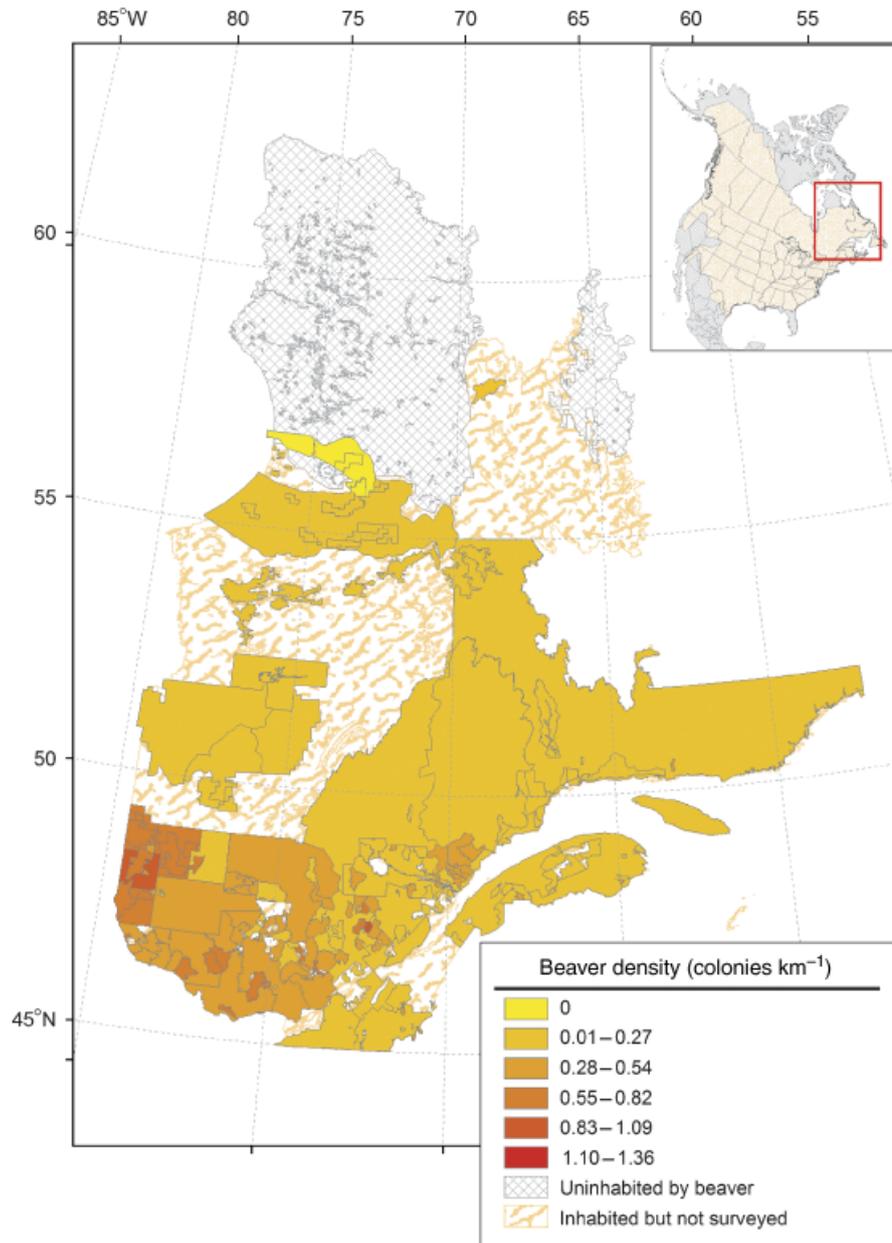


Fig. 1 Local abundance of North American beaver (*Castor canadensis*) across the province of Québec. Densities were derived from 161 helicopter surveys conducted between 1976 and 2004. The average number of active beaver colonies per km² for each survey area was calculated by locating active colonies along watercourses and dividing this number by the total area. Inset: the approximate North American range of *C. canadensis*.

calculated by comparing beaver densities predicted by best-fit models applied to current climate normals and GCM-predicted climate futures.

Results

The highest beaver densities in Québec are found in the southwest; in other southern portions of the province, beaver densities are variable, but generally declining from west to east (Fig. 1). Moving northwards, beaver densities decline sharply around 49°N and then form a long tail of low densities spanning more than 9° of latitude (Fig. 2a).

Partial regressions on two principal component axes (scaled PCA) derived from all climate and nonclimate variables revealed that climate variables alone explained 17.4% of the variation in beaver density, nonclimate variables alone explained 1.5%, and climate and nonclimate variables jointly explained 33.3% (leaving 47.7% unexplained). In other words, climate variables explained 97.1% of the variation that could be explained by a combination of climate and nonclimate variables (Fig. 3).

Both stepwise multivariate linear regression and regression trees selected a model with only two of the possible 24 climate variables (T_{avgann} and T_{maxmam} for stepwise, PET and T_{mindjf} for regression tree). The multivariate regression on all 24 climate variables had an r^2 of 0.67, the chosen stepwise model (with two climate variables) had an r^2 of 0.57, and the regression against the top two climatic PCA axes had an r^2 of 0.51. The selection of only two variables using both model selection techniques is presumably due to the high collinearity of climate variables (the first principal component accounted for 80% of all variation in the 24 climate variables and the first two principal components accounted for 92% of all variation).

Exploring univariate predictive power of climate and nonclimate variables, the majority of variation in square-root transformed beaver density across Québec can be accounted for by several univariate relationships (Table 2). The top univariate climate predictors include agroclimatic indices [e.g., PET and growing degree days (GDD)] and temperature variables (e.g., maximum, minimum, and average seasonal air temperatures) (Table 2). The top nonclimate predictors include

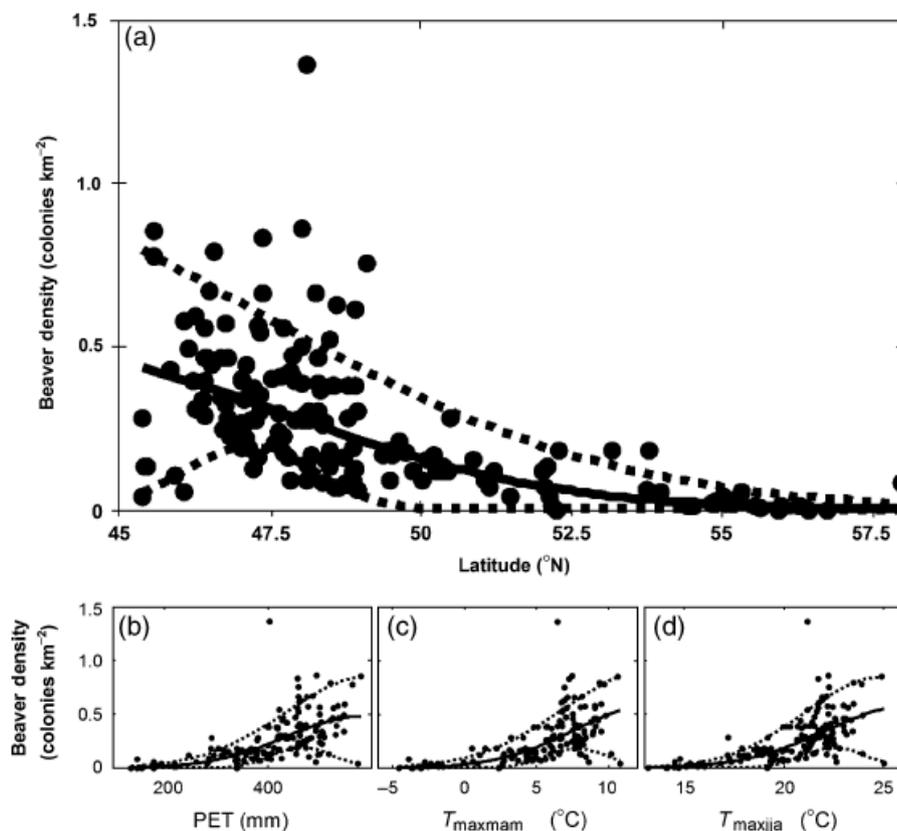


Fig. 2 Variation in local beaver density across Québec as a function of (a) latitude and the top-three univariate climate predictors, including (b) potential evapotranspiration (PET), (c) average maximum March–April–May temperature (T_{maxmam}), and (d) average maximum June–July–August temperature (T_{maxjja}). Lines represent the normal equations that best describes the 10th (dashed line), 50th (solid line), and 90th (dashed lines) percentiles of beaver density.

latitude, black bear density, and deciduous and shrub land covers (Table 2).

Using the top 10 climate variables to predict the 10th, 50th, and 90th percentiles of untransformed beaver densities, a normal model provided a better fit (based on pseudo- r^2 values appropriate for quantile regression) than a linear or quadratic model in 27 of 30 instances (Table 3). The fit of the quadratic model was frequently only marginally weaker than the normal model, but when this was the case, the quadratic curve was invariably concave (i.e., c was always positive), meaning that, similar to the normal model, the slope of the relationship between climate and abundance accelerated from low to high beaver density (i.e., from the edge to the interior of the range).

Overall, the best three predictors of the 10th, 50th, and 90th percentiles collectively and the 50th percentile in particular, are PET, average maximum March–April–May temperature ($T_{\max\text{mam}}$), and average maximum June–July–August temperature ($T_{\max\text{jja}}$) (Table 3). Each of these three climate variables assumes a normal relationship with percentiles of beaver density, with the slope of the curve peaking at intermediate climate values corresponding to the approximate midpoint of beaver's distribution in Québec, then flattening to vary-

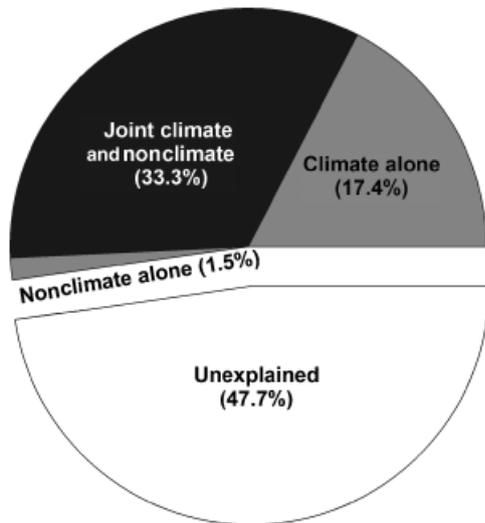


Fig. 3 Partial regression analysis estimating the variation in beaver density explained by climate and nonclimate variables. PCA was calculated on all 24 climate variables and the scores of each site on the first two axes were retained. Similarly, a principal component analysis (PCA) was performed on all 36 nonclimate variables and the scores of each site on the first two axes were retained. Each group uniquely accounts for only a small amount of variation in beaver density, whereas a much larger proportion is explained jointly by climate and nonclimate variables. Thus, a model including climate variables alone can account for >95% of the total variation explained by climate and nonclimate variables in combination.

ing extents at warmer climate values corresponding with southern Québec (Figs 2b–d).

For the top three climate variables, beaver climate sensitivity (predicted change in density per unit change in climate) is highest in the southern half of Québec and declines northward as the present day range limit is approached (Fig. 4 1a–c). GCM-projected change between now and 2055 in these climate variables peaks at high latitudes and generally diminishes southward (Fig. 4 2a–c). These climate projections differ marginally from other GCM and emission scenarios on a regional basis, but, in general, tend to be intermediate or conservative relative to other model and scenario combinations (Fig. 5). Combining projected climate change and beaver climate sensitivity, the largest absolute changes in density (future density–present density) are consistently predicted to occur in the southern half of Québec (Fig. 4 3a–c). Considering the present northern range limit of beaver distribution in Québec (Fig. 4 1a–c), relatively small and spatially restricted range expansion is predicted to occur (Fig. 4 3a–c). Thus, beavers are presently restricted to regions in Québec with average annual temperature above -5.1°C , maximum summer temperature above 15.2°C , maximum spring temperature above -1.4°C , and PET above 200 mm. By 2055, these conditions are expected to expand northwards and be associated with a northern range expansion of <100 km in most regions of northern Québec (Fig. 4 3a–c), with the exception of the westcentral portion of the range limit where a ~ 200 km expansion is predicted.

Discussion

Beaver density across Québec follows a roughly logistic envelope pattern, with high but variable density across the southern portion of the province, a sharp decline in density at about 49°N , and a long tail of low density extending as far as 58°N . Although several climate and nonclimate variables were strong univariate predictors of variation in beaver abundance, 97% of the variation explained by nonclimate variables could be accounted for by climate variables. Furthermore, four PCA axes that included all climate and nonclimate variables (two axes derived from 24 climate variables and two derived from 36 nonclimate variables) explained less variation in beaver density ($r^2 = 0.51$) than the three top climate univariate models, each based on a single climate variable ($r^2 = 0.55$ – 0.56). Although stepwise regression and regression tree procedures both selected multivariate models over univariate models, in both cases the selected models contained only two climate variables, had only marginally higher explanatory power than the top univariate models ($r^2 = 0.57$ vs. 0.55 – 0.56 for top univariate climate models despite the positive r^2 -bias

Table 2 Results from univariate regression of square-root transformed beaver density as a linear function of climate and nonclimate variables

Climate			Nonclimate				
Variable	Sign	R^2	P	Variable	Sign	R^2	P
PET	+	0.562	0.000	Latitude	-	0.495	0.000
$T_{\max\text{mam}}$	+	0.559	0.000	Beardensity	+	0.399	0.000
$T_{\max\text{jja}}$	+	0.546	0.000	CdecidB	+	0.375	0.000
T_{avgjja}	+	0.503	0.000	CshrubsB	-	0.359	0.000
GDD	+	0.502	0.000	CmixedB	+	0.352	0.000
$T_{\max\text{son}}$	+	0.489	0.000	CconiferB	-	0.309	0.000
T_{avgmam}	+	0.486	0.000	CmossrockB	-	0.251	0.000
T_{avgann}	+	0.466	0.000	Limitedroads	+	0.239	0.000
T_{iso}	+	0.448	0.000	Beaverharvest	+	0.199	0.000
T_{minmam}	+	0.432	0.000	Roads	+	0.166	0.000
T_{minjja}	+	0.431	0.000	Longitude	-	0.063	0.001
T_{maxdjf}	+	0.426	0.000	Riverbuffer	+	0.055	0.003
T_{avgson}	+	0.421	0.000	Lakebuffer	-	0.049	0.005
T_{minson}	+	0.360	0.000	Lakeshoreline	-	0.048	0.005
P_{seas}	-	0.315	0.000	Rivershoreline	+	0.032	0.023
T_{avgdjf}	+	0.303	0.000	Wolfdensity	+	0.027	0.039
T_{mindjf}	+	0.262	0.000	CrockB	-	0.021	0.069
P_{avgmam}	+	0.220	0.000	Largelakes	-	0.013	0.153
T_{seas}	-	0.158	0.000	Slope $\leq 2^\circ$	-	0.011	0.176
P_{avgann}	+	0.146	0.000	Slope $> 30^\circ$	-	0.011	0.178
P_{avgdjf}	+	0.141	0.000	Slope $\leq 30^\circ$	+	0.011	0.179
P_{avgjja}	+	0.121	0.000	Smalllakes	-	0.010	0.214
P_{avgson}	+	0.021	0.069	Shardrock	-	0.007	0.296
				Slope $\leq 30^\circ\text{B}$	+	0.007	0.307
				Slope $> 30^\circ\text{B}$	-	0.007	0.307
				Ssoftrock	-	0.006	0.329
				Wetlandbuffer	+	0.006	0.337
				Wetlandshoreline	+	0.006	0.347
				Sgranite	+	0.004	0.400
				Smineral	-	0.004	0.451
				Slope $\leq 2^\circ\text{B}$	-	0.002	0.598
				Slimestone	+	0.001	0.642
				Slope $\leq 10^\circ\text{B}$	+	0.001	0.732
				Slope $\leq 10^\circ$	-	0.001	0.752
				Sorganic	-	0.001	0.765
				CbuiltupB	-	0.000	0.811
				CurbanB	+	0.000	0.825
				CagricB	+	0.000	0.916

inherent in stepwise and regression tree procedures; Freedman, 1983), and included climate variables that were highly ranked as univariate predictors. Accordingly, we used univariate climate models because of their high predictive power in this application (in both absolute terms and relative to the alternatives), their parsimony, their ability to inform about potential mechanisms, and their compatibility with quantile regression.

Univariate climate–abundance relationships formed a logistic envelope pattern, with a long tail of low beaver density at low climate values, ramping up to high but

Table 3 Quantile regression pseudo- r^2 -values explaining the variation in the 10th, 50th, and 90th percentile of beaver densities using the top 10 univariate climate predictors and three different models (linear, quadratic, and normal)

Climate variable	Linear (%)			Quadratic (%)			Normal (%)		
	10	50	90	10	50	90	10	50	90
PET	0.207	0.323	0.285	0.208	0.366	0.328	<i>0.239</i>	<i>0.366</i>	<i>0.340</i>
$T_{\max\text{mam}}$	0.205	0.297	0.262	0.208	0.356	0.328	<i>0.254</i>	<i>0.360</i>	<i>0.334</i>
$T_{\max\text{jja}}$	0.192	0.306	0.286	0.195	0.346	0.337	<i>0.247</i>	<i>0.346</i>	<i>0.357</i>
T_{avgjja}	0.187	0.258	0.214	0.189	0.306	0.239	<i>0.220</i>	<i>0.309</i>	<i>0.239</i>
GDD	0.177	0.314	0.294	0.192	0.336	0.295	<i>0.241</i>	<i>0.346</i>	<i>0.314</i>
$T_{\max\text{son}}$	0.171	0.294	0.278	0.186	0.311	0.279	<i>0.217</i>	<i>0.315</i>	<i>0.295</i>
T_{avgmam}	0.191	0.249	0.193	0.194	0.281	0.205	<i>0.207</i>	<i>0.285</i>	<i>0.207</i>
T_{avgann}	0.173	0.263	0.237	0.189	0.283	0.243	<i>0.212</i>	<i>0.290</i>	<i>0.241</i>
T_{iso}	0.231	0.244	0.170	0.238	0.245	0.183	<i>0.273</i>	<i>0.299</i>	<i>0.280</i>
T_{minmam}	0.172	0.233	0.207	0.188	0.243	0.211	<i>0.219</i>	<i>0.252</i>	<i>0.203</i>

Values in italics indicate the highest pseudo- r^2 , with the normal model performing best in 27 of 30 cases (90%). Note that the quantile-adapted pseudo- r^2 presented here is not comparable with the traditional r^2 presented in Table 2; both are valid for comparisons of relative explanatory power within but not across tables.

PET, potential evapotranspiration; GDD, growing degree days.

variable densities at high climate values. Thus, relatively warm climates appear necessary, but not sufficient for beavers to attain high densities in Québec. Presumably, beavers often occur at low densities in warm regions because not all localities within these regions provide the types of habitats, watercourses, and topography that beavers also require. On the other hand, beaver can clearly survive and reproduce in the extreme climatic and habitat conditions that prevail in far northern Québec (where average annual temperature is -5°C , lakes are free of ice for only 4 months per year, and the only trees present are riparian shrubs; Lenormand *et al.*, 2002), but appear to be unable to attain high densities in these regions.

Relatively few studies have examined correlations between climate and abundance across species' ranges because typically only presence/absence data are available (Scott *et al.*, 1993; Guisan & Zimmerman, 2000; but see Lichstein *et al.*, 2002). However, the range limits of many plants and animals appear to coincide with climatic isotherms (Root, 1988) and climatic predictors of range limits often outperform nonclimate predictors (Thuiller *et al.*, 2004), regardless of the trophic level under consideration (Huntley *et al.*, 2004). We selected climate variables for modeling purposes because they were slightly better predictors of beaver density and are more commonly and consistently projected in climate change scenarios than nonclimate variables. However, we could have explained nearly as much variation in

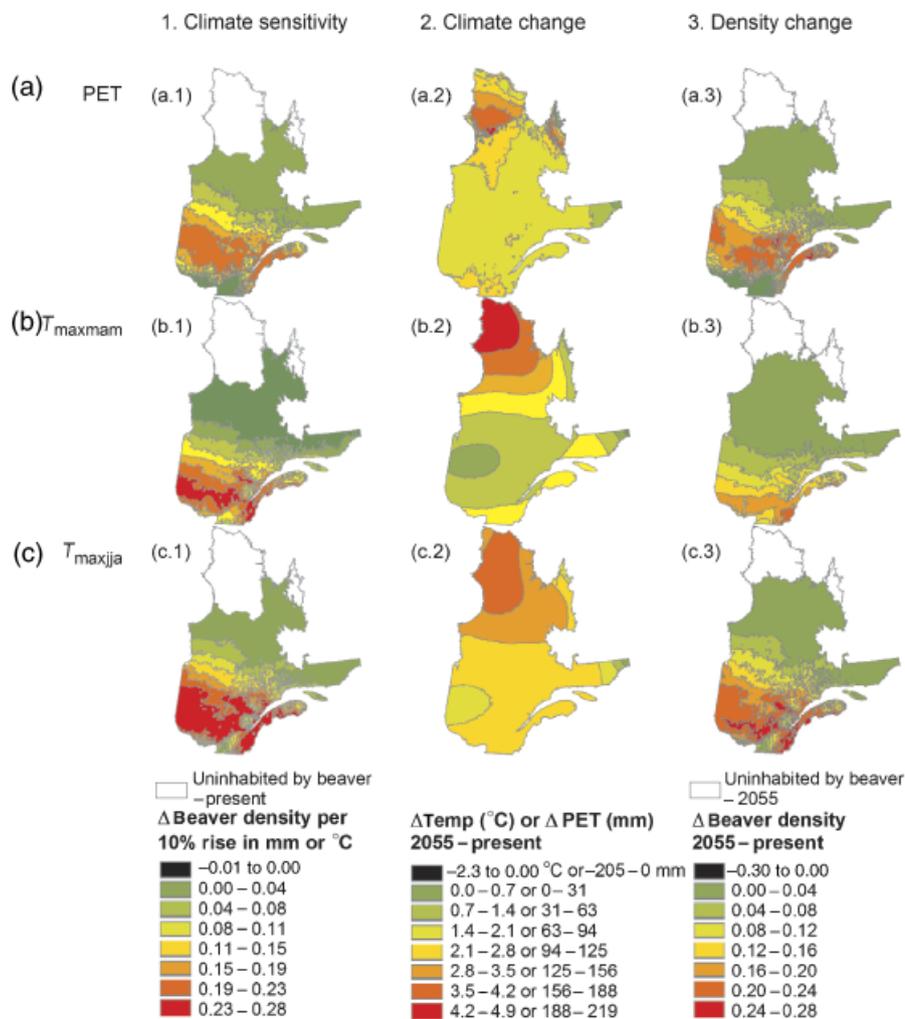


Fig. 4 Predicted changes in (1) beaver density (colonies km^{-2}) with a 10% increase in climate variables (climate sensitivity), (2) climate from present to the year 2055 (climate change) based on the CGCM1 GA1 model, and (3) beaver density change across Québec from present to the year 2055 (density change) based on three climatic variables with best-fit models: (a) potential evapotranspiration (PET), (b) average maximum March–April–May temperature (T_{\maxmam}), and (c) average maximum June–July–August temperature (T_{\maxjja}). White areas indicate regions not inhabited by beavers at present (column 1; climate sensitivity) and in the future (column 3; density change). Projection of future range limits is based on matching the current isotherm delineating the northern most location of beaver at present, then using the GCM projection of the location of this isotherm in 2055 [(a.3) $\text{PET} = 200 \text{ mm}$, (b.3) $T_{\maxmam} = -1.4 \text{ °C}$, (c.3) $T_{\maxjja} = 15.2 \text{ °C}$].

beaver density with several land cover variables and, based on results from our partial regression analysis, the variation explained would have overlapped extensively with that explained by climate variables. In other words, the independent effect of climate on beaver density (i.e., variation in climate not correlated with variation in nonclimate variables) was relatively weak. These results emphasize that (1) climate variables can serve as an effective proxy for the suite of climatic and nonclimatic factors that determine animal abundance and distribution but (2) the validity of using climate proxies to project animal responses to climate change hinges critically on the persistence of current correla-

tions between climate, habitat, and other environmental features (Pearson & Dawson, 2003; Lawler *et al.*, 2006).

We found general support for our hypothesis that the climate sensitivity of beaver abundance (change in abundance per unit change in climate) peaked in the interior of the range. The high variability of beaver densities in southern Québec, combined with our lack of data from jurisdictions south of Québec, prevented us from clearly differentiating the fit of normal models (with accelerating then decelerating slope from the edge to the interior) from quadratic models (with continuously accelerating slope from the edge to the interior; Table 3). However, this distinction is less important to

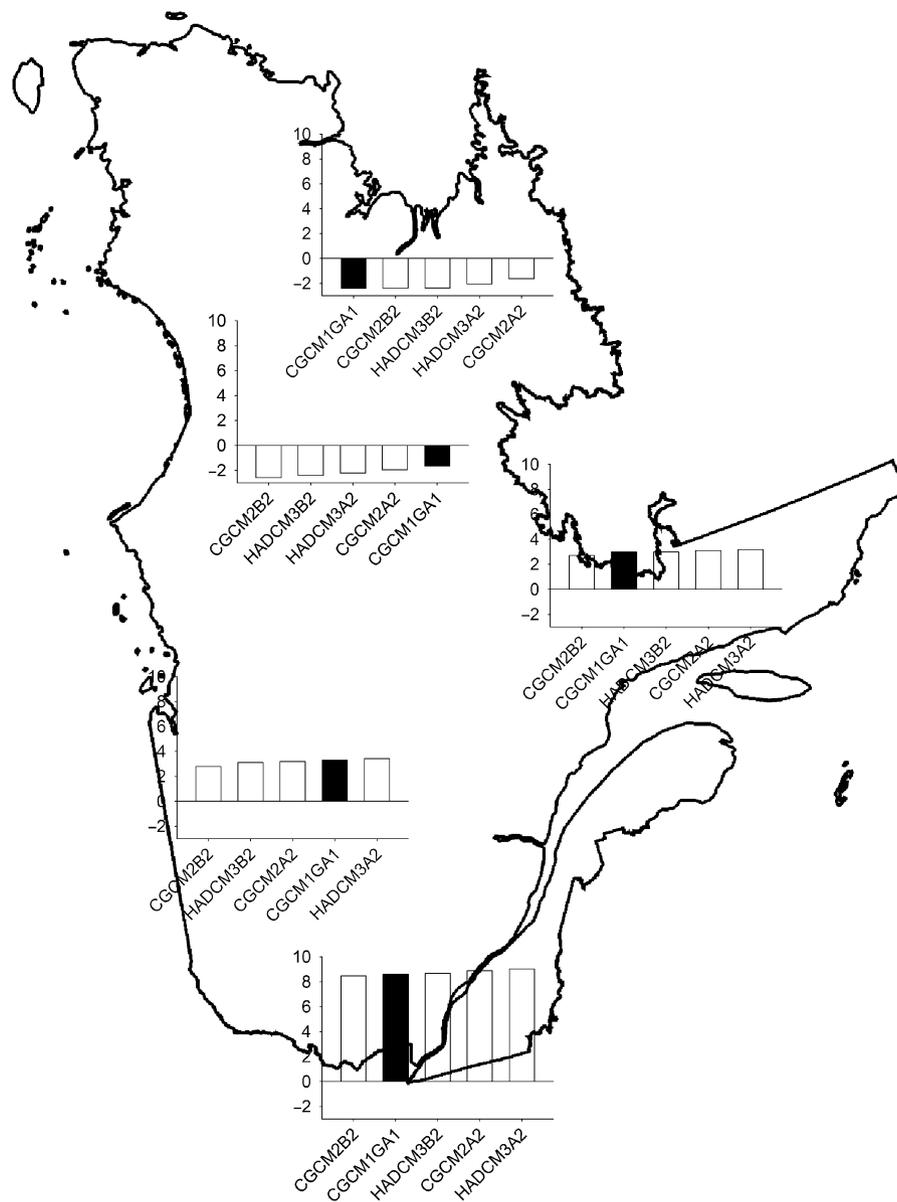


Fig. 5 Climate model and emissions scenario comparison for projected 2055 average annual temperature (T_{avgann} ; °C) for different regions of Québec. The climate model and emission scenario combination used in this study (black bar; CGCM1 GA1) generated similar predictions as two other models each with two different emission scenarios (white bars; CGCM2 A2, B2 and HADCM3 A2, B2). Results are similar if other climate variables are used as the basis of comparison (e.g., T_{maxmam} , T_{maxjja} ; not shown here), except CGCM1 GA1 projections of T_{maxjja} increases are consistently conservative across Québec relative to the other climate model and emission scenario combinations.

the general conclusion of the study than the agreement of both models that climate sensitivity is low at the northern edge of the range and accelerates towards the range interior.

Combining our best climate envelope models of beaver density with current GCM projections of future climate change, beavers are predicted to be characterized by only modest range expansion, but substantial

increases in density within the interior of their range. We acknowledge the numerous limitations in using a correlative climate envelope approach, including the fact that we fail to directly account for biotic interactions, evolutionary change, or dispersal (Pearson & Dawson, 2003), and that the present relationships among abundance, distribution, and climate may not remain the same in the future (Lawler *et al.*, 2006).

Consequently, in using this approach, we assume that the relationships among climate, beaver abundance, and beaver distribution reflect some direct or indirect form of causality, that this causality will remain the same in the face of climate change, and that beaver responses and climate change will occur at a similar pace. Based on beaver's well-studied ecology (Slough & Sadleir, 1977; Allen, 1983; Howard & Larson, 1985; Novak, 1987), we expect that this will be the case only if there is a concomitant increase in abundance and/or productivity of their primary food sources (deciduous shrubs and trees) adjacent to waterways, and if other forms of environmental and anthropogenic changes (e.g., fire frequency, conversion of forests into agricultural and developed lands, trapping intensity) do not override the effects of climate change in this region. The pattern of dispersal and settlement of the reintroduced European beavers (*Castor fiber*) in Scandinavia provides a useful precedent for predicting how beavers colonize new habitats and alter their abundance in currently occupied habitats. This example indicates an important role of long distance dispersal within watersheds, followed by back-filling of suitable habitats between the dispersal front and the established population core (Hartman, 1995), as well as persistent influences of initial territory establishment on long-term patterns of beaver distribution and abundance (Campbell *et al.*, 2005). The present pattern of North American beaver abundance across Quebec, as reflected in our dataset, will also be strongly influenced by historical recolonization events, following repeated large-scale overharvest, population depletion/extirpation episodes that have occurred in northeastern North America as recently as the 1930s (Müller-Schwarze & Sun, 2003). Thus, although patterns of individual movement and territory settlement may account for some of the unexplained variation in large-scale patterns of beaver abundance, they do not appear to preclude the emergence and persistence of strong climate–abundance associations.

Conclusions

Our central conclusion is that there is much to be gained by incorporating information about how abundance varies across species ranges when using spatial climate variability as a basis for predicting the impacts of climate change. Species–climate envelope models relying on presence/absence data can predict expected range shifts in the face of climate change, but cannot predict where the largest changes in abundance will occur. The associated emphasis on monitoring range boundaries to detect expansions or contractions has led to the discovery of sensitive bioindicators of the impacts of climate change and has improved our understanding

of the ecological niche, threshold responses to environmental change, the nature of adaptation, speciation and co-evolution, species interactions, and invasion dynamics (Parmesan & Yohe, 2003; Holt & Keitt, 2005; Perry *et al.*, 2005; Wilson *et al.*, 2005). However, the current importance placed on monitoring range edges may cause the largest impacts of climate change to go undetected if tails of low abundance near species' range limits combined with linear variation in climate render relationships between climate and abundance weakest at the periphery of the range. Because changes in relative abundance are less frequently monitored by researchers and less easily perceived by the general public than changes in species presence or absence, some of the most dramatic responses to climate change in the interior of species range are likely being overlooked.

Achieving good measures of relative abundance across adequate spatial scales is difficult, in particular for species that are widely distributed, highly mobile, and difficult to observe directly. Population ecologists have overcome these difficulties to generate excellent abundance estimates for many populations, but due to research priorities and constraints, have tended to conduct these estimates year after year in one or very few localities. To adequately answer the questions posed by climate change, we need to add a spatial component to population–climate research that encompasses the range of climate variability projected by GCMs. Given the current paucity of data on how the abundance of most species varies with spatial climate variability, progress in this important area of research requires capitalizing on currently available coarse indices of abundance, as well as generation of new and better data on variation in abundance across the range.

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