Interacting Effects of Climate Change, Landscape Conversion, and Harvest on Carnivore Populations at the Range Margin: Marten and Lynx in the Northern Appalachians

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Abstract: *Assessing the effects of climate change on threatened species requires moving beyond simple bioclimatic models to models that incorporate interactions among climatic trends, landscape change, environmental stochasticity, and species life history. Populations of marten (*Martes americana*) and lynx (*Lynx canadensis*) in southeastern Canada and the northeastern United States represent peninsular extensions of boreal ranges and illustrate the potential impact of these threats on semi-isolated populations at the range margin. Decreased snowfall may affect marten and lynx through decreased prey vulnerability and decreased competitive advantage over sympatric carnivores. I used a spatially explicit population model to assess potential effects of predicted changes in snowfall by 2055 on regional marten and lynx populations. The models' habitat rankings were derived from previous static models that correlated regional distribution with snowfall and vegetation data. Trapping scenarios were parameterized as a 10% proportional decrease in survival, and logging scenarios were parameterized as a 10% decrease in the extent of older coniferous or mixed forest. Both species showed stronger declines in the simulations due to climate change than to overexploitation or logging. Marten populations declined 40% because of climate change, 16% because of logging, and 30% because of trapping. Lynx populations declined 59% because of climate change, 36% because of trapping, and 20% in scenarios evaluating the effects of population cycles. Climate change interacted with logging in its effects on the marten and with trapping in its effects on the lynx, increasing overall vulnerability. For both species larger lowland populations were vulnerable to climate change, which suggests that contraction may occur in the core of their current regional range as well as among smaller peripheral populations. Despite their greater data requirements compared with bioclimatic models, mesoscale spatial viability models are important tools for generating more biologically realistic hypotheses regarding biotic response to climate change.*

Keywords: connectivity, conservation planning, focal species, *Lynx canadensis*, *Martes americana*, population viability analysis, resource selection function, spatially explicit population model

Interacción de los Efectos del Cambio Climático, Conversión del Paisaje y Cosecha de Poblaciones de Carnívoros en el Margen de su Distribución: Marta y Lince en el Norte de las Apalaches

Resumen: *La evaluación de los efectos del cambio climático en especies amenazadas requiere ir más allá de los modelos bioclimáticos simples para usar modelos que incorporan las interacciones entre tendencias climáticas, cambios en el paisaje, estocasticidad ambiental e historia de vida de las especies. Las poblaciones de marta (*Martes americana*) y lince (*Lynx canadensis*) en el sureste de Canadá y noreste de Estados Unidos representan extensiones peninsulares de su distribución boreal e ilustran el impacto potencial de estas amenazas sobre poblaciones semi aisladas en el margen de su distribución. La disminución de nevadas puede afectar a martas y linces por medio de la disminución de la vulnerabilidad de presas y de la ventaja competitiva sobre carnívoros simpátricos. Utilicé un modelo poblacional espacialmente explícito para evaluar los efectos*

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potenciales de los cambios previstos en la caída de nieve a 2055 sobre poblaciones regionales de marta y lince. Las clasificaciones de hábitat del modelo fueron derivadas de modelos estáticos previos que correlacionaban la distribución regional con datos de la caída de nieve y la vegetación. Los escenarios con cacería fueron incluidos como una disminución proporcional de 10% en la supervivencia, y los escenarios con tala de árboles fueron incluidos como una disminución de 10% en la extensión de bosques de coníferas maduros o mixtos. Ambas especies mostraron declinaciones más fuertes en las simulaciones debido a cambio climático que por la sobreexplotación o el desmonte. Las poblaciones de marta disminuyeron 40% debido al cambio climático, 16% debido al desmonte y 30% debido a la cacería. Las poblaciones de lince disminuyeron 59% debido al cambio climático, 36% debido a la cacería y 20% en escenarios que evaluaron los efectos de los ciclos poblacionales. El cambio climático interactuó con la tala en sus efectos sobre la marta y con la cacería en sus efectos sobre el lince, lo que incrementó la vulnerabilidad en general. En ambas especies, las poblaciones en tierras bajas fueron vulnerables al cambio climático, lo que sugiere que la contracción puede ocurrir en el centro de su distribución regional actual y en poblaciones periféricas más pequeñas. No obstante el mayor requerimiento de datos en comparación con modelos bioclimáticos, los modelos de viabilidad a mesoescala espacial son herramientas importantes para la generación de hipótesis más realistas biológicamente en relación con la respuesta biótica al cambio climático.

Palabras Clave: análisis de viabilidad poblacional, conectividad, especies fócales, función de selección de recursos, *Lynx canadensis*, *Martes americana*, modelo poblacional espacialmente explícito, planificación de la conservación

Introduction

Among the factors driving the current wave of anthropogenic extinctions, the impact of climate change is increasingly being recognized as comparable to that of habitat loss, overexploitation, and invasive species (Sala et al. 2000). Nevertheless, the effects of climate change on biodiversity have primarily been assessed for large assemblages of species with simple bioclimatic or "climatic envelope" models that predict changes in a species range without considering the dynamics of individuals and populations and with simple rules governing dispersal (Peterson et al. 2004; Thomas et al. 2004). Models with finer spatial scale and increased biological realism are needed to explore the interacting effects of climatic trends, landscape change, and life-history patterns on species distribution and viability (Pearson & Dawson 2003). Intensive field studies documenting demographic response to climatic variations, although valuable, generally occur at a spatial scale that is too limited to provide insights into the regional-scale metapopulation dynamics relevant to conservation planning. Although regional-scale models combining climate and habitat data have been developed (e.g., Pearson et al. 2004), they have not yet been incorporated into biologically realistic dispersal and viability models. I combined an individual-based spatially explicit population model (SEPM; Dunning et al. 1995) with regional-scale habitat data to assess how climate change might interact with habitat loss and overexploitation to affect the distribution and viability of two mammalian carnivores, the marten (*Martes americana*) and the lynx (*Lynx canadensis*), in the northern Appalachians region of the northeastern United States and southeastern Canada.

Marten and lynx occur in the northern Appalachians as semidisjunct populations separated from larger northerly populations by the St. Lawrence river and adjacent agricultural lands. Both species are considered threatened in portions of the region but differ in their basic habitat requirements and the factors responsible for their decline (Ray 2000). The region has been identified as a global hotspot of latent extinction risk because of the presence of many species, such as marten and lynx, that are expected to be vulnerable to landscape change due to the large area requirements for viable populations (Cardillo et al. 2006). Lynx are relatively abundant and commercially trapped in the Gaspé region of Québec but are threatened or extirpated elsewhere in the northern Appalachians region. Marten are more abundant and widespread but less is known about their relative abundance across the region than for the lynx (Ray 2000).

Lynx distribution is correlated with snowfall on a regional scale (Hoving et al. 2005), and marten distribution in Maine is correlated with both snowfall and the distribution of a potential competitor, the fisher (*Martes pennanti*) (Krohn et al. 1995). Snow causes marten and lynx, with their small ratio of body mass to foot area, to gain a competitive advantage over sympatric carnivores and may also affect prey abundance and vulnerability (Krohn et al. 1995; Mowat et al. 2000). Marten also show an association with older forest (Powell et al. 2003). This may be due to lower predation risk in forest with high canopy closure or the use for denning or foraging of the subnivean openings associated with coarse woody debris (Powell et al. 2003). Marten distribution and demographic rates are affected by the loss of closed-canopy forest due to logging (Bissonette et al. 1997; Chapin et al. 1998; Payer & Harrison 2003). Because larger native carnivores such as the gray wolf (*Canis lupus*) have been extirpated from the northern Appalachians region, mesocarnivores such as the lynx and marten are often proposed as flagship species whose conservation can catalyze awareness of regional environmental issues or as focal species whose status may be suggestive of broader biotic trends (Lambeck 1997).

My goals were first to evaluate the potential of SEPM as mesoscale tools for assessing the effects of climate change. A case study of small and semi-isolated populations at the range margin may highlight contrasts between predictions of mechanistic models such as SEPM and simpler bioclimatic models. An additional goal was to compare patterns of threat for the two carnivore species to help design more effective multispecies conservation strategies and promote coordinated planning across jurisdictions.

Methods

The study area encompassed the northern Appalachians/Acadia ecoregion, which consists of Maine, New Hampshire, Vermont, northern New York state, Nova Scotia, New Brunswick, and southern Québec. I incorporated previously developed habitat models (Carroll 2005; Hoving et al. 2005) into an SEPM to evaluate the contrasts between such static habitat models and a dynamic model incorporating varying assumptions as to population cycles and the effects of increased trapping mortality, logging, and climate change (Tables 1 & 2).

Because no systematic regional-scale survey data exist for these species, the static models were built with reported lynx locations (primarily from trapping reports) and marten harvest data (Carroll 2005; Hoving et al. 2005). Thus, the models were built on the assumption that species distribution or habitat quality is correlated with patterns evident in data on trapping harvest. Trapping data are more spatially extensive in this region than commonly used alternatives, such as museum records and incidental sightings, and are strongly correlated with such data at regional scales in other areas (Carroll et al. 2001). The regional-scale lynx distribution model took the form $\mathrm{logit}(p) = -12.78 + -0.052 \times \mathrm{DECID} + 0.0049 \times \mathrm{SNOW}$, where DECID is proportion of the landscape in deciduous forest and SNOW is annual snowfall (Hoving et al. 2005).

The marten model took the form marten harvest/100 km^2 $= 54.97756 + 0.495844 \times \mathrm{SNOW} + 7.351139 \times (\mathrm{CON} + \mathrm{MIX})$, where (CON + MIX) is percentage of older conifer and mixed forest ($n = 54$, $p < 0.001$, $R^2 = 0.44$ for the multivariate model) (Carroll 2005). In this model, SNOW incorporated a threshold such that the effect of the variable was constant above 3000 mm/year. Marten model selection was based on three criteria: (1) low AIC (Akaike 1973) among competing models when applied to the primary data set (the northern Appalachians excluding the Adirondacks), (2) generality, or consistently high predictive power when applied to validation data sets from other geographic areas (the Adirondacks and central Quebec), and (3) interpretability and consistency with habitat associations documented from intensive field studies (e.g., Chapin et al. 1998; Payer & Harrison 2003). The snowfall variable was present in the top candidate models and showed high generality between data sets. Nevertheless, other variables in the top models showed more variation among regions, due in part to high correlations among candidate variables. For example, a model containing snowfall and human impact variables (roads and population) showed lowest AIC for the primary data set but was not selected due to its poor generality and lack of support from previous field studies (Carroll 2005). The resolution of habitat data grids derived from the marten and lynx models was 1 km, but this was subject to limitations on the scale of the snowfall and vegetation data described below.

Table 1. Base parameters used in the PATCH model of marten and lynx population dynamics.

*Species and parameter**	*Value*	
Marten		
territory size (km^2)	4.0	
maximum dispersal distance (km)	40	
survival rates (maximum)	good year	poor year
young, year 1	0.87	0.32
subadult/adult >1 year	0.87	0.87
at senescence (>7 years)	0.40	0.40
fecundity rates (maximum)	good year	poor year
subadult – year 2	0	0
adult >2 years	3.3	0.93
at senescence (>7 years)	0.87	0.32
Lynx		
territory size (km^2)	90.0	
maximum dispersal distance (km)	268	
survival rates (maximum)		
young, year 1	0.77	
subadult – year 2	0.77	
adult – >2 years	0.99	
at senescence (>9 years)	0.44	
fecundity rates (maximum)		
subadult – year 2	2.4	
adult >3 years	2.9	
at senescence (>7 years)	2.2	

Cycle of demographic multipliers

	Year								
	1	2	3	4	5	6	7	8	9
fecundity	1.0	0.80	0.20	0.25	0.25	0.25	0.25	0.40	0.60
survival	1.0	0.89	0.67	0.56	0.56	0.56	0.56	0.67	0.89

**Fecundity is number of female offspring per adult female.*

To assess the potential effects of climate change on marten and lynx habitat suitability, I created versions of these models based on predicted annual snowfall for 2055. These predictions were derived from output of the Parallel Climate Model, a general circulation model (GCM) developed by a consortium of researchers in support of the Intergovernmental Panel on Climate Change

Table 2. Alternate scenarios used to parameterize marten survival and lynx fecundity and survival in the PATCH simulations of the two species' distribution and viability in the northern Appalachians region.

- Marten
  - trapping intensity and trapping extent
    - base scenario 1 (B1): survival set at base level except survival in parks 120% of base level (common to all scenarios)
    - base scenario 2 (B2): survival in trapped areas 90% of base level, survival in untrapped areas 100% of base level
    - base scenario 3 (B3), increase in area open to trapping: survival in trapped areas 90% of base level, survival in untrapped areas 90% of base level
    - base scenario 4 (B4), increase in trapping intensity in currently open areas: survival in trapped areas 80% of base level, survival in untrapped areas 100% of base level
  - extent of timber harvest
    - double the percentage of regenerating forest (up to a maximum of 100%), with corresponding decrease in the percentage of conifer/mixed forest
    - logging scenario 1 (L1): above combined with base scenario 1
    - logging scenario 2 (L2): above combined with base scenario 2
    - logging scenario 3 (L3): above combined with base scenario 3
    - logging scenario 4 (L4): above combined with base scenario 4
  - restoration
    - convert all regenerating forest to conifer/mixed forest
    - restoration scenario 1 (R1): above combined with base scenario 1
    - restoration scenario 2 (R2): above combined with base scenario 2
    - restoration scenario 3 (R3): above combined with base scenario 3
    - restoration scenario 4 (R4): above combined with base scenario 4
  - amount of annual snowfall (climate change)
    - annual snowfall as predicted for 2055, based on IPCC Scenario A2 (see text)
    - base scenario 2 with 2055 snowfall (FB2)
    - base scenario 4 with 2055 snowfall (FB4)
    - logging scenario 2 with 2055 snowfall (FL2)
    - restoration scenario 2 with 2055 snowfall (FR2)
- Lynx
  - degree and extent of population cycling
    - no cycling, fecundity and survival set at mean rates of cycle (A1)
    - cycling only in Gaspé, elsewhere fecundity and survival set at mean rates of cycle (B1)
    - cycling throughout region, using demographic multipliers as in Table 7 (C1)
  - trapping intensity
    - no cycling, survival in Gaspé population and central Québec set at 90% of base level (A2)
    - cycling only in Gaspé, survival in Gaspé population and central Québec set at 90% of base level (B2)
    - cycling throughout region, survival in Gaspé and central Québec population set at 90% of base level (C2)
  - territory size
    - no cycling, territory size set at 36 km^2 (A136)
    - no cycling, survival in Gaspé population and central Québec set at 90% of base level, territory size set at 36 km^2 (A236)
    - cycling only in Gaspé, territory size set at 36 km^2 (B136)
    - cycling throughout region, territory size set at 36 km^2 (C136)
  - amount of annual snowfall (climate change)
    - annual snowfall as predicted for 2055, based on IPCC Scenario A2 (see text)
    - scenario A1 (above) with 2055 snowfall (FA1)
    - scenario B1 (above) with 2055 snowfall (FB1)
    - scenario B2 (above) with 2055 snowfall (FB2)
    - scenario C1 (above) with 2055 snowfall (FC1)

(IPCC) (Kiehl & Gent 2004). The IPCC A2 climate-change scenario is in the intermediate-to-high range among the 35 scenarios evaluated by the IPCC in its assumptions regarding rate of growth in carbon emissions, with an approximate doubling of emissions between 2005 and 2055 (Peterson et al. 2004). Because GCM predictions are available only at coarse resolutions (here approximately 200 km), I interpolated the percent change in annual snowfall predicted by the GCM and then multiplied that prediction by the finer-scale data for current annual snowfall to produce a "sharpened" estimate of future snowfall patterns (Peterson et al. 2004). Current annual snowfall data incorporated a lake effect (Carroll 2005) and thus differed slightly from that used by Hoving et al. (2005).

Marten Dynamic Models

An SEPM, such as the PATCH model I used here (Schumaker 1998), assesses population viability in a landscape context by combining information on the spatial arrangement of habitat patches with data on a species demographic response to different types of habitat (Carroll et al. 2003). PATCH, a female-only model designed for studying territorial vertebrates, linked the survival and fecundity of individual animals to geographic information system (GIS) data on mortality risk and habitat productivity measured at the location of the individual or pack territory (Schumaker 1998). Territories were allocated by intersecting the GIS data with an array of hexagonal cells. The different habitat types in the GIS maps were assigned weights based on the relative levels of fecundity and survival expected in those habitat classes. Base survival and reproductive rates, derived from published field studies, were then supplied to the model as a population projection matrix (Table 1; Caswell 2001). The model scaled these base matrix values based on the mean of the habitat weights within each hexagon, with lower means translating into lower survival rates or reproductive output.

The simulations incorporated demographic stochasticity with a random number generator. In the marten simulations that incorporated environmental stochasticity, two matrices were available with similar survival rates but with either high or low fecundity to simulate variation in marten productivity with alternate-year mast cycles (Table 1). Adult organisms were classified as either territorial or floaters. The movement of territorial individuals was governed by a site-fidelity parameter, but floaters must always search for available breeding sites. Movement decisions used a directed random walk that combined varying proportions of randomness, correlation (tendency to continue in the direction of the last step), and attraction to higher quality habitat. Nevertheless, there was no knowledge of habitat quality beyond the immediately adjacent territories.

For a large carnivore such as the wolf, it is clear from field studies which regional-scale factors are linked to fecundity (prey density) and which are linked to survival (e.g., roads) (Carroll 2003). For mesocarnivores such as marten and lynx, it is more difficult to map, on a regional scale, proximal influences on fecundity and survival such as prey density and large woody structure (Powell et al. 2003). Instead I related species abundance to regional-scale habitat factors such as extent of older forest (Bissonette et al. 1997; Chapin et al. 1998; Payer & Harrison 2003) and then made more speculative links between these factors and the fecundity and survival maps (grids) that are necessary inputs to the PATCH model. Here I assumed that habitat factors such as snowfall and older conifer or mixed forest would influence both fecundity (through prey abundance and vulnerability) and survival (e.g., through refuge from predators and increased competitive ability vs. sympatric mesocarnivores) (Powell et al. 2003).

I determined demographic rates (Table 1) by evaluating the range and mean of rates reported in published field and modeling studies (Schneider & Yodzis 1994; Hodgman et al. 1997; Fryxell et al. 1999) and calibrating PATCH model parameters so that they matched rates documented for equivalent habitat categories in those studies. The fecundity and survival grids were then derived by dividing the mapped marten regression model output into 20 ranked classes of equal area. Both fecundity and survival grids varied between sets of scenarios that differed in their assumptions on extent of logging and climate change (Table 2). In addition, within each set of scenarios I varied the survival grid to explore the effects of alternate options for trapping management on marten viability. I created alternate survival grids by multiplying the initial grid by the factors specified in four alternate scenarios (Table 2). I combined the regression output with data on management class (e.g., trapped versus untrapped areas) to create the survival grid because, although actual marten survival is linked to both trapping intensity and habitat (e.g., extent of closed forest) (Chapin et al. 1998), the regression model was necessarily built only on data from trapped areas. Thus, the contrast in survival between trapped and untrapped areas must be added in the form of a conceptual model.

I created simplified landscape-change scenarios based on the assumption that timber harvest in the near future would occur in the same general areas (of 10 km^2 in size) that have supported recent logging (Table 2). Due to data confidentiality restrictions in Canada, the 10-km^2 scale was that of the hexagons over which vegetation data were summarized (Carroll 2005). In the logging scenarios, the percentage of regenerating forest was doubled within each hexagon (up to a maximum of 100%), with a corresponding decrease in the percentage of conifer or mixed forest. Development of a realistic forest-succession model was precluded by both the lack of high-resolution vegetation data and the broad geographic scale of the analysis. I also evaluated scenarios incorporating input layers based on future snowfall predictions to assess the effects of climate change alone and in interaction with other threat factors on marten viability (Table 2). One hundred simulations of 200 years each were performed for each scenario, with demographic statistics tallied from year 190. The habitat map remained constant throughout each 200-year simulation, rather than being dynamically updated at each time step. These simulation results were thus equilibrium predictions, which depict the capacity of an area to support a carnivore species over the long term (200 years).

Lynx Dynamic Models

Lynx population dynamics in boreal habitats have been linked to cyclic change in habitat quality as it relates to snowshoe hare (*Lepus americanus*) density (Mowat et al. 2000). The extent of cycling in northern Appalachian populations of lynx and hare is poorly known compared with the record from boreal habitats (Hodges et al. 2000). Lynx trapping data from southern Quebec suggest pronounced year-to-year variation in population size in this region (range of coefficient of variation of trapping harvest 1985–2003 for nine management units: 82.02–200.61%, mean 125.40%; Quebec Ministry of Wildlife and Parks, unpublished data). Population cycles and environmental stochasticity tend to disproportionately affect small and isolated subpopulations (Gilpin & Soulé 1986), conditions that characterize lynx at their range margin in the northern Appalachians.

The initial input grid was derived by dividing the static habitat model output into 20 equal-interval ranked classes. I incorporated several scenarios of population cycling into the lynx model by scaling the habitat-quality values derived from the static model to lynx demographic performance at different points in the population cycle (Table 1). I parameterized lynx demographic rates (Table 1) based on the rates reported in field studies (reviewed in Steury & Murray 2004). Scenarios were parameterized to evaluate the contrasts between three assumptions concerning the prevalence of cycling in the region's lynx populations: (1) no cycling, (2) cycling only in the Gaspé population (here termed "core-only cycling"), and (3) cycling throughout the region (Table 2).

Because the Gaspé lynx population is the largest in the region and the only population subject to trapping, variation in trapping pressure in Gaspé could potentially affect the viability of protected lynx populations in adjacent jurisdictions. Therefore, I also created scenarios that evaluated the effects of increased trapping (parameterized as a 10% proportional decrease in survival rate in Gaspé) and the interaction between trapping and population cycles (Table 2). I also evaluated scenarios incorporating input layers based on future snowfall predictions to assess the effects of climate change alone and in interaction with other threat factors on lynx viability (Table 2). The average size of lynx territories in this region is poorly known but may be smaller than those in boreal regions. The majority of the scenarios (Table 2) used a territory size (90 km^2) similar to that used in other regional lynx models (Hoving et al. 2004, 2005). Nevertheless, I repeated a subset of the scenarios with a smaller home range size (36 km^2) to evaluate sensitivity of results to this parameter. The regional-scale static lynx model of Hoving et al. (2005), in contrast with models at finer scales (e.g., Hoving et al. 2004), does not include variables representing forest age. Therefore, I did not evaluate scenarios assessing the effects of logging on lynx, which may be more appropriately evaluated at the subregional scale using more detailed vegetation data (e.g., Hoving et al. 2004).

Five hundred simulations of 200 years each were performed for each scenario, with demographic statistics tallied from year 190. Lynx simulations, unlike those for marten, set site fidelity at medium, such that each territory holder would search for a new territory when their existing territory became a sink (Schumaker 1998). This allowed lynx migration during unfavorable stages of the population cycle (Mowat et al. 2000).

Results

Marten

Results from base scenario 2 (Fig. 1a) approximated current marten distribution in both trapped and untrapped portions of the mainland of its range in the northern Appalachians; however, discrepancies between model predictions and current distribution were greater in isolated subpopulations. The results did not consistently rate areas with failed or difficult reintroductions (southern Vermont and Fundy Park [New Brunswick]) and highly imperiled

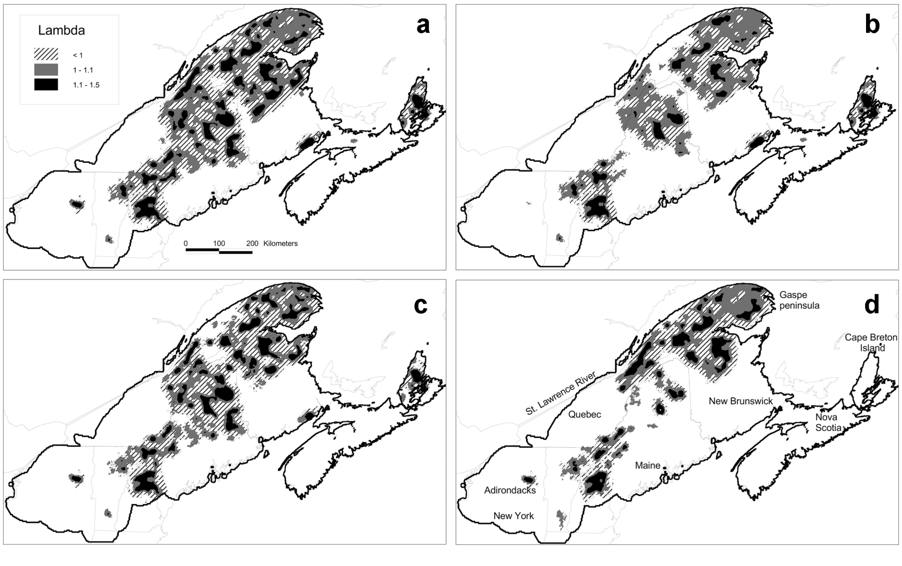

Figure 1. Demographic potential and distribution of martens in the northern Appalachians region under (a) current landscape conditions (scenario B2, Table 2), (b) increased trapping pressure (scenario B4), (c) increased timber harvest (scenario L2), and (d) decreased snowfall (scenario FB2). Population growth rate (lambda) predicted by the PATCH model simulations. Areas with < 50% probability of occupancy are white. Because the raw results would be difficult to distinguish on a regional-scale map, the demographic structure shown represents output of the PATCH model averaged over a 300-km^2 moving window.

populations (Cape Breton Island) as less suitable than areas with successful reintroductions (mainland Nova Scotia) or less-imperiled populations (Adirondacks). Under base scenario B2, strong source habitat was predicted in northern New Brunswick, northeastern Maine, New Hampshire's White Mountains, and portions of the central Gaspé peninsula. Simulations without environmental stochasticity showed higher population sizes, with the most dramatic change in peripheral populations. Percent increase due to removal of environmental stochasticity from scenario B2 was 10.9% in Maine, 5.0% in New Hampshire, 6.6% in southern Québec, 5.7% in New Brunswick, and 7.1% on Cape Breton Island. Smaller populations showed greater effects, with 16.0% in New York, 28.0% in Vermont, and 85.7% in mainland Nova Scotia.

The logging scenarios reduced the percentage of the region in older conifer-mixed forest from 47.6% to 43.0%. The restoration scenarios increased the percentage of the region in older conifer-mixed forest from 47.6% to 52.4%. This proportionally small change caused large changes in marten population size in some areas (Table 3). Contrasts in the sensitivity of marten population size by state or province to alternate trapping scenarios (B1 through B4) suggested that New York and Vermont populations are more influenced by contrasting trapping mortality scenarios than those in New Hampshire, Maine, and Maritime Canada (Table 3, Fig. 2). Among jurisdictions that are currently trapped, vulnerability to increased trapping intensity (population loss between B2 and B4) was greater in Maine (39.2%) and especially New York (76.1%) than in southern Québec (29.3%) or New Brunswick (32.9%) (Table 3). Among jurisdictions that are not currently trapped, vulnerability to initiation of trapping (B2 vs. B3) was greater in mainland Nova Scotia (85.3%) and Vermont (77.6%) than in New Hampshire (18.0%) or Cape Breton Island (23.3%) (Table 3). Canadian populations were more influenced by differences between the logging scenarios (e.g., L2 vs. R2: Table 3, Fig. 2) than those in the northeastern United States. Mainland Nova Scotia showed a large effect of habitat restoration, although even restored habitat remained vulnerable to trapping mortality due to the population's small size and isolation.

Interaction between the effects of trapping and logging, as shown by differences in slopes of the three lines in Figure 2, was most evident in New Brunswick (28.5% population loss from R2 to R4 vs. 50.8% loss from L2 to L4) (Table 3). Populations were predicted extirpated from Cape Breton Island and the rest of Nova Scotia under all climate-change scenarios (Table 3, Figs. 1 & 2). The large population in Maine was also greatly reduced under climate change, and the New Brunswick population was moderately vulnerable (Table 3). Under the base scenario, the regional marten population declined 40.08% due to

Table 3. Relative size of marten and lynx populations predicted to inhabit various states and provinces under alternate PATCH scenarios (Table 2), expressed as a multiple of population size under the base scenario (scenario B2 [marten] and B1 and B136 [lynx, for simulations with 90 km^2 and 36 km^2 home ranges, respectively]).

	Scenario														
	B1	*B3*	*B4*	*L1*	*L2*	*L3*	*L4*	*R1*	*R2*	*R3*	*R4*	*FB2*	*FB4*	*FL2*	*FR2*
Marten															
jurisdiction															
Maine	1.13	0.95	0.61	1.10	0.90	0.88	0.51	1.14	1.05	1.00	0.66	0.33	0.27	0.12	0.45
New Hampshire	0.99	0.82	0.99	0.99	0.97	0.79	0.97	0.99	1.01	0.82	0.96	0.89	0.87	0.88	0.91
New York	1.80	0.92	0.24	1.76	0.96	0.96	0.24	1.76	1.00	0.88	0.24	0.97	1.03	0.26	1.01
Vermont	1.00	0.22	1.00	0.88	0.86	0.16	0.92	1.03	1.11	0.26	0.98	0.91	0.86	0.96	1.03
Southern Quebec	1.11	0.97	0.71	0.96	0.81	0.80	0.53	1.23	1.13	1.10	0.84	0.87	0.72	0.61	0.97
New Brunswick	1.12	0.95	0.67	0.97	0.77	0.75	0.38	1.28	1.18	1.08	0.84	0.56	0.42	0.32	0.69
Cape Breton Island	0.98	0.77	0.99	0.75	0.74	0.55	0.76	1.20	1.23	0.96	1.19	0.00	0.00	0.00	0.00
Mainland Nova Scotia	1.00	0.15	1.00	0.15	0.15	0.00	0.15	17.35	18.77	3.13	16.49	0.00	0.00	0.00	0.00
Overall	1.11	0.91	0.70	1.00	0.84	0.78	0.54	1.22	1.15	1.01	0.84	0.60	0.50	0.39	0.71

	Scenario											
	A1	*C1*	*A2*	*B2*	*C2*	*A136*	*A236*	*C136*	*FA1*	*FB1*	*FB2*	*FC1*
Lynx												
jurisdiction												
Maine	0.87	0.70	0.67	0.71	0.43	0.94	0.75	0.76	0.05	0.10	0.00	0.07
New Hampshire	1.03	0.39	1.03	1.03	0.37	1.01	0.63	1.01	0.36	0.31	0.33	0.00
New York	1.01	0.64	1.01	1.00	0.61	1.00	0.81	1.00	0.64	0.63	0.63	0.25
Southern Québec	1.09	0.93	0.22	0.37	0.23	1.07	0.95	0.22	0.80	0.66	0.04	0.66
New Brunswick	0.95	0.79	0.76	0.80	0.55	0.99	0.82	0.85	0.22	0.34	0.06	0.26
Cape Breton Island	1.18	0.06	1.08	0.96	0.07	1.02	0.50	1.01	0.00	0.00	0.00	0.00
Overall	0.99	0.79	0.57	0.64	0.39	1.01	0.84	0.61	0.41	0.41	0.08	0.34

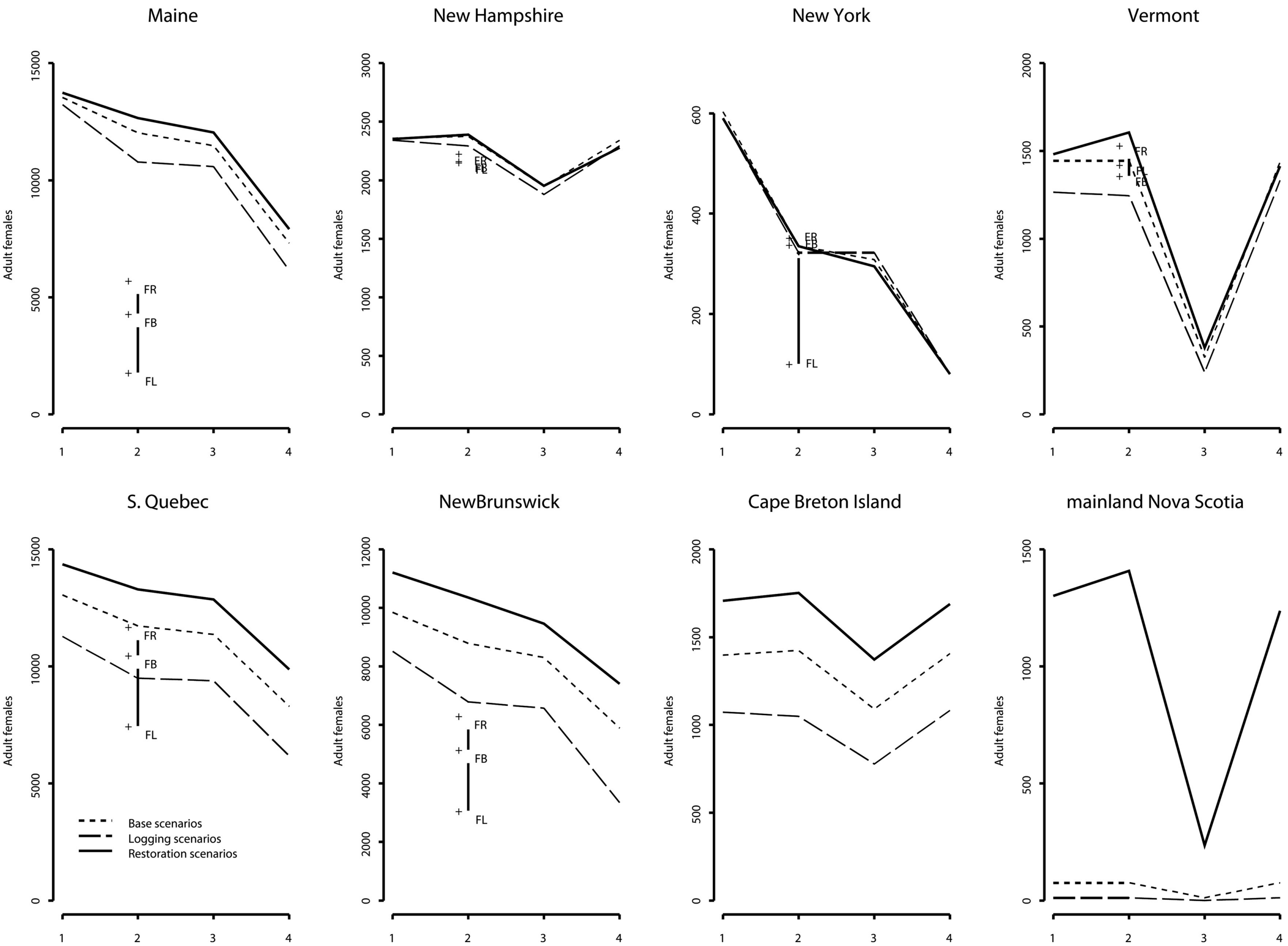

Figure 2. Response of predicted marten population size by state or province to alternate PATCH scenarios described in Table 2. The x-axis shows scenarios 1 through 4 under base, logging, and restoration conditions (Table 2). The vertical line above the x-axis position for scenario 2 shows climate change scenarios FB2, FL2, and FR2 (Table 2). Because population predictions from PATCH (y-axis) are expressed as number of adult (territorial) females, total population size including males and young would be two or more times the figure reported here. Populations were predicted extirpated from Cape Breton Island and mainland Nova Scotia under all climate change scenarios.

climate change (B2 vs. FB2). This compares with a 16.27% decline in the logging scenarios (B2 vs. L2) and a 29.73% decline in the trapping scenarios (B2 vs. B4) (Table 3).

The contrast in the relative vulnerability of different regions to the threat scenarios was also expressed by an increase in sink habitat, fragmentation of range, and ultimately extirpation of the smaller peripheral populations. Increase in trapping intensity in currently trapped jurisdictions (B2 vs. B4) resulted in fragmentation of formerly continuous range into two large subpopulations (in northern New Brunswick and Gaspé and in northern Maine), two smaller untrapped populations (northern New Hampshire and Cape Breton Island), and loss of the Adirondack subpopulation (Fig. 1b). Results from an increase in logging intensity (L2) showed a similar pattern of fragmentation except that the northern Maine subpopulation retained more source habitat and connectivity to the south than in the trapping scenarios, and the Adirondack subpopulation persisted (Fig. 1c). Climate change greatly reduced marten distribution in Maine, fragmenting the regional population into a large population in northern New Brunswick and Gaspé and a remnant isolate in the mountains of northern New Hampshire (Fig. 1d). Restoration partially mitigated this range contraction by maintaining distribution in northern and western Maine.

Lynx

The distribution of lynx in the PATCH simulations with no environmental stochasticity was similar to that predicted by the static habitat model adapted from Hoving et al. (2005), with core populations in Gaspé and northern New Brunswick and smaller populations in northern

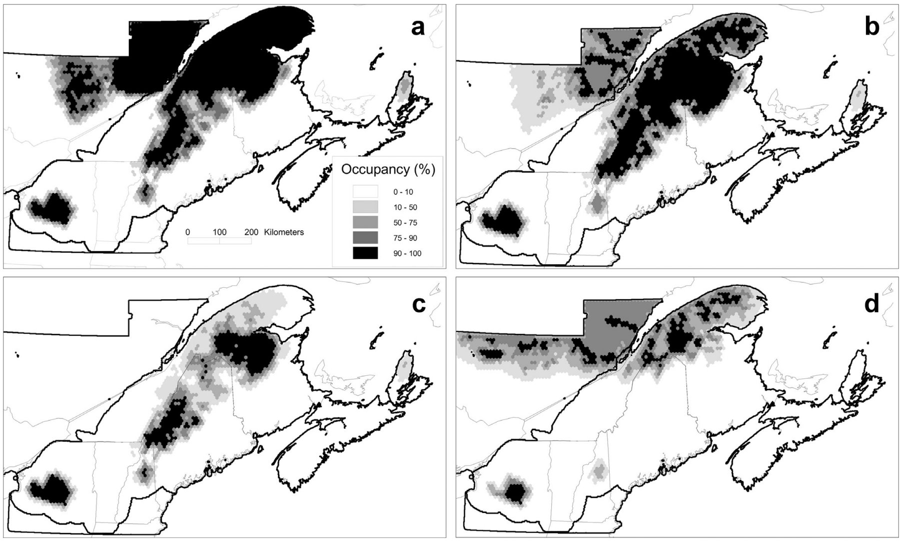

Figure 3. Distribution of lynx predicted by the PATCH model simulations in the northern Appalachians region under (a) no population cycling (scenario A1, Table 2), (b) population cycling only in Gaspé (scenario B1), (c) population cycling only in Gaspé with increased trapping pressure (scenario B2), and (d) decreased snowfall (scenario FB1). Unlike with marten, lynx population simulations included areas north of the St. Lawrence River within the outer black line.

Maine, the Adirondacks, and Cape Breton Island (Fig. 3a). Nevertheless, the fragmented distribution of lynx habitat within the northeastern United States and Cape Breton Island, combined with the negative effect of population cycling, caused a smaller proportion of potential habitat there to be occupied in the PATCH simulations than in the static model or in simulations in more continuous habitat (i.e., boreal regions) (Fig. 3b). The viability of these peripheral populations was sensitive to assumptions concerning the intensity of population cycling (e.g., scenarios A1 vs. C1; Table 3). In the scenarios where population cycling was confined to the Gaspé population (B1), lynx populations in Maine and New Brunswick were larger than when either none (A1) or all (C1) of the region experienced cycling (Table 3). These populations benefited from dispersal from Gaspé during high points of the population cycle (B1), but this effect was negated when these areas also experienced population cycles directly (C1). Increased trapping in the Gaspé (A2) had a negative effect on New Brunswick and Maine populations (Table 3). When these peripheral areas (New Brunswick and Maine) also experienced cycling (C2), the population decrease it caused was additive to the decline caused by trapping in Gaspé (Table 3). When the territory size parameter was set at 36 km^2 rather than 90 km^2, the effects of population cycling and trapping on peripheral populations (C136 and A236) were reduced because all populations were then larger (Table 3).

Under the core-only cycling base scenario, the regional lynx population declined 59.48% due to climate change alone (scenario B1 vs. FB1; Table 3). This compares with a 20.09% decline in the population-cycling scenarios (A1 vs. C1) and a 36.09% decline in the trapping scenarios (B1 vs. B2; Table 3). The effects of climate change on lynx viability varied between jurisdictions, with small peripheral populations (Cape Breton Island) and lowland populations (Maine) most vulnerable to climate change (Table 3, Fig. 4). Mountainous or more northerly populations (New Brunswick) were moderately vulnerable to climate change, whereas the core Gaspé population, at the northern limits of the study area, was least vulnerable. Interaction between the threats from trapping and climate change caused a Gaspé population affected by climate change to become highly vulnerable to additional threats from trapping (B2 vs. FB2, Table 3).

DISCUSSION

Although bioclimatic models, which evaluate impacts on a large number of species based on correlations between range boundaries and climatic factors (Thomas et al. 2004), are valuable as a first stage in the analysis of the effects of climate change (Pearson & Dawson 2003), they should form part of a hierarchy of models of increasing complexity (Pearson & Dawson 2003; Hannah et al. 2005). As with most species, the quantitative relationship between demographic rates and habitat is poorly documented for mesocarnivores such as marten and lynx. Despite these data gaps, SEPMs can form a useful intermediate or mesoscale level in this spatial hierarchy of models. Integration of climate change projections into an SEPM can reveal the interaction of climate change with other anthropogenic threats such as landscape conversion and overexploitation, and how these threats are mediated through characteristics of the species' biology such as home range size and dispersal ability. The results of an SEPM can thus provide novel insights into the prioritization of strategies for species restoration, highlighting the vulnerability of small populations and the influence of linkages between populations.

The PATCH results suggest that climate change will strongly affect both regionally scarce carnivore species,

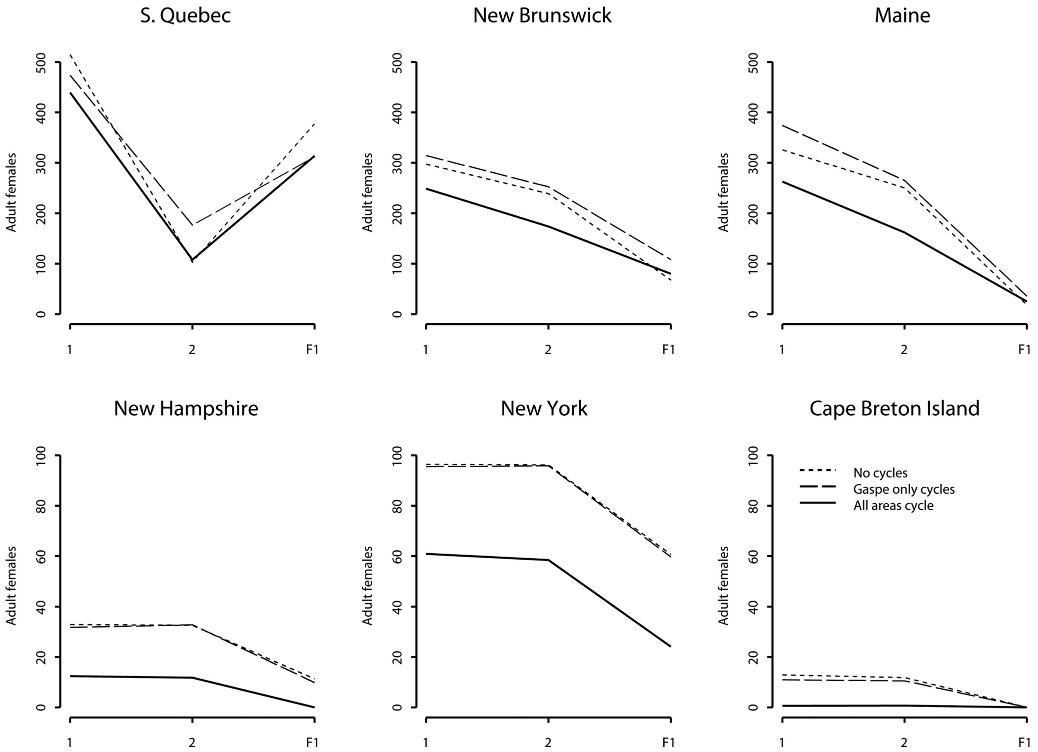

Figure 4. Response of predicted lynx population size by state or province to alternate PATCH scenarios described in Table 2. The x-axis shows scenario groups 1 (base scenario), 2 (increased trapping), and F1 (decreased snowfall) under various population cycling assumptions (no cycling [A1, A2, and FA1], cycling only in Gaspé [B1, B2, and FB2], and cycling in all areas [C1, C2, FC1], Table 2). Because population predictions from PATCH (y-axis) are expressed as number of adult (territorial) females, total population size including males and young would be two or more times the figure reported here.

such as the lynx, and relatively abundant species, such as the marten, although lynx remain substantially more vulnerable than marten. Regional marten and lynx populations showed stronger declines due to climate change alone than in the overexploitation or logging scenarios, but climate change interacted with logging for the marten and trapping for the lynx to increase overall vulnerability in a more than additive manner (Table 3). These results illustrate the threats small and semi-isolated populations face at their range margins in the relatively near future, as climate change interacts with habitat conversion and direct exploitation (e.g., trapping) to form an extinction vortex (Gilpin & Soulé 1986). Exacerbating these threats, these populations span national boundaries with contrasting social and regulatory contexts.

Nevertheless, the SEPM results should be interpreted in the context of several methodological limitations. Snowfall, the climate parameter present in the habitat models, not only correlates with marten and lynx distribution but also has a well-documented functional link to their demography (Krohn et al. 1995; Mowat et al. 2000). Nevertheless, a broad suite of other climatic variables are likely to indirectly influence marten and lynx distribution via effects on habitat structure (forest composition) and the composition of vertebrate communities (e.g., prey and sympatric carnivore species). Future extensions of SEPMs to model multispecies interactions would be useful in analyzing the effects of climate change and landscape conversion on the spread of competitor species such as coyote (*Canis latrans*) and fisher and on shifts in prey communities. The utility of model predictions for conservation will also increase as more realistic forest succession and landscape-change models and detailed regional-scale climate models are developed.

Both marten and lynx models predicted distribution and viability more successfully in the central portion of the regional distribution than they predicted the success of reintroductions to small, isolated habitat areas. Nevertheless, reintroductions may have failed due to other factors than habitat suitability, such as high densities of sympatric carnivore species (Trombulak & Royar 2001). The model predicts lynx could occur in the southwestern Adirondacks, an area where lynx are not currently extant and where attempts at reintroduction have failed (Ray 2000). This area owes its predicted suitability to heavy snowfall due to a lake effect. Nevertheless, annual snowfall may be a poor surrogate for lynx habitat in these areas if snow crusting (which affords a competitive advantage to sympatric carnivores such as bobcat [*Lynx rufus*]) is increased at the southern range limit by frequent melt-thaw events (M. McCollough, personal communication).

Analysis was limited to a single IPCC emissions scenario (A2) from a single GCM. Nevertheless, although precipitation predictions vary more between GCMs than do temperature predictions in many regions, both show a general agreement (the same direction and magnitude of change) in the portion of eastern North America where this study was located (Raper and Giogi 2005). Other IPCC scenarios such as the B2 are also commonly analyzed in assessments of climate change impacts on species. The B2 scenario generally shows climate changes, and resultant biotic effects, of similar direction and spatial pattern but somewhat lower magnitude than does the A2 scenario (Thuiller et al. 2006). For example, 44% of African mammals were predicted to be threatened by climate change under scenario A2 versus 38% under scenario B2 (Thuiller et al. 2006).

In addition, although the magnitude of climate change in the scenarios is based on GCM simulations, the magnitude of trapping and logging effects is more arbitrary. The assumption that trapping might result in a 10% reduction in survival falls in the lower range of additive mortality from trapping described in the literature (Brand & Keith 1979), which is appropriate given that the Gaspé lynx population is managed in a relatively precautionary manner due to its isolation from larger populations. The logging scenarios were parameterized based on a 10% decrease in the regional extent of older conifer forest, which represents a doubling of the extent of the transitional (recent clearcut) forest type. Due to the fact that the analysis region spans many jurisdictions, no comprehensive estimate of current logging rate is available. Subregional logging rates vary greatly between jurisdictions and over time in response to economic trends. The parameterization used thus represents an exploratory look at effects of a plausible variation in rate of harvest, rather than a prediction of future effects.

The SEPM results highlight contrasts between the two carnivore species in four major factors: the nature of threat processes, the scale of population processes, the level of environmental stochasticity, and the patterns of landscape connectivity experienced by the species. In particular, environmental stochasticity differed in amplitude and temporal scale between the species and interacted with the spatial and temporal scale of the species population dynamics to affect vulnerability. Although the prevalence of lynx population cycles has long been known (Elton & Nicholson 1942), marten trapping data from this region suggest variation of a similar magnitude but with a shorter cycle length, perhaps due to alternate-year mast production by beech (*Fagus grandifolia*; Jakubas et al. 2005). Such productivity pulses, which are common in temperate forest ecosystems (Ostfeld & Keesing 2000), may significantly affect the ability of the small populations typical of species at high trophic levels to persist in the face of climate change.

The SEPM results showed that peripheral marten and lynx populations, such as those in New York (marten), Nova Scotia (marten and lynx), and Maine and New Hampshire (lynx), are highly vulnerable compared with larger core populations. The climate-change scenarios suggested that decreased snowfall will also have a high impact on marten in areas such as northern Maine, where they are relatively abundant under current conditions but which lack mountainous refugia. Larger marten populations in northern New Brunswick, and to a lesser extent western Maine, may also be vulnerable to the interaction of the effect of logging with both climate change and trapping (Table 3).

Except for the core Gaspé population, lynx habitat was occupied in the SEPM results due to a combination of site habitat value and proximity to sources of dispersers. The demographic importance of dispersers was accentuated by population cycling. Although the extent of cycling in the region's lynx populations is poorly known, the SEPM scenarios (Figs 3 & 4) illustrate the complex manner in which cycling in this core population could potentially affect peripheral populations. Lynx populations in Maine and New Brunswick were larger in scenarios where population cycling was confined to the Gaspé population than when either none or all of the region experienced cycling. Although Maine and New Brunswick lynx populations benefited from dispersal from Gaspé during high points in the population cycle, this effect was erased by negative impacts when these areas also experienced population cycles directly because these smaller populations were highly vulnerable to the impacts of cycling. This result contrasts with the relatively small impact of cycling in nonspatial lynx population models (Steury & Murray 2004). In addition, these peripheral areas were vulnerable to the indirect impacts of increased trapping pressure in the Gaspé (Table 3; Fig. 4).

Climate change appeared to have an even greater impact on the viability of lynx than on the viability of marten in the region, with lynx distribution effectively contracting to the Gaspé peninsula. As with the marten, small peripheral populations (Cape Breton Island) and lowland populations (Maine) were most vulnerable to the effects of climate change. Nevertheless, because core habitat for the lynx is already limited to the Gaspé peninsula, northward range contraction was more pronounced than for marten. Mountainous or more northerly populations (New Brunswick) were moderately vulnerable to climate change, whereas the core Gaspé population, at the northern limits of the study area, was least vulnerable. Nevertheless, the Gaspé population lacks large reserves closed to trapping and may not be sustainable under current trapping levels and the effects of climate change.

Conservation Planning for Multiple Carnivore Species

Habitat types associated with high fecundity and survival differ between the two species. For marten, industrial forestry has both direct (loss of structure) and indirect (increased access and trapping) effects on viability, but the two effects have different temporal scales (Hodgman et al. 1997; Chapin et al. 1998). Some evidence of an interaction between the effects of trapping pressure and habitat loss (Chapin et al. 1998) appeared in the SEPM model (Table 3). Further analysis of how the spatial distribution of logging and of no-trapping refugia influences the impact of these processes may be informative. The ability of wildlife agencies to affect trapping pressure through creation of single-species refugia, however, may be limited where most harvest occurs as an incidental take. For example, the northern Appalachians is one of the only areas where lynx are sympatric with high-density populations of coyotes (due in part to extirpation of the wolf), and most lynx harvested in the region are caught in snares set for coyotes (H. Jolicoeur, personal communication). In this case increased road development may result in more severe long-term impacts on vulnerable carnivore populations than if incidental trapping risk were low.

For both species the interaction of management (i.e., logging and trapping policy) with regional gradients in vegetation type and climate is critical in this region characterized by islands of boreal habitat. My results suggest that it will be difficult to sustain small peripheral populations (such as in Nova Scotia for the marten or Nova Scotia and northern Maine for the lynx) of either species in the face of climate change. The strong impact of climate change in the results imply not that conservation action to address other threats will be useless, but that it is essential to move toward more precautionary management of populations that may today still appear robust. Unless steps are taken now to begin more regionally coordinated management of these species, they may also suffer a range contraction in areas that are now considered the core of their regional range (Gaspé for the lynx, northern Maine for the marten). A key component of a precautionary management strategy will be improved monitoring of the response of populations to climate change and other stressors and an adaptive management policy concerning trapping harvest and habitat conservation.

Due to the limited ability of regional-scale models to discern factors such as forest structure or prey density that directly limit distribution and the additional limitations inherent in complex models such as SEPMs, the quantitative predictions from the PATCH scenarios should be interpreted cautiously. Nonetheless, model results are highly relevant to carnivore conservation policy because they generate hypotheses concerning regional population dynamics and offer heuristic tools to evaluate how carnivore populations may be linked across jurisdictions. Because marten and lynx populations in the northern Appalachians represent peninsular extensions of broader boreal ranges, demographic decline due to increased threats and environmental stochasticity is rapidly expressed as fragmentation of peripheral from core populations. Because of the interaction between the effects of climate change and other habitat threats in the SEPM scenarios, it is important to integrate model results into reserve selection algorithms to help build regional conservation plans that enhance the persistence of carnivore populations in the face of climate change through reduction in trapping of vulnerable populations and habitat restoration in critical core areas and linkages (Araújo et al. 2004). Despite the greater data requirements of mesoscale spatial viability models when compared with bioclimatic models, they are important tools for generating more biologically realistic hypotheses regarding biotic response to climate change.

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