



©SUSAN C. MORSE

Carnivore Restoration in the Northeastern U.S. and Southeastern Canada

A Regional-Scale Analysis of Habitat and Population Viability for Wolf, Lynx, and Marten

Report 2: Lynx and Marten Viability Analysis

Carlos Carroll, Ph.D.



©SUSAN C. MORSE

We are ambitious. We live for the day when grizzlies in Chihuahua have an unbroken connection to grizzlies in Alaska; when wolf populations are restored from Mexico to the Yukon to Maine; when vast forests and flowing prairies again thrive and support their full range of native plants and animals; when humans dwell on the land with respect, humility, and affection.

Toward this end, the Wildlands Project is working to restore and protect the natural heritage of North America. Through advocacy, education, scientific consultation, and cooperation with many partners, we are designing and helping create systems of interconnected wilderness areas that can sustain the diversity of life.



P.O. Box 455

Richmond, VT 05477

802/434-4077

info@wildlandsproject.org

www.wildlandsproject.org

Carnivore Restoration in the Northeastern U.S. and Southeastern Canada

A Regional-Scale Analysis of Habitat and Population Viability for Wolf, Lynx, and Marten

Report 2: Lynx and Marten Viability Analysis

Carlos Carroll, Ph.D.

May 2005

Carlos Carroll is a research ecologist with the Klamath Center for Conservation Research (P.O. Box 104, Orleans, CA 95556; carlos@klamathconservation.org). He received his B.A. in Biology from UC Santa Cruz (1994) and his M.S. in Wildlife Science (1997) and Ph.D. in Forest Science (2000) from Oregon State University. His research has focused on the conservation of mammalian carnivores throughout North America.

Suggested citation:

Carroll, Carlos. 2005. Carnivore Restoration in the Northeastern U.S. and Southeastern Canada: A Regional-Scale Analysis of Habitat and Population Viability for Wolf, Lynx, and Marten (Report 2: Lynx and Marten Viability Analysis). Wildlands Project Special Paper No. 6. Richmond, VT: Wildlands Project. 46 pp.

This study was commissioned by the Wildlands Project, Richmond, Vermont, and was funded through the generous support of the Fine Family Foundation, Sweet Water Trust, and Henry P. Kendall Foundation.

©2005 Wildlands Project

CONTENTS

[2]
Executive Summary

[4]
Introduction

[6]
Methods

[15]
Results

[35]
Discussion

[44]
Acknowledgments

[45]
References

EXECUTIVE SUMMARY

THE RESEARCH DESCRIBED HERE, AND IN A companion report on the wolf, seeks to develop a comprehensive analysis of habitat, population viability, and conservation needs for three focal carnivores in the Northern Appalachians region of the northeastern U.S. and southeastern Canada: American marten (*Martes americana*), lynx (*Lynx canadensis*), and eastern gray wolf (*Canis lupus*, or *C. lycaon*). All three species are considered threatened in portions of the region but differ in their basic habitat requirements and the factors responsible for their decline. Carnivore conservation in the Northern Appalachians faces fundamental challenges due in part to the expected impacts of climate change on species such as the lynx and marten, which are primarily associated with boreal regions. Habitat for these species at the southern limits of their range is already fragmented by climate and human-associated factors such as conversion of forest to farmland and urban areas. Because of the small and semi-isolated carnivore populations of the region, climate change can interact with habitat conversion and direct exploitation (trapping) to form an “extinction vortex” that may affect both regionally scarce species such as the lynx and relatively abundant species such as the marten.

Species recovery efforts that span national boundaries face challenges due to contrasting social and regulatory contexts. For example, lynx are relatively abundant and commercially trapped in the Gaspé region of Québec, but threatened or extirpated elsewhere in the Northern Appalachians region. Broad-scale analyses such as this one that encompass all components of the regional metapopulation, although necessarily less detailed than state/province-level efforts, may provide important insights as to the underlying drivers of species vulnerability that can make conservation policy more effective.

In the first stage of this analysis, I developed regional-scale models that relate GIS habitat data to the relative fecundity and survival rates shown by marten, lynx and wolf in differing habitats. Marten distribution was predicted by relating marten trapping harvest to environmental factors, and lynx distribution was predicted using a previously published model (Hoving et al. 2005). Snowfall is an important habitat factor in both the marten and lynx models, because decreased snowfall is linked to decreased prey abundance and/or vulnerability, and decreased competitive advantage over sympatric carni-

vores. Therefore, projecting these initial regional habitat models forward to 2055 using snowfall predictions from the IPCC’s general circulation models resulted in dramatic changes in the extent of suitable habitat in the region. Marten habitat was effectively eliminated from Nova Scotia, southern New Brunswick, and eastcentral Maine, and predicted marten abundance was reduced in more northerly areas. Lynx habitat contracted to the Gaspé peninsula (Québec), northernmost New Brunswick, and scattered areas in the northeastern U.S.

In the second step, I incorporated these static habitat models into a spatially-explicit population model (SEPM) called PATCH. This model goes beyond the simpler habitat models by simulating populations of individual animals on the landscape, allowing assessment of how population size and connectivity influence persistence. PATCH also allowed assessment of novel future scenarios that included increased trapping pressure, increased or decreased timber harvest, and the interaction of these with climate change.

For marten, an increase in trapping intensity results in fragmentation of formerly continuous range into two large subpopulations (in northern New Brunswick/northern Gaspé and northern Maine) and two smaller untrapped populations (northern New Hampshire and Cape Breton Island), and loss of the Adirondack subpopulation. An increase in logging intensity results in a similar pattern of fragmentation. Climate change sharply reduced marten distribution in Maine, fragmenting the regional population into a larger population in northern New Brunswick/northern Gaspé and a remnant isolate in the mountains of northern New Hampshire. Restoration (decreased logging) mitigated this range contraction to some extent by maintaining distribution in northern and western Maine. The climate change scenarios suggest that decreased snowfall will have high impact on marten, not only in small isolated populations such as Cape Breton Island, but also in areas such as northern Maine where they are relatively abundant under current conditions, but which lack mountainous refugia.

For lynx, small peripheral populations (Cape Breton Island) and lowland populations (Maine) were also most vulnerable to the effects of climate change. However, because core habitat for the lynx is already limited to the Gaspé peninsula, northward range contraction was more

pronounced. Mountainous or more northerly populations (New Brunswick) were moderately vulnerable to climate change, while the core Gaspé population, at the northern limits of the study area, was least vulnerable. However, the threats from trapping and climate change interacted, causing a Gaspé population affected by climate change to become highly vulnerable to additional threats from trapping. These results suggest areas such as Gaspé that hold robust lynx populations under current conditions will not be able to sustain current threat levels when coupled with the effects of climate change.

Because marten, lynx, and (potentially) wolf 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. This occurs at differing scales; the wolf suffers from the isolation of the Northern Appalachians from populations north of St. Lawrence River, the lynx from potential disconnection of the U.S. from the Gaspé population, and the marten from potential loss of contact between peripheral populations in New Hampshire, Vermont, and Nova Scotia from core populations in northern Maine/northern New Brunswick/Gaspé.

The PATCH analysis highlighted areas that may serve as critical linkages to maintain viability of outlying populations. While there is some overlap between the linkage areas highlighted, the substantial contrasts in linkage needs between these three carnivore species, a small subset of the region's threatened species, implies that identifying and protecting linkages requires a science-based approach

rather than a rapid assessment based on human perceptions of landscape pattern.

Until recently, the effects of climate change on biodiversity were assessed using simple "climatic envelope" models that predicted changes in a species range without considering the dynamics of individuals and populations and the ability to disperse to new habitat. This study is thus the first comprehensive assessment of the how climate change will interact with other threats to affect carnivore population viability. The results reported here help focus conservation action on policy changes and critical habitat areas which will be key to preventing the loss of these vulnerable species from large portions of the Northern Appalachians in the next century.

The strong impact of climate change in our results imply, not that conservation action to address other threats will be useless, but on the contrary, that it is essential to move towards more precautionary management of populations that may today still appear robust. Unless steps are taken now to begin more precautionary and regionally-coordinated management of these species, they may suffer range contraction in areas that are now considered the core of their regional range (Gaspé for the lynx, northern Maine for the marten). These results imply that reduction in trapping of vulnerable populations and habitat restoration in critical core areas and linkages may have a large effect in sustaining regional lynx and marten populations in the face of climate change. For all three species, effective conservation strategies must be binational and take into account the dynamic ecosystem context within which recovery will occur.

INTRODUCTION

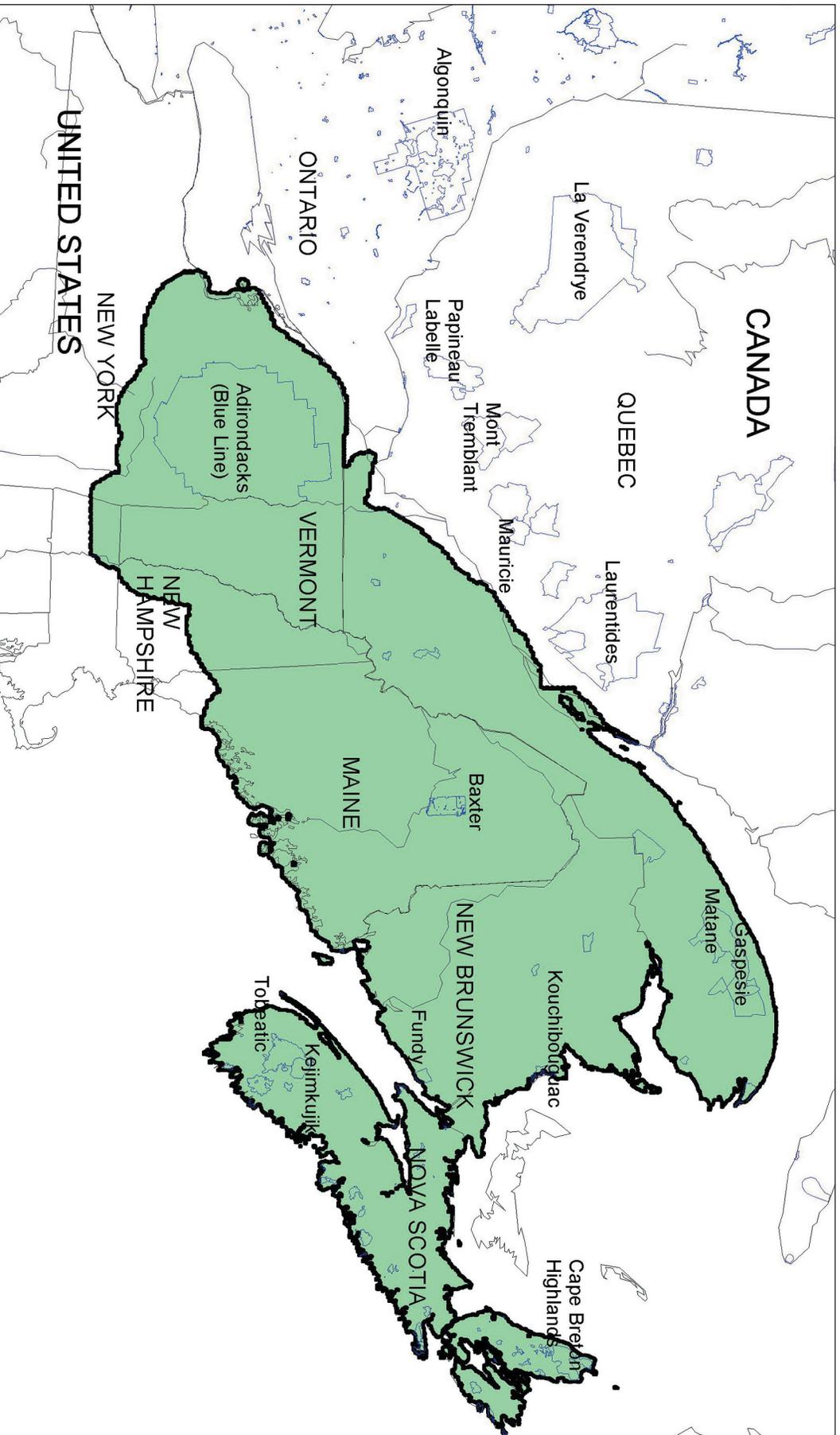
IN THE AREA OF THE NORTHEASTERN U.S. AND southeastern Canada known as the Northern Appalachians ecoregion (Figure 1), European settlement led initially to loss of most of the larger carnivore species due to deforestation and direct persecution (Litvaitis 1993). More recent trends towards reforestation and increased regulation of hunting and trapping have created a potential for restoration of extirpated or threatened carnivore species (Trombulak and Royar 2001). However, increased development of rural lands as well as lack of coordination across jurisdictions have hampered recovery efforts (Paquet et al. 1999). The research described in this report and Carroll (2003) seeks to develop a comprehensive analysis of recovery potential in the region for the lynx (*Lynx canadensis*), American marten (*Martes americana*), and eastern gray wolf (*Canis lupus*, or *Canis lycaon* after Wilson et al. [2000]). All three species are considered threatened in portions of the region but differ in their basic habitat requirements and the factors responsible for their decline (Harrison and Chapin 1998, Ray 2000, Ray et al. 2002). A comprehensive analysis of viability needs for the three species can result in a stronger and more efficient restoration strategy than would separate single-species recovery efforts (Carroll et al. 2001, Carroll et al. 2003).

Whereas Carroll (2003) described the results of the wolf viability analysis, here I report results for phase two of the carnivore study, which concerns the marten and lynx. Carnivore restoration is a major focus of The Wildlands Project's (TWP) conservation strategy in the northeastern U.S. and southeastern Canada. TWP is currently using the results reported here to aid in the design of a regional conservation network based on both focal species (Lambeck 1997) and ecological representation principles. The reserve selection software MARXAN (Possingham et al. 2000) is being used to help identify optimal combinations of habitat to both 1) ensure the long-term viability of the region's native carnivore species, and 2) represent the full complement of the region's ecological systems and vegetation communities. The carnivore study's results will also aid ongoing single-species-based restoration projects and promote coordinated planning across jurisdictions to preserve and restore connectivity in the U.S./Canada transboundary region.

My analysis adapts techniques developed in carnivore

restoration projects in the Rocky Mountain region (Carroll et al. 2001, 2003), but also builds upon earlier carnivore habitat analyses for the northeastern U.S. (e.g., wolf: Harrison and Chapin 1998, Mladenoff and Sickley 1999, Quinby et al. 1999, 2000; lynx: Hoving et al. 2003, 2004, 2005; American marten: Krohn et al. 1995, Chapin et al. 1998, Payer and Harrison 2003). Past habitat models for these species can be termed either empirical (derived from statistical analysis of occurrence data) or conceptual (derived from expert knowledge-based rules regarding habitat associations). Because the wolf was extirpated from Northern Appalachians a century ago, no occurrence data is available from which to build regional empirical models. A conceptual model of wolf habitat across the region was developed by Harrison and Chapin (1998), and Mladenoff and Sickley (1999) extrapolated an empirical model developed in the northcentral U.S. to the U.S. Northern Appalachians. The lynx is still extant in the region, with a relatively large and heavily trapped population on the Gaspé peninsula of Québec. The lynx is extant but protected in adjacent areas of New Brunswick, and threatened in peripheral areas of its range in northern Maine and Nova Scotia (Ray et al. 2002). A reintroduction attempt to the Adirondacks (New York) was unsuccessful (Brocke et al. 1999). The first regional habitat models have been recently developed from occurrence data (Hoving et al. 2005). Marten are the most abundant of the three species, but paradoxically, less is known about their relative abundance across the region than for the lynx. Marten are trapped in Maine, Québec, northern New Brunswick, and the Adirondacks, extant but protected in New Hampshire, and threatened or extirpated from Vermont and Nova Scotia (Ray 2000). Marten have been the focus of many reintroduction attempts in the region, with varying success (Trombulak and Royar 2001). Previous studies have examined relationships between marten and both snowfall and a potential competitor, the fisher (*Martes pennanti*), in Maine (Krohn et al. 1995) and predictive habitat models have been developed for that state (Hepinstall et al. in prep.). On a regional level, some efforts have been made to compile expert opinion on relative marten abundance. However, this study is the first to develop regional-scale (i.e., multi-state/province) empirical models for marten.

FIGURE 1 Map of the study area in southeastern Canada and the northeastern United States. The marten study area boundary, which was limited to the Northern Appalachians region by the extent of available vegetation data, is shown in green. Major parks and wildlife reserves are outlined in blue. Wolf and lynx study areas extended north of the St. Lawrence River.



METHODS

THE STUDY AREA FOR THE MULTI-CARNIVORE viability analysis is based on the Northern Appalachians/Acadia ecoregion (Figure 1), which encompasses Maine, New Hampshire, Vermont, northern New York state, Nova Scotia, New Brunswick, Prince Edward Island, and southern Québec. Prince Edward Island was excluded from the analyses due to its isolation and highly-modified landscape with low suitability for the three carnivore species. The lynx and wolf analysis area was expanded to include potential source habitat in the Laurentides region of southeastern Ontario and Québec north of the St. Lawrence valley. However, I discuss results from these areas only to the extent that they influence carnivore populations in the Northern Appalachians.

In the first step of the modeling process, I developed regional-scale models that relate geographic information systems (GIS) habitat data to the relative fecundity and survival rates shown by marten and lynx in differing habitats. In the second step, I incorporated these static habitat models into a spatially-explicit population model (SEPM), PATCH (Schumaker et al. 1998).

Development of static models

Marten In order to explore regional marten habitat associations, I developed regression models to predict marten harvest density from environmental variables. The variables considered fall into six categories: vegetation, satellite imagery, geographic, topographic, climatic, and human-impact associated (Table 1). Vegetation variables were derived from a data layer developed by The Nature Conservancy (TNC) from two sources. The source of vegetation data for the United States was the National Land Cover Dataset (NLCD)(Vogelmann et al. 2001). The NLCD was developed by the Multi-Resolution Land Characterization Consortium of governmental agencies in order to provide a seamless vegetation map spanning the conterminous United States. These data were derived from Landsat TM data at a resolution of 30 m. They contain 21 landcover classes and therefore represents a spatially-detailed but thematically coarse data layer when compared with e.g., the vegetation maps produced by the Gap Analysis Programs (GAP) of the individual states (Scott et al. 1993). In Canada, several provincial vegetation data lay-

ers were crosswalked to the NLCD classification scheme (TNC, unpublished). Data of various ages was used in creating the TNC vegetation layer: 1990-92 for the United States, 1980-2001 for New Brunswick, 2000 for Nova Scotia, and ~2003 for Québec. Despite the thematic coarseness of the NLCD system, and data inconsistencies between jurisdictions, the TNC layer represents the first detailed vegetation data available for this region. However, it does not extend into adjacent regions north of the St. Lawrence River. Because of data confidentiality restrictions, this data was provided for use in this study summarized over hexagons of 10 km² in size, such that each hexagon contained data on the percent of that area falling within each vegetation type. The NLCD vegetation system classifies recent clearcuts as transitional or regenerating forest, whereas the conifer, mixed, and deciduous forest classes represent older stands. The regenerating forest class may also contain some naturally sparse stands (G. Kehm, pers. comm.). A map of the extent of regenerating forest (Figure 2) illustrates the scale of the data, as well as potential inconsistencies in mapping between jurisdictions and ownerships.

I also derived potential explanatory variables from MODIS satellite imagery (Wharton and Myers 1997). The tasseled-cap indices of brightness, greenness, and wetness (Crist and Cicone 1984) are a standardized means of representing the three principal axes of variation in six spectral bands of the MODIS imagery. "Pseudo-habitat" variables such as greenness that are derived directly from unclassified satellite imagery are correlated to varying degrees with ecological factors such as net primary productivity and green phytomass (Cihlar et al. 1991, Merrill et al. 1993, White et al. 1997) and have proved useful in modeling wildlife distributions (Mace et al. 1999). MODIS images from two seasonal dates (March and July 2002) were compared. I also evaluated other variables developed by the MODIS program from that imagery: Leaf Area Index (LAI), Enhanced Vegetation Index (EVI), and a forest cover layer (Wharton and Myers 1997).

Geographic variables that may be surrogates for unmeasured regional environmental gradients (Carroll et al. 1999) were also evaluated. These included northing, easting, and distance from ocean or large lake. Topographic variables included latitude-adjusted elevation and topographic ruggedness or complexity (Carroll et al. 2001). The climatic variable evaluated was annual

snowfall. Annual snowfall data for the U.S. originated from the PRISM model (Daly et al. 1994), while snowfall data for Canada was predicted based on a model similar to that developed by Hoving et al. (2005), relating weather station data to geographic coordinates, elevation, and distance to water. Human impact-related variables included road density and habitat effectiveness, a metric that combines road density, local human population density, and interpolated human population density (Merrill et al. 1999). Differences between jurisdictions in trapping reg-

ulations and socioeconomic factors driving trapper effort might be expected to have a large effect on trapping harvest. Therefore jurisdiction (state or province) was evaluated as a “nuisance” variable in an alternate set of models.

The marten trapping data acquired from state and provincial wildlife agencies was merged into a composite database. Although some jurisdictions provided longer time series of data, trapping data was only available for all jurisdictions for the period 1999-2003. Trapping data was collected at the spatial scale of wildlife management units

TABLE 1 Data layers evaluated in the development of the regression model for marten harvest density.

Data Layer	Code	Resolution	Reference
<i>Vegetation variables</i>			
Vegetation type (NLCD system)		variable	TNC unpublished
Percent conifer	CON		
Percent mixed	MIX		
Percent regenerating forest	REG		
Percent deciduous forest	DECID		
Percent forest (MODIS)		1 km	Wharton and Myers 1997
Percent beech (U.S. only)			
<i>Satellite imagery metrics</i>			
July LAI		1 km	Wharton and Myers 1997
July EVI		1 km	Wharton and Myers 1997
March Brightness		1 km	Crist and Cicone 1984
March Greenness	MGRN	1 km	Crist and Cicone 1984
March Wetness		1 km	Crist and Cicone 1984
July Brightness		1 km	Crist and Cicone 1984
July Greenness		1 km	Crist and Cicone 1984
July Wetness		1 km	Crist and Cicone 1984
<i>Geographic variables</i>			
Albers northing			
Albers easting			
Distance to ocean			
<i>Topographic variables</i>			
Latitude-adjusted elevation		90 m	USGS unpublished
Topographic ruggedness		90 m	USGS unpublished
<i>Climatic variables</i>			
Average annual snowfall	SNOW	2 km	Daly et al. 1994
<i>Human-impact associated variables</i>			
Road density		1:100,000	USGS unpublished
Habitat effectiveness	HAB	1 km	Merrill et al. 1999
Jurisdiction	JUR	1:100,000	

which averaged 3801 km² in size (SD 1842 km²). Use of trapping data to model marten habitat associations is based on the assumption that trapping harvest correlates well with marten abundance. This assumption is supported by results from previous studies. For example, models developed from sightings data predicted lynx and wolverine trapping harvest in the Canadian Rockies (Carroll et al. 2001). However, variation in trapping effort may distort this relationship. The trapping data was examined for evidence of environmental stochasticity and cyclic patterns. The extent of the marten regression analysis was limited to areas with open trapping of martens, as low (incidental) trapping harvest in closed areas is obviously an artifact of management. However, the resulting model was then extrapolated to areas closed to marten trapping in order to evaluate habitat suitability across the region irrespective of trapping closure. Field knowledge of relative abundance in untrapped areas can provide a validation of model results. However, model performance may be poorer if habitat conditions are present in untrapped areas that are not represented in trapped areas. Marten trapping data from the Adirondacks was reported at a scale (townships) that was much finer than that from other jurisdictions. Therefore, the Adirondack data was excluded from initial model construction, and instead used in model validation. Data from Québec north of the St. Lawrence River was also used in model validation, although because the TNC vegetation layer did not extend to that area, only models that did not contain vegetation variables could be validated there.

Lynx Unlike in the case of the marten, regional-scale empirical models have been developed for the lynx from occurrence data (Hoving et al. 2005). Within the Northern Appalachians, only limited areas (the Gaspé peninsula) are open to lynx trapping. Therefore the trapping database I assembled contained too few management units with lynx trapping to build a robust empirical model. Hoving et al. (2005) made use of sightings data to circumvent this problem. The optimal model selected by Hoving et al. (2005) took the form $\text{logit}(p) = -12.78 + -0.052 \cdot \text{DECIDUOUS-FOREST} + 0.0049 \cdot \text{SNOWFALL}$. The explanatory variables available in this study (MODIS landcover data and PRISM snowfall data) differed somewhat from the inputs used by Hoving et al. (2005). I adapted the static model developed by Hoving et al. (2005) for use in the PATCH simulations, evaluated the magnitude of the contrast caused by the different input variables, and then validated the model's generality using lynx trapping data from both north and south of the St. Lawrence River.

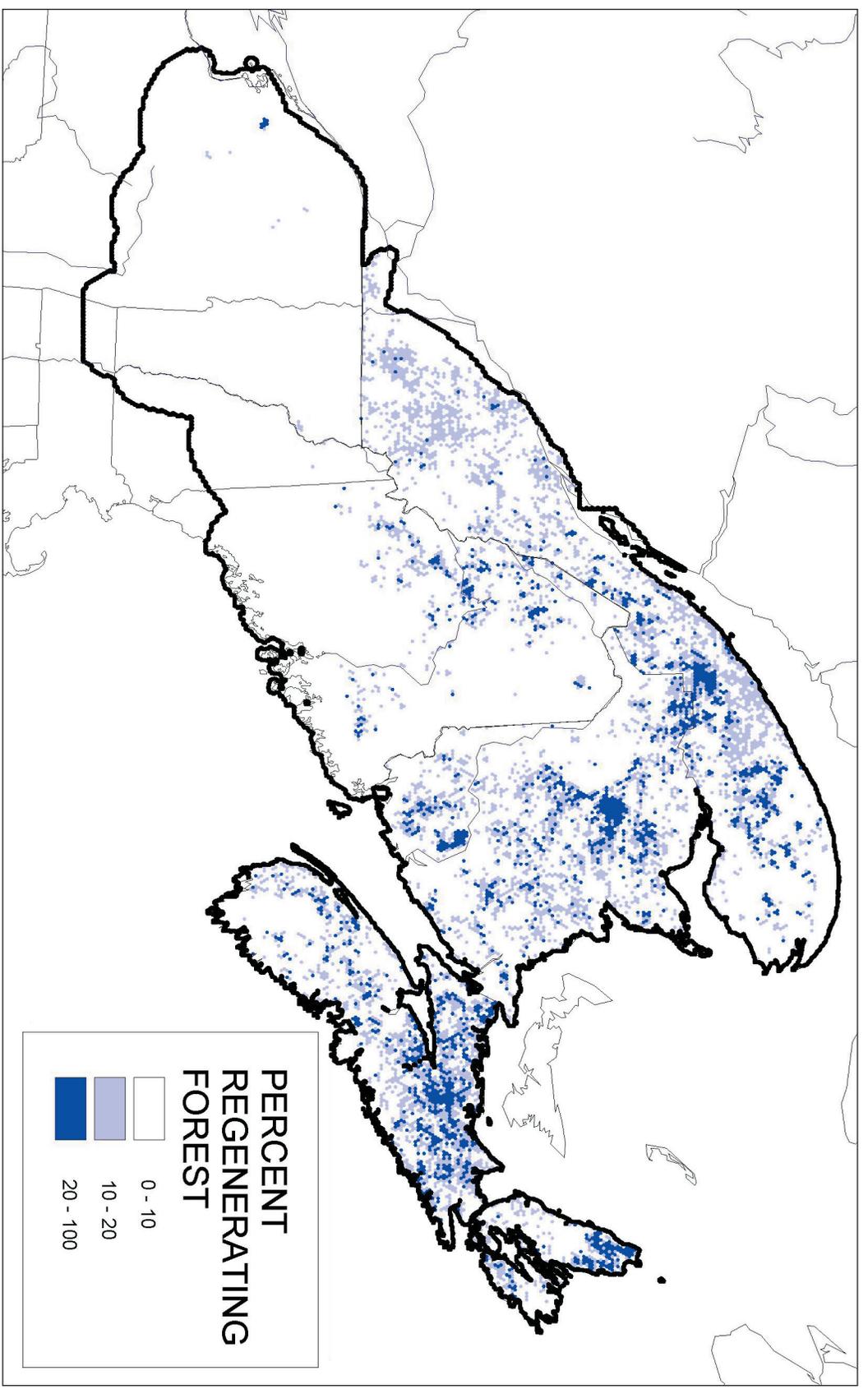
Static models incorporating climate change

In order to assess the potential effects of climate change on marten and lynx habitat suitability, I created versions of the marten regression model developed here, as well as the lynx model of Hoving (2005) 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 (IPCC) (Kiehl and Gent 2004). I used output from the IPCC A2 climate change scenario because this has been characterized as representative of the range of scenarios evaluated by the IPCC. The A2 scenario assumes an intermediate rate of growth in carbon emissions, with an approximate doubling of emissions between 2005 and 2055. This is due to a regionally diverse world with continuously increasing global population and divergent rates of economic and technological development. Because GCM predictions are available only at coarse resolutions (here ~200 km), I interpolated the percentage 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).

Dynamic models

Marten The model used in this study, PATCH (Schumaker 1998), is an example of a spatially-explicit population model (Dunning et al. 1995, Kareiva and Wennergren 1995). These models are useful in assessing population viability in a landscape context because they combine information on the spatial arrangement of habitat patches with data on how a particular species responds to different types of habitat (Carroll et al. 2003). The PATCH model is designed for studying territorial vertebrates, and links the survival and fecundity of individual animals to GIS data on mortality risk and habitat productivity measured at the location of the individual or pack territory (Schumaker 1998). Territories are allocated by intersecting the GIS data with an array of hexagonal cells. The GIS maps are assigned weights based on the relative levels of fecundity and survival rates expected in the various habitat classes. Survival and reproductive rates are then supplied to the model as a population projection matrix (Tables 2 and 3) (Caswell 2001). The model scales the matrix values based on the hexagon scores, with lower

FIGURE 2 Percentage regenerating forest in the Northern Appalachians as derived from a multi-jurisdiction vegetation data layer produced by The Nature Conservancy.



scores translating into higher mortality rates and lower reproductive output. The simulations incorporate demographic stochasticity with a random number generator. In the case of survival, a uniform random number between zero and one is selected. An individual dies if this number is less than the sum of the probabilities of making a transition between the current age class and every other class. A random number is also selected to force the number of offspring in a year to take on integer values. Environmental stochasticity is incorporated by drawing each year's base population matrix from a randomized set of matrices whose elements were drawn from a truncated normal distribution. In the marten simulations that incorporated environmental stochasticity, two matrices were available with similar survival rates, but either high or low fecundity to simulate observed variation in marten productivity with alternate year masting cycles (Table 2). Adult organisms are classified as either territorial or floaters. The movement of territorial individuals is governed by a site fidelity parameter, but floaters must always search for available breeding sites. Movement decisions use a directed random walk that combines varying proportions of randomness, correlation (tendency to continue in the direction of the last step), and attraction to higher quality habitat. However, there is 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 to survival (e.g., roads) (Carroll 2003). For mesocarnivores such as the marten and lynx, it is more difficult, if not impossible, to map, on a regional scale, proximal influences on fecundity and survival such as prey density and large woody structure. Instead I attempt to relate species abundance to more distal regional-scale habitat factors such as extent of older forest, and then make more speculative links between these factors and the fecundity and survival layers that are necessary inputs to the PATCH model. Here I assumed that habitat factors such as snowfall and older conifer/mixed forest would influence both fecundity (through prey abundance and vulnerability) and survival (through refuge from predators, increased competitive ability versus sympatric mesocarnivores, etc.) (Powell et al. 2003). The fecundity grid was derived directly from the marten regression model output and was unchanged over all scenarios. In order to explore the effects of alternate management options for trapping and timber harvest on marten viability, the survival grid was created by multiplying the marten regression model output by the factors specified in

several alternate scenarios (Table 4). 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 (extent of closed forest) (Chapin et al. 1998), the regression model was necessarily built using only data from trapped areas. Thus the contrast in survival between trapped and untrapped areas must be added in the form of a conceptual model. In addition to contrasts between areas open or closed to marten trapping, I assigned higher survival to parks closed to all trapping. These areas are likely to have higher survival than areas closed to marten trapping but open to trapping of other species, due to incidental mortality in the latter areas. Such parks without any trapping form only 0.8% of the Northern Appalachians region, so this decision has little effect on results.

I created simplified landscape change scenarios based on the assumption that timber harvest in the near future would occur in the same general areas (at the scale of the 10 km² "landscapes" over which the vegetation data was summarized) that have supported recent logging (Table 4). One hundred simulations of 200 years each were performed for each scenario. These simulation results are equilibrium predictions, in that current predictions depict the current capacity for an area to support a carnivore species over the long-term (200 years), which may, due to past overharvest or other lag effects, differ from the number of animals currently inhabiting that area. I also evaluated scenarios incorporating input layers based on future

TABLE 2 Base parameters used in the PATCH model of marten population dynamics. Fecundity is given as number of female offspring per adult female.

Parameter		
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

snowfall predictions in order to assess the effects of climate change alone and in interaction with other threat factors on marten viability (Table 4).

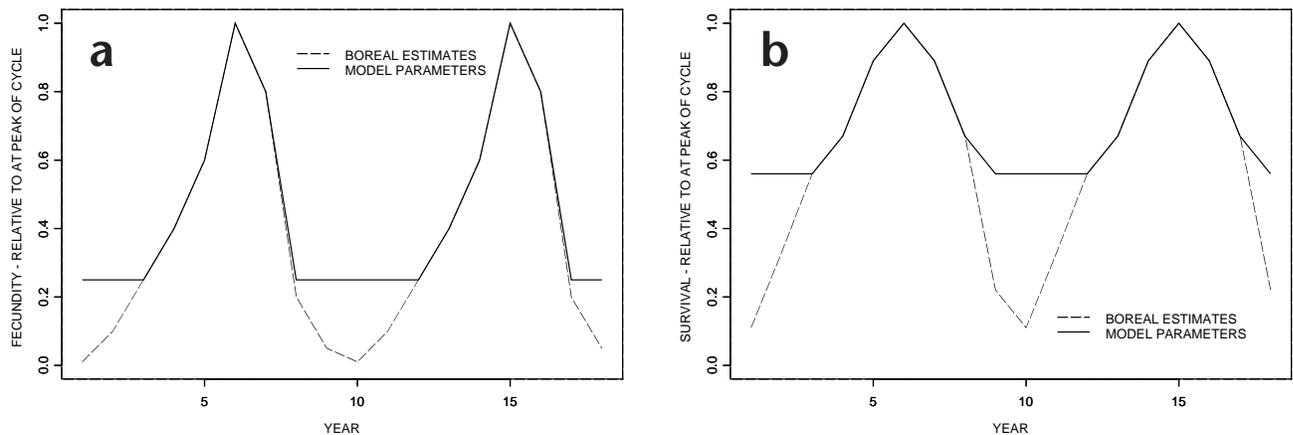
Lynx Because static habitat models had previously been developed for the lynx, the primary purpose of the lynx modeling was to evaluate the contrasts between such stat-

ic models and a dynamic model incorporating varying assumptions as to population cycles, as well as the effects of increased trapping mortality (Table 5). The regional-scale static lynx model of Hoving et al. (2005), in contrast to models at finer scales (e.g. Hoving et al. 2004), did not include variables representing forest age. Additionally, the older deciduous forest type that is included in the region-

TABLE 3 Base parameters used in the PATCH model of lynx population dynamics. Fecundity is given as number of female offspring per adult female.

Parameter										
Territory size (km ²)	90.0									
Maximum dispersal distance (km)	268									
<i>Survival rates (maximum)</i>										
young, year 1	0.77									
subadult - year 2	0.77									
adult >2 years	0.99									
at senescence (>9 years)	0.44									
<i>Fecundity rates (maximum)</i>										
subadult - year 2	2.4									
adult >3 years	2.9									
at senescence (>7 years)	2.2									
<i>Cycle of demographic multipliers</i>										
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	

FIGURE 3 Demographic rate multipliers used to evaluate the influence of cycling on lynx populations (Table 3). As shown in the figure, the multipliers used for a) fecundity and b) survival created a cycle with lower variance than that documented in boreal populations.



al-scale model of Hoving et al. (2005) is not as heavily affected by logging as is coniferous forest in this region. Therefore, I did not evaluate scenarios assessing the effects of logging on lynx, which may be more appropriate to evaluate at the subregional scale using more detailed vegetation data (e.g., Hoving et al. 2004).

Lynx population dynamics in boreal habitats have been closely linked to cyclic change in habitat quality as it relates to snowshoe hare density and other factors such as (Mowat et al. 2000). The extent of cycling in Northern Appalachians lynx populations is poorly known compared to the record from boreal populations. However, the lynx trapping data used in this study do suggest pronounced year-to-year variation in population size in this region (range of CV of trapping harvest 1985-2003 for 9 management units: 82.02-200.61%, mean 125.40%), and time

series analyses suggest cycling is evident in Gaspé lynx populations (D. Murray, pers. comm.). Cycles, as an extreme form of environmental stochasticity, tend to disproportionately impact small and isolated subpopulations (Gilpin and Soulé 1986), conditions that characterize lynx at their range margin in the Northern Appalachians. I incorporated several cyclic habitat change scenarios into the lynx model by scaling the static-model-based habitat quality values to lynx demographic performance at different points in the cycle (Table 3, Figure 3). 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 ("half-cycling"), and 3) cycling throughout the region (Table 5).

Because the Gaspé lynx population is the largest in the region and the only population subject to trapping,

TABLE 4 Alternate scenarios used to parameterize marten survival in the PATCH simulations.

Effects of changes in trapping intensity and trapping extent

B1 - Base scenario 1 - Survival set at base level except survival in parks 120% of base level (common to all scenarios)

B2 - Base scenario 2 - Survival in trapped areas 90% of base level, survival in untrapped areas 100% of base level

B3 - Base scenario 3 (increase in area open to trapping)- Survival in trapped areas 90% of base level, survival in untrapped areas 90% of base level

B4 - Base scenario 4 (increase in trapping intensity in currently open areas) - Survival in trapped areas 80% of base level, survival in untrapped areas 100% of base level

Effects of changes in extent of timber harvest

Logged scenarios - Doubling of the percentage of regenerating forest, with corresponding decrease in the percentage of conifer/mixed forest

L1 - Logged scenario 1 - Above combined with base scenario 1

L2 - Logged scenario 2 - Above combined with base scenario 2

L3 - Logged scenario 3 - Above combined with base scenario 3

L4 - Logged scenario 4 - Above combined with base scenario 4

Restored scenarios - Convert all regenerating forest to conifer/mixed forest

R1 - Restored scenario 1 - Above combined with base scenario 1

R2 - Restored scenario 2 - Above combined with base scenario 2

R3 - Restored scenario 3 - Above combined with base scenario 3

R4 - Restored scenario 4 - Above combined with base scenario 4

Effects of changes in snowfall due to climate change

Annual snowfall as predicted for 2055, based on IPCC Scenario A2 (see text).

FB2 - Base scenario 2 with 2055 snowfall

FB4 - Base scenario 4 with 2055 snowfall

FL2 - Logged scenario 2 with 2055 snowfall

FR2 - Restored scenario 2 with 2055 snowfall

TABLE 5 Alternate scenarios used to parameterize lynx fecundity and survival in the PATCH simulations.

Effects of changes in degree and extent of population cycling

- A1 - No cycling, fecundity and survival set at mean rates of cycle
- B1 - Cycling only in Gaspé, elsewhere fecundity and survival set at mean rates of cycle
- C1 - Cycling throughout region, using demographic multipliers as in Table 7

Effects of changes in trapping intensity

- A2 - No cycling, survival in Gaspé population and central Québec set at 90% of base level
- B2 - Cycling only in Gaspé, survival in Gaspé population and central Québec set at 90% of base level
- C2 - Cycling throughout region, survival in Gaspé and central Québec population set at 90% of base level

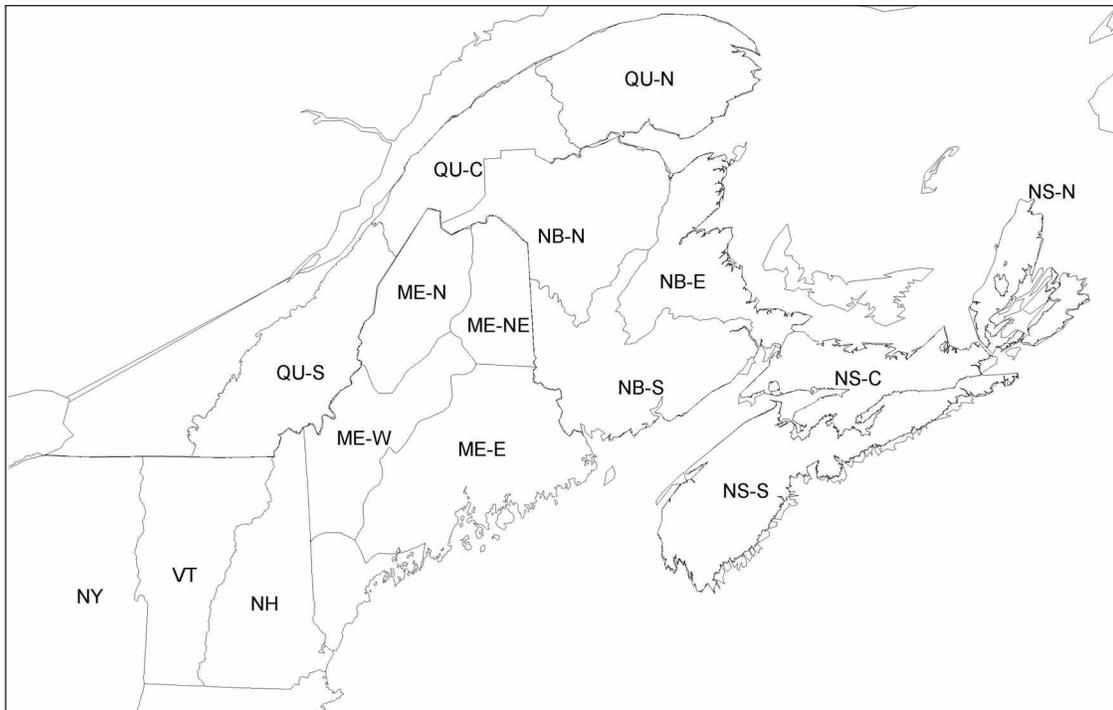
Sensitivity of results to assumptions as to territory size

- A1(36) - No cycling, fecundity and survival set at mean rates of cycle, territory size set at 36 km²
- C1(36) - Cycling throughout region, fecundity and survival set at mean rates of cycle, territory size set at 36 km²
- A2(36) - No cycling, survival in Gaspé population and central Québec set at 90% of base level, territory size set at 36 km²

Effects of changes in snowfall due to climate change

- Annual snowfall as predicted for 2055, based on IPCC Scenario A2 (see text).
- FA1 - Scenario A1 (above) with 2055 snowfall.
 - FB1 - Scenario B1 (above) with 2055 snowfall.
 - FB2 - Scenario B2 (above) with 2055 snowfall.
 - FC1 - Scenario C1 (above) with 2055 snowfall.

FIGURE 4 Subregions used in the irreplaceability-vulnerability analysis.



there has been concern as to the effects of variation in trapping pressure in Gaspé on 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), as well as the interaction between trapping and population cycles (Table 5). The average size of lynx territories in this region is poorly known in comparison to those in boreal regions, but recent field research in Maine suggests female home range sizes of 53 km² (J. Vashon, pers.comm.). Hoving et al. (2004, 2005) analyzed lynx habitat selection over circular landscapes of 100 km² in area, a size similar to that documented in boreal regions (Mowat et al. 2000). Although the base scenarios reported here were performed using a similar territory size (90 km²), I repeated a subset of the scenarios using a smaller home range size (36 km²) to evaluate sensitivity of results to this parameter. I also evaluated scenarios incorporating input layers based on future snowfall predictions in order to assess the effects of climate change alone and in interaction with other threat factors on lynx viability (Table 5).

Five hundred simulations of 200 years each were performed for each scenario, with demographic statistics were tallied from year 190. Lynx simulations, unlike those for marten and wolf, 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 choice was to allow lynx migration during unfavorable stages of the habitat cycle.

Irreplaceability/vulnerability analysis

I adapted an approach that sets priority areas for conservation action based on their irreplaceability and vulnerability in order to minimize the loss of options for conservation planning during an interim period where new reserves are being achieved in some areas while habitat loss is occur-

ring elsewhere (Pressey and Taffs 2001). An area's irreplaceability is the relative contribution it makes to reaching a conservation goal, here species persistence (Margules and Pressey 2000). I defined irreplaceability in this context as the relative value of an area as source habitat. Source habitat value depends on both the quality of a patch and its landscape context. Vulnerability, the likelihood that a site's conservation value will be reduced over time, is measured here as the predicted decline in demographic value (λ) between low threat and high threat scenarios (marten: between scenarios B2 and B4 for trapping, between scenarios R2 and L2 for logging, and between scenarios B2 and FB2 for climate change [Table 4]; lynx: scenarios A1 versus C1 for population cycling, scenarios B1 versus B2 for trapping pressure, and scenarios B1 versus FB1 for climate change [Table 5]). Values were plotted on a graph of irreplaceability (y-axis) versus vulnerability (x-axis) and the graph divided into four quadrants. The upper right quadrant, which includes sites with high irreplaceability and high vulnerability, contains the highest priority sites for conservation (Pressey and Taffs 2001). This is followed in priority by the upper left and lower right quadrants and, finally, by the lower left quadrant, containing sites that are relatively replaceable and face less severe threats. Areas in the lower-left quadrant somewhat misleadingly show low threat values because they contain sink habitat that is becoming less influential as it becomes less likely to be occupied by the species. Areas under threat tend to move clockwise through the irreplaceability/vulnerability graph from secure source to threatened source to threatened sink and ultimately to uninhabited (intersection of axes). In order to divide the study region into subunits that were relevant to both species ecotypes and regulatory contexts, I created 16 subregions by dividing the larger jurisdictions (Maine, New Brunswick, Nova Scotia, and southern Québec) into three to four subunits each based on ecosystem boundaries (Figure 4).

RESULTS

Marten static model results

Patterns in marten trapping data The areas showing highest density of marten harvest include the northern half of Maine, the northern third of New Brunswick, and the Laurentides region of Québec to the north of the St. Lawrence River (Figure 5). A strong biannual cycle in trapping harvest is evident in all trapped jurisdictions to the south of the St. Lawrence River (Figure 6a) and is synchronous across jurisdictions. This biannual cycle is not evident in trapping data from north of the St. Lawrence River in Québec (Figure 6b). Marten harvest density showed a significant positive correlation with annual snowfall ($\text{cor} = 0.53, p < 0.001$), latitude-adjusted elevation ($\text{cor} = 0.56, p < 0.001$), habitat effectiveness ($\text{cor} = 0.71, p < 0.001$), MODIS March tasseled-cap greenness ($\text{cor} = 0.57, p < 0.001$), conifer forest ($\text{cor} = 0.27, p < 0.049$), and regenerating forest ($\text{cor} = 0.29, p = 0.032$). Annual snowfall showed a threshold in its positive effect above 3000 mm per year. Some of these correlations are likely spurious due to strong correlations amongst several of the potential explanatory variables. Annual snowfall and latitude-adjusted elevation are strongly positively correlated with each other and with percent conifer, as expected. Landscapes that have high snowfall/elevation also tend to have high MODIS tasseled-cap March greenness (likely a surrogate for conifer forest) and high habitat effectiveness (perhaps due to sparse settlement and road building in mountainous areas). More surprisingly, landscapes that have high habitat effectiveness also tend to have high percent regenerating forest (recent clearcuts) ($\text{cor} = 0.32, p = 0.019$). These correlations makes it difficult to identify a best model from alternate models containing one of these variables. The counterintuitive positive correlation between habitat effectiveness (lack of human activity) and regenerating forest (recent clearcuts) may be an issue of spatial and temporal scale, e.g., most recent logging may be occurring in the most remote parts of the region if other areas were logged in the past and now have less merchantable timber, and the scale of a trapping management unit may hold large clearcuts but still contain landscapes of older forest that support marten.

Marten regression model Among the alternate models considered in the analysis of the primary marten data set

(Maine, New Brunswick, and southern Québec data), a model containing annual snowfall and habitat effectiveness showed lowest AIC, whether or not the effect of jurisdiction was considered (Table 6, Figure 7). Although the jurisdiction covariate had a significant effect on marten harvest (Table 7), in order to maximize model generality and allow extrapolation to untrapped jurisdictions, a final model was selected from the set of models without the jurisdiction variable. The high coefficient values shown by the habitat effectiveness variable in the multivariate models containing it (Table 6) made predictions from these models similar to those from the univariate model for habitat effectiveness. The snowfall/habitat effectiveness model did not show lowest AIC when tested against data from other areas (Adirondacks and Québec), in fact it was nearly the poorest AIC model (Table 7). Therefore, the results of the AIC comparison can be summarized as indicating 1) a group of models dominated by habitat effectiveness showed lowest AIC but had poor generality when extrapolated to adjacent regions, and 2) an alternate set of models containing snowfall plus either March tasseled-cap greenness or forest type, but not containing habitat effectiveness, show ΔAICs that would exclude them from consideration in a strictly AIC-based model selection (i.e., $\Delta\text{AICs} > 2$), but showed greater interpretability and agreement with field data (e.g., Chapin et al. 1998, Powell et al. 2003). Although both types of models were highly significant ($p < 0.001$), the lowest AIC model showed an R^2 of 0.57, versus a model using snowfall and older conifer/mixed forest which showed an R^2 of 0.44. A significant model that did not have the best AIC was selected for use in the subsequent dynamic modeling in order to 1) incorporate field knowledge on marten habitat relations and thus improve model generality, and 2) allow creation of landscape change scenarios relevant to management. I also chose a model containing vegetation type over one containing less interpretable variables such as tasseled-cap greenness because landscape change trends (e.g., changes in logging intensity) can be used to predict changes in extent of forest types more easily than they can be linked to changes in greenness. This is an example of why information criteria (AIC [Akaike 1983] and BIC [Schwarz 1978]) based model selection is only one factor in identifying the most informative model for

FIGURE 5 American marten trapped per 100 km² based on a multi-jurisdiction trapping harvest database assembled for this study from data provided by state and provincial wildlife agencies.

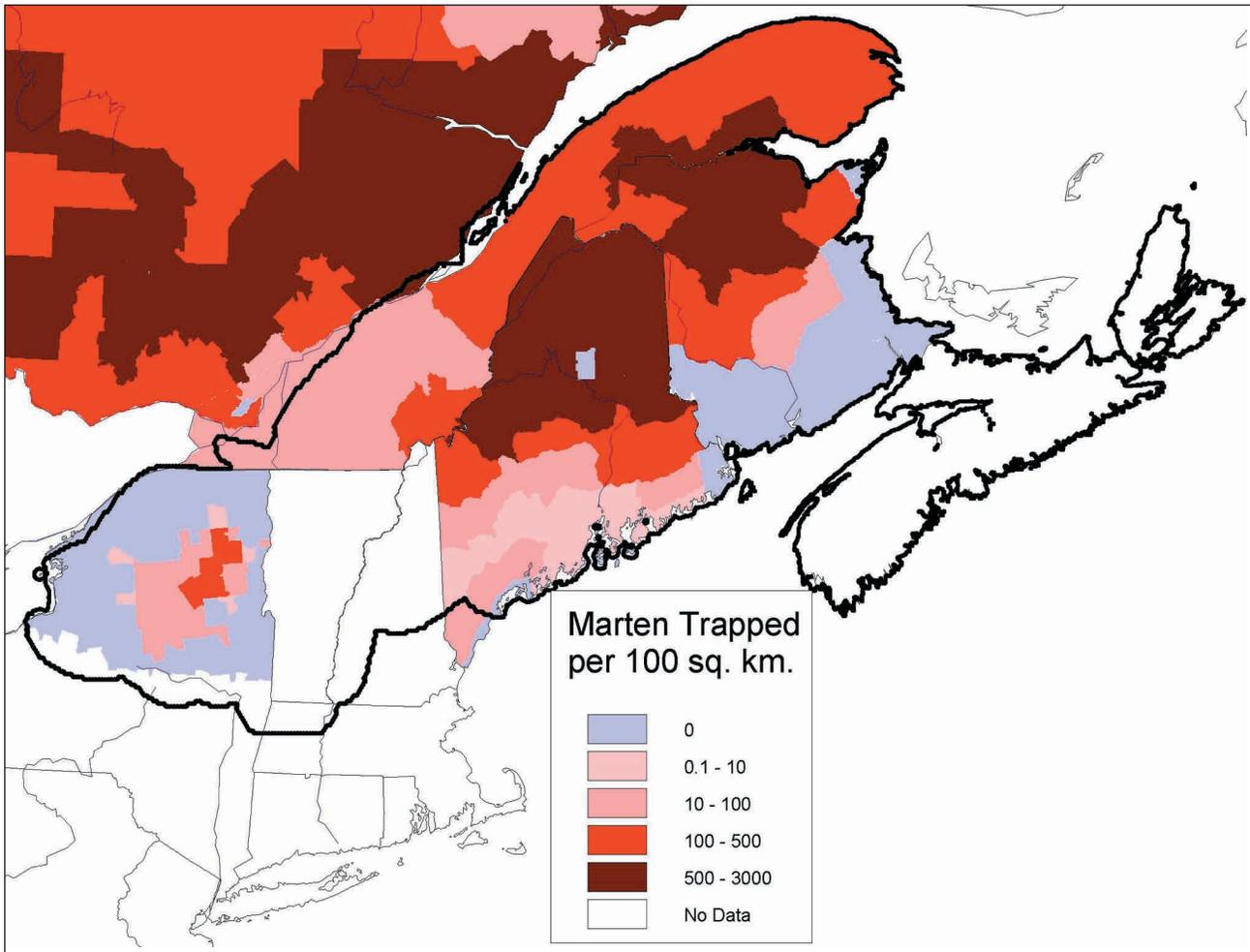


FIGURE 6 Temporal pattern in marten harvest shown by trapping data from (a) several jurisdictions in the Northern Appalachians region, and (b) compared with data that includes areas north of the St. Lawrence River.

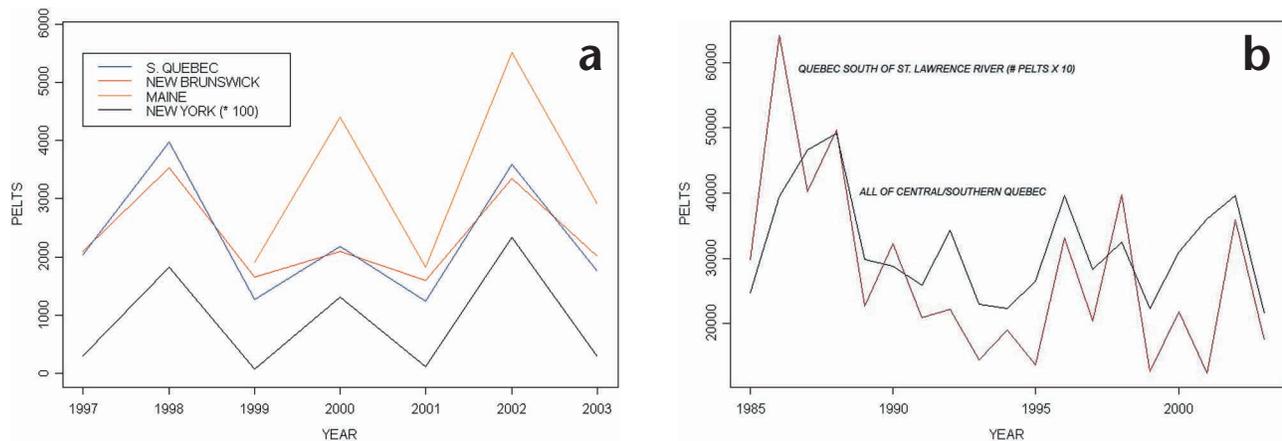


FIGURE 7 Marten habitat suitability in the Northern Appalachians region as developed from a regression model based on correlations between marten trapping data and both annual snowfall and habitat effectiveness (the inverse of human population and road density).

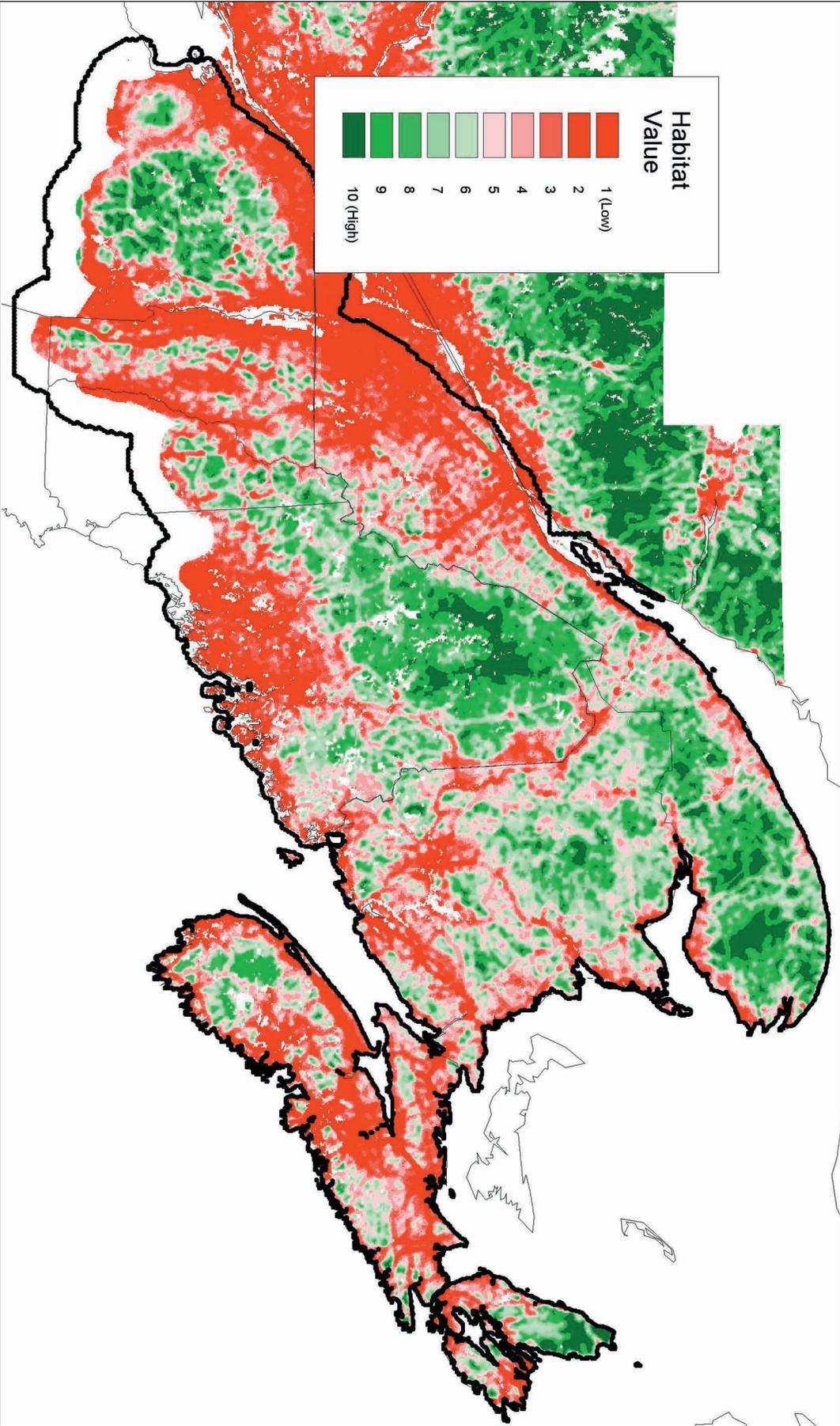


TABLE 6 Rankings of alternate regression models for marten harvest density (n=54).

	AIC*	Δ AIC	Δ AIC <i>within group</i>
<i>Model set without jurisdiction variable</i>			
HAB	580.86	3.17	2.90
MGRN	597.12	19.43	19.16
SNOW	599.39	21.70	21.43
SUM(CON,MIX)	610.28	32.59	32.32
SNOW, HAB	577.96	0.27	0.00
SNOW, MGRN	587.05	9.36	9.09
SNOW, CON, MIX	594.99	17.30	17.03
SNOW, SUM(CON,MIX)	593.15	15.46	15.19
SNOW, SUM(REG, CON, MIX)	593.38	15.69	15.42
SNOW, SUM(CON,MIX,DECID)	594.48	16.79	16.52
SNOW, CON, MIX, HAB	580.67	2.98	2.71
SNOW, SUM(CON,MIX), HAB	578.82	1.13	0.86
SNOW, SUM(REG, CON, MIX), HAB	578.54	0.85	0.58
SNOW, REG, HAB	579.95	2.26	1.99
<i>Model set with jurisdiction variable</i>			
SNOW, MGRN, JUR	586.44	8.75	
SNOW, HAB, JUR	577.69	0.00	
SNOW, CON, MIX, JUR	590.23	12.54	
SNOW, CON, MIX, HAB, JUR	578.74	1.05	
SNOW, SUM(CON,MIX), JUR	587.80	10.11	
SNOW, SUM(REG, CON, MIX), JUR	586.67	8.98	
SNOW, SUM(REG, CON, MIX), HAB, JUR	578.54	0.85	<i>*(for So. PQ, NB, ME data)</i>

TABLE 7 Results of validation of alternate marten regression models with data from jurisdictions (central Québec, Adirondacks [ADKs]) not used in the original regressions. Vegetation data were unavailable for central Québec, so models containing vegetation variables were not validated there.

	AIC (for all Québec data)	AIC (for ADKs)
HAB	855.31	364.17
MGRN	844.14	358.88
SNOW	855.02	365.48
SUM(CON,MIX)	N/A	359.33
SNOW, MGRN	832.10	357.38
SNOW, HAB	856.60	366.11
SNOW, REG, HAB	N/A	367.81
SNOW, CON, MIX	N/A	352.24
SNOW, CON, MIX, HAB	N/A	353.18
SNOW, SUM(CON,MIX)	N/A	357.26
SNOW, SUM(CON,MIX), HAB	N/A	352.89
SNOW, SUM(REG, CON, MIX)	N/A	357.57
SNOW, SUM(REG, CON, MIX), HAB	N/A	353.05

a particular modeling application (Taper 2004). The regression model selected took the form:

$$\text{Marten trapped per } 100 \text{ km}^2 = 54.97756 + 0.495844 * \text{SNOW} + 7.351139 * (\text{CON} + \text{MIX})$$

where SNOW is annual snowfall, incorporating a threshold at 3000 mm per year, and (CON+MIX) is percent of older conifer and mixed forest (n=54, p < 0.001, R² = 0.44 for the multivariate model).

Distribution of suitable habitat Areas that showed the highest density of marten harvest (the northern half of Maine and the northern third of New Brunswick) not surprisingly showed high predicted habitat suitability in the snowfall/conifer/mixed model (Figure 8). However, the Gaspé peninsula of Québec shows higher suitability than expected based on marten harvest density. The regression model predicts fine-grained variation in habitat suitability, e.g., within northern Maine, that is not discernable from the raw trapping harvest data. When change in snowfall to 2055 was incorporated into the regression model, suitable habitat was effectively eliminated from Nova Scotia, southern New Brunswick, and eastcentral Maine (Figure 9), and predicted marten abundance was reduced in more northerly areas.

Marten dynamic model results

Predicted equilibrium distribution and demographic structure As compared to species with larger home ranges such as the wolf, the PATCH results for marten show a finer-scale pattern of distribution of sources and sinks. The demographic structure shown in Figures 10, 12, and 13 represents the PATCH marten output averaged over a 300 km² moving-window. This is for cartographic reasons only, because the raw results would be difficult to distinguish on a regional-scale map. All summary statistics were based on the unaveraged results. The base scenario 2 (Figure 10a) approximates fairly well current marten distribution in the mainland of its range in the Northern Appalachians. However, PATCH overpredicts the extent of the Cape Breton Island population and predicts a potential population around Fundy Park where reintroduction efforts have met mixed success. Little habitat potential is predicted for southern Nova Scotia where a reintroduction effort appears to have been successful, and the extent of the Adirondack population may be underpredicted. Discrepancies between model predictions and current distributions are thus greatest in isolated subpopulations.

Under base scenario 2, strong source habitat is predicted in northern New Brunswick, northeastern Maine, New Hampshire's White Mountains, and portions of the central Gaspé peninsula. These PATCH predictions differ from the areas of highest habitat suitability in the static model (Figure 8) in that the northern Gaspé peninsula, and isolated areas of habitat in southern New Brunswick, Vermont, and Nova Scotia show lower than expected lambda in PATCH (Figure 10a).

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 base scenario 2 was 10.9% in Maine, 5.0% in New Hampshire, 16.0% in New York, 28.0% in Vermont, 6.6% in southern Québec, 5.7% in New Brunswick, 7.1% on Cape Breton Island, and 85.7% in mainland Nova Scotia.

Comparison of marten scenarios: effects of landscape change 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%. However, this proportionally small change caused large changes in marten population size in some areas. Predicted population size for the various states and provinces ranges from near 12,000 for Maine and Québec to less than 500 for New York and mainland Nova Scotia (Table 8). Because population predictions from PATCH 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. Contrasts in the sensitivity of marten population size by state/province to alternate trapping scenarios (1 through 4)(Figure 11) suggest that New York and Vermont populations are more influenced by differences between the trapping mortality scenarios than those in New Hampshire, Maine, and Maritime Canada. Among jurisdictions that are currently trapped, vulnerability to increased trapping intensity (population loss between base scenario 2 and base scenario 4) is greater in Maine (39.2%) and especially New York (76.1%) than in southern Québec (29.3%) or New Brunswick (32.9%). Among jurisdictions that are not currently trapped, vulnerability to initiation of trapping (base scenario 2 versus base scenario 3) is greater in mainland Nova Scotia (85.3%) and Vermont (77.6%) than in New Hampshire (18.0%) or Cape Breton Island (23.3%). Contrasts in the sensitivity of marten population size by state/province to alternate log-

FIGURE 8 Marten habitat suitability in the Northern Appalachians region as developed from a regression model based on correlations between marten trapping data and both annual snowfall and percent of coniferous or mixed forest.

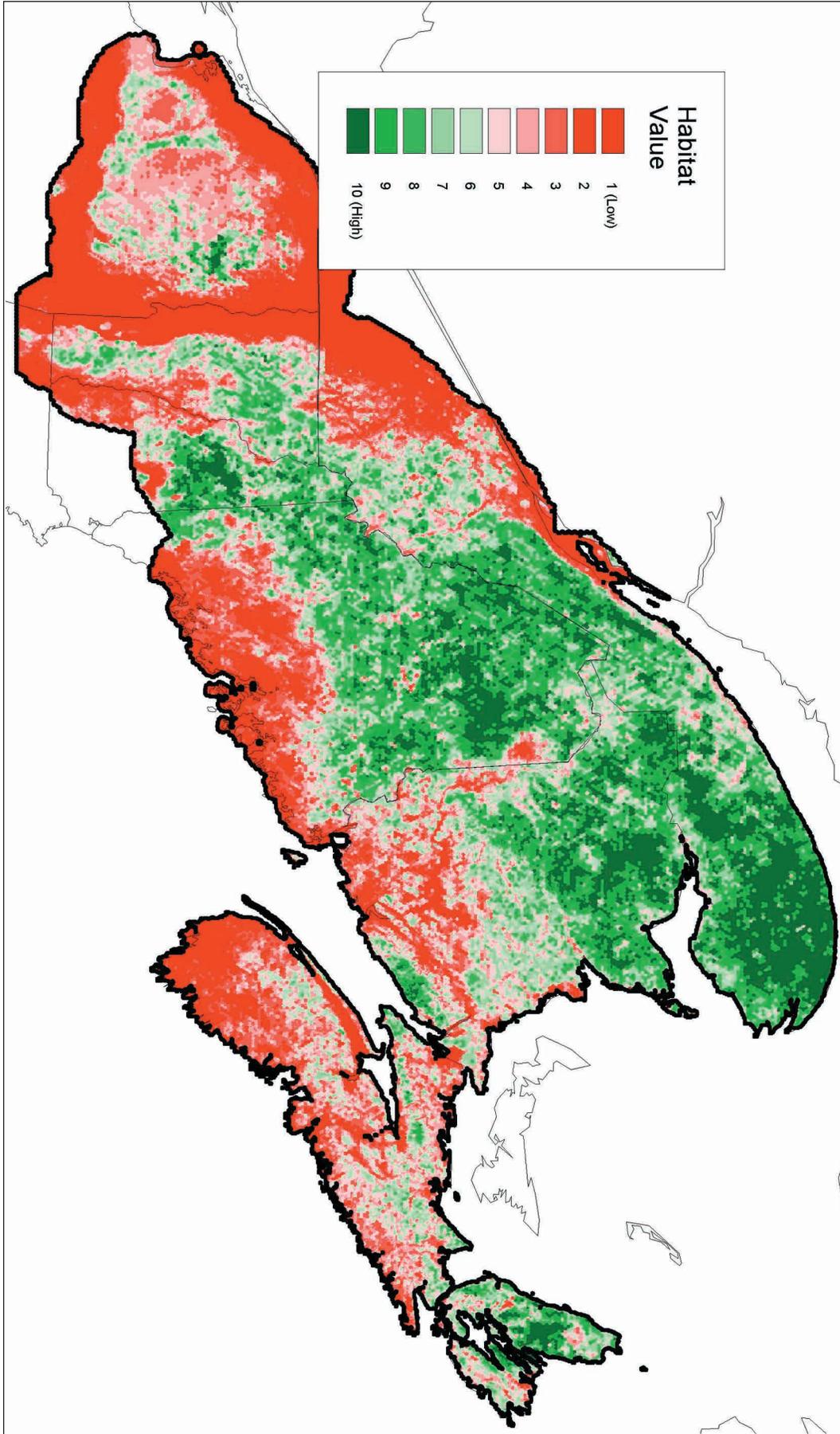


FIGURE 9 Marten habitat suitability in the Northern Appalachians region as developed from a regression model based on correlations between marten trapping data and both annual snowfall and percent of coniferous or mixed forest, with annual snowfall as predicted for 2055 under IPCC climate change scenario A2.

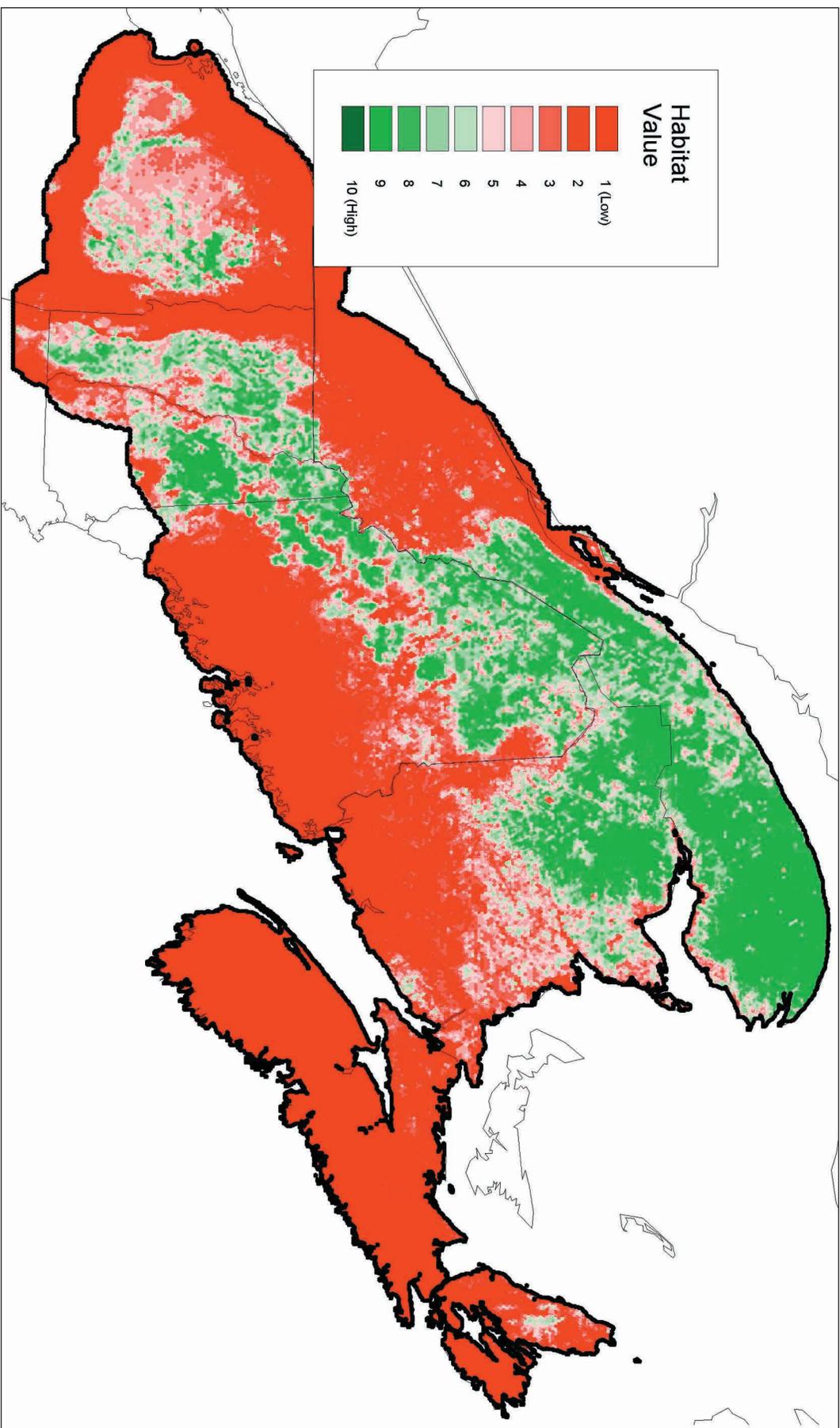
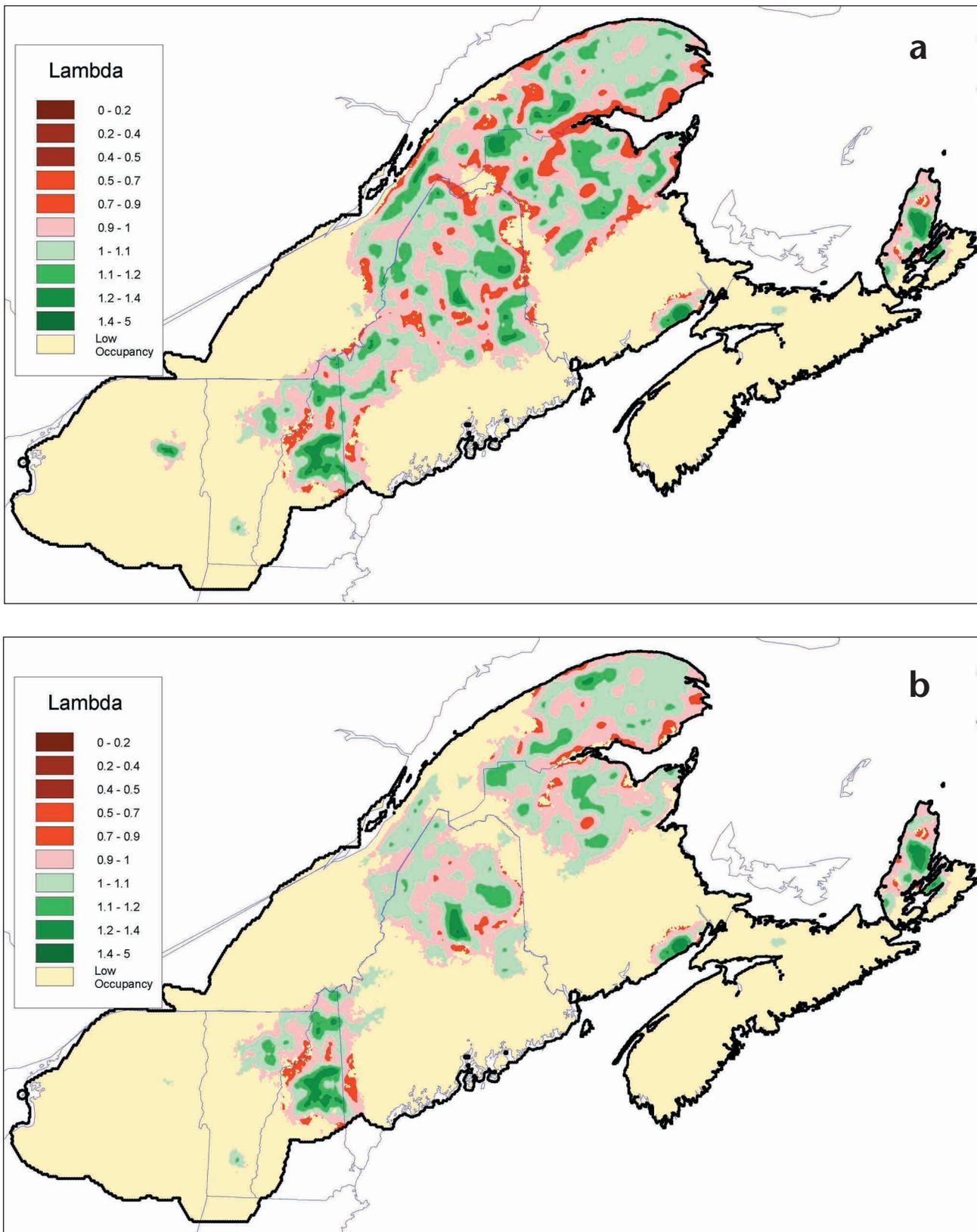


FIGURE 10 Comparison of demographic potential and distribution of marten under (a) current landscape conditions (base scenario 2, Table 4) and (b) the increased trapping pressure scenario (base scenario 4, Table 4). Legend shows population growth rate (λ) values predicted by the PATCH model simulations. Areas in green are population sources, whereas areas in red are sinks. Areas with less than 50% probability of occupancy are shown in yellow.



ging scenarios (e.g., logged 2 versus restored 2)(Figure 11) suggest that Canadian populations are much more influenced by differences between the logging scenarios than those in the northeast United States. In particular, mainland Nova Scotia shows a large effect of habitat restoration, though even restored habitat remains vulnerable to trapping mortality due to the population's small size and isolation. Differences in slopes of the three lines in Figure 11 indicate an interaction between trapping and logging effects. The most interaction between the effects of trapping and logging is evident in New Brunswick (28.5% population loss from restoration scenarios 2 to 4 versus 50.8% loss from logging scenario 2 to 4). The effects of climate change on marten distribution and viability were most pronounced in Nova Scotia (Table 8). However, the large population in Maine also was greatly reduced under

climate change, and the New Brunswick population was moderately vulnerable (Table 8).

The contrast in the relative vulnerability of different regions to the threat scenarios is also evident in changes in distribution and demography, as expressed by increase in sink habitat, fragmentation of range, and ultimately loss of viability (extirpation) of the smaller peripheral populations. Increase in trapping intensity in currently trapped jurisdictions (base scenario 2 versus base scenario 4) results in fragmentation of formerly continuous range into two large subpopulations (in northern New Brunswick/northern Gaspé and northern Maine) and two smaller untrapped populations (northern New Hampshire and Cape Breton Island), and loss of the Adirondack subpopulation (Figure 10b). Increase in logging intensity (logged scenario 2) results in a similar pattern of fragmentation as shown by the trapping

FIGURE 11 Response of predicted marten population size by state to scenarios. The x axis shows scenarios 1 through 4, with the solid lines showing “restored” scenarios, dotted lines showing base scenarios, and long-dashed lines showing “logged” scenarios (Table 4). Because population predictions from PATCH 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.

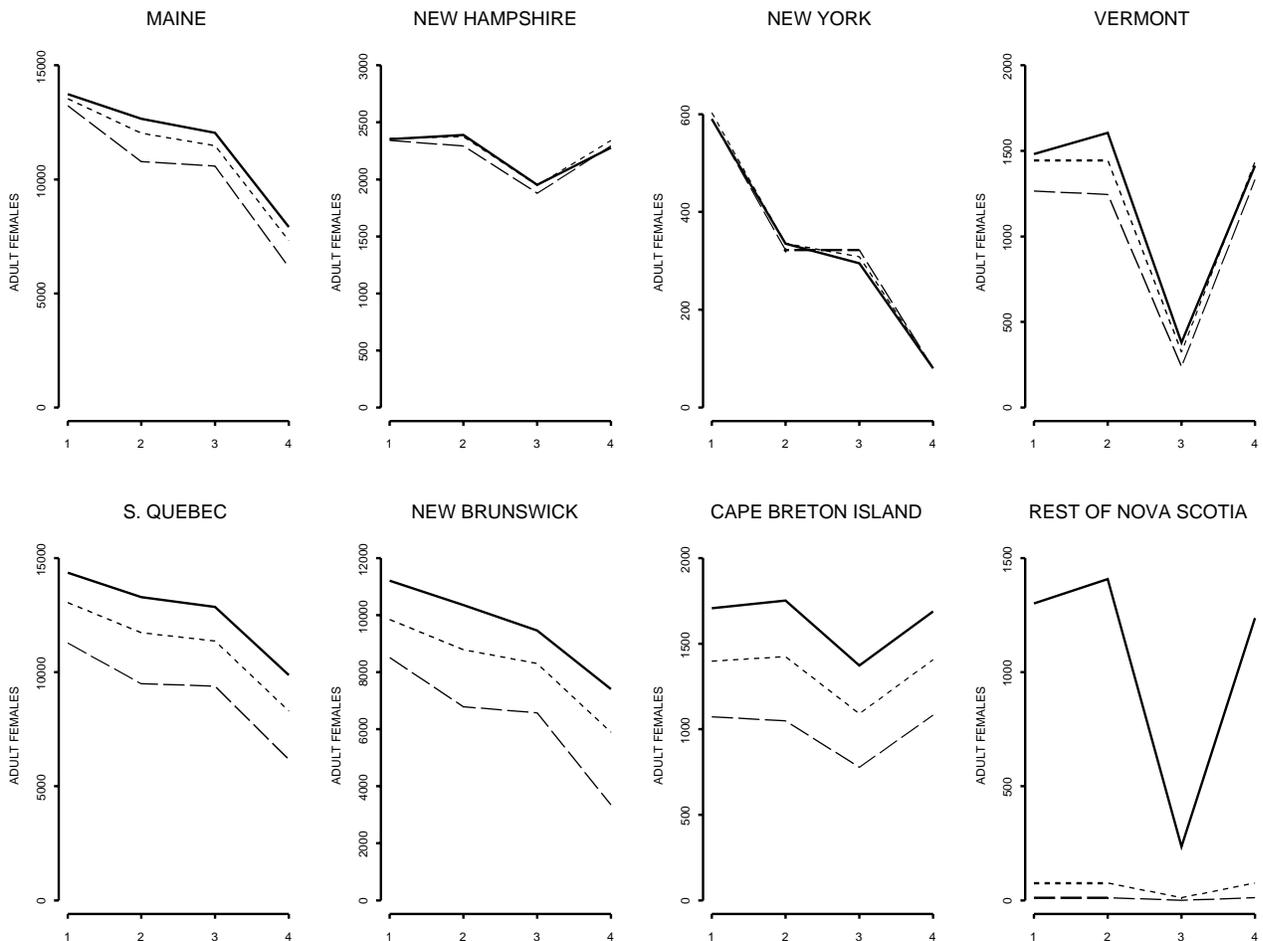


FIGURE 12 Comparison of demographic potential and distribution of marten under (a) the increased timber harvest scenario (logging scenario 2, Table 4) and (b) the decreased timber harvest scenario (restoration scenario 2, Table 4). Legend shows population growth rate (lambda) values predicted by the PATCH model simulations. Areas in green are population sources, whereas areas in red are sinks. Areas with less than 50% probability of occupancy are shown in yellow.

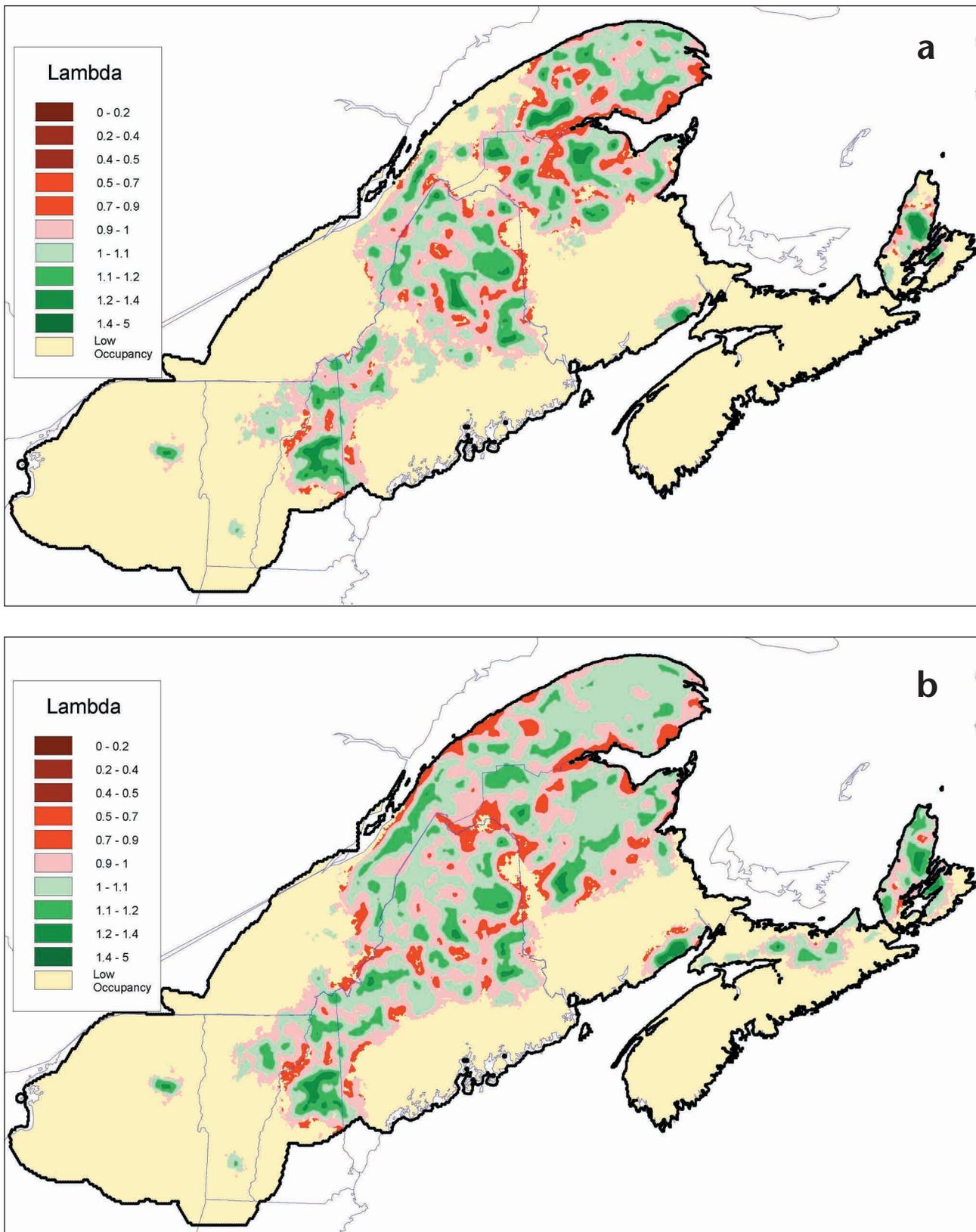
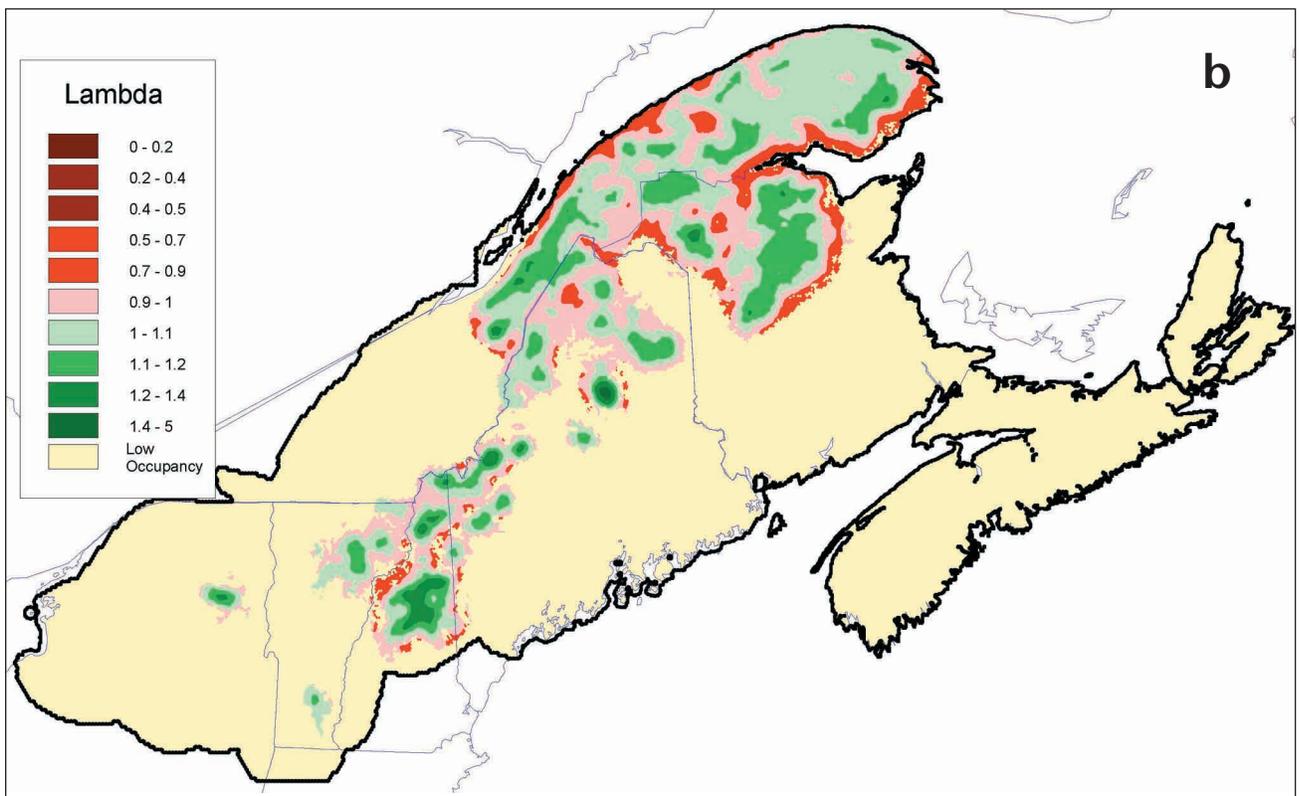
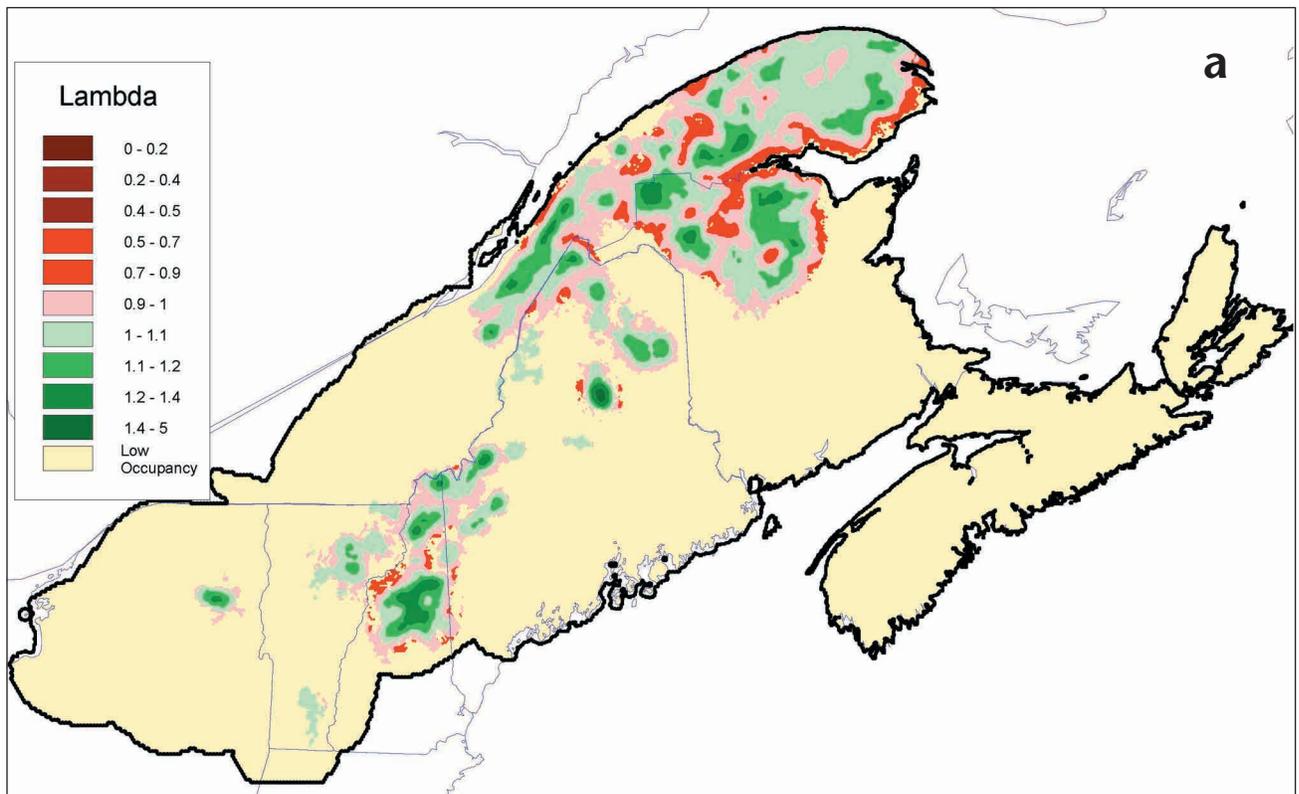


FIGURE 13 Comparison of demographic potential and distribution of marten under (a) the decreased snowfall scenario (climate change scenario FB2, Table 4) and (b) the decreased snowfall plus restoration scenario (climate change scenario FR2, Table 4). Legend shows population growth rate (lambda) values predicted by the PATCH model simulations. Areas in green are population sources, whereas areas in red are sinks. Areas with less than 50% probability of occupancy are shown in yellow.



scenarios, differing in that the northern Maine subpopulation retains more source habitat and connectivity to the south than in the trapping scenarios, and the Adirondack subpopulation persists (Figure 12a). Decrease in logging intensity (restored scenario 2) results in a similar pattern of distribution as shown by the base scenario except for range expansion in Nova Scotia and central New Brunswick (Figure 12b). Climate change sharply reduced marten distribution in Maine, fragmenting the regional population into a larger population in northern New Brunswick/northern Gaspé and a remnant isolate in the mountains of northern New Hampshire (Figure 13a). Restoration mitigated this range contraction to some extent by maintaining distribution in northern and western Maine (Figure 13b).

Lynx static and dynamic model results

Based on comparison of the lynx static model shown in Hoving et al. (2005) with an adapted model substituting other vegetation and snowfall data sources (Figure 14), it appears appropriate to apply the model with the alternate data sources. The MODIS vegetation data for percent deciduous forest appears to match the TNC data well in the U.S. but to lead to overprediction of lynx habitat in southeastern Canada. The adapted version of the Hoving et al. (2005) model (using MODIS data) was significantly correlated with lynx harvest density in central and southern Québec ($cor=0.62$, $p<0.001$). When change in snowfall to 2055 was incorporated into the model of Hoving

(2005), suitable habitat was eliminated from Cape Breton Island and greatly reduced in Maine and New Brunswick.

The distribution of lynx in the PATCH simulations with no environmental stochasticity matches 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 Maine, the Adirondacks, and Cape Breton Island (Figure 15a). However, the fragmented distribution of lynx habitat within the northeast U.S. and Cape Breton Island, combined with the negative effect of population cycling, causes a smaller proportion of potential habitat there to be occupied in the PATCH simulations when compared with the static model or with simulations in more continuous habitat (i.e., boreal regions)(Figure 15a versus 15b, Table 9). This cause these peripheral populations to be sensitive to extirpation given changes in the assumptions concerning the intensity of population cycling (e.g., scenarios A1 vs. C1). In the scenarios where cycling was confined to the Gaspé population (B1), lynx populations in Maine and New Brunswick benefitted (were larger) than when either none (A1) or all (C1) of the region experienced cycling. These populations benefitted from dispersal from Gaspé during cyclic highs (B1), but this effect was negated when these areas also directly experienced population cycles (C1). Increased trapping in the Gaspé (A1 vs. A2) had a significant negative ripple effect on New Brunswick and Maine populations. When these peripheral areas (New Brunswick and Maine) also experienced cycling (C1 vs. C2), the population decrease caused by cycling was addi-

TABLE 8 Number of adult female marten predicted to inhabit various states and provinces in the PATCH scenarios (Table 5). Because population predictions from PATCH 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.

Scenario	B1	B2	B3	B4	L1	L2	L3	L4	R1	R2	R3
<i>Jurisdiction</i>											
Maine	13530	12020	11469	7306	13224	10775	10571	6142	13734	12652	12040
New Hampshire	2357	2373	1947	2340	2340	2291	1878	2295	2352	2389	1952
New York	603	335	308	80	590	322	322	80	590	335	295
Vermont	1444	1444	324	1438	1264	1245	237	1332	1482	1606	380
Southern Québec	13046	11725	11360	8291	11278	9490	9388	6178	14367	13290	12863
New Brunswick	9840	8786	8304	5893	8518	6786	6572	3339	11215	10358	9465
Cape Breton Island	1397	1423	1091	1406	1072	1049	778	1082	1707	1752	1373
Mainland Nova Scotia	75	75	11	75	11	11	0	11	1301	1408	235

tive to the decline caused by trapping in Gaspé. In contrast, the Gaspé population itself, though vulnerable to increased trapping, because of its large size did not show further additive vulnerability due to cycling (A2 vs. C2). Effects of increased trapping in Gaspé under the half-cycling assumption (B1 vs. B2; Figure 16) were thus similar to those under the no cycling assumption (A1 vs. A2). When the territory size parameter was set at 36 km² rather than 90 km², the effects of cycling on peripheral populations (A1(36) vs. C1(36)) were not as dramatic, because all populations were now larger. Trapping scenarios (A1(36) vs. A2(36)) also showed this effect, but were not as sensitive as the cycling scenarios to the territory size parameter.

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 9, Figure 17). Mountainous or more northerly populations (New Brunswick) were moderately vulnerable to climate change, while the core Gaspé population, at the northern limits of the study area, was least vulnerable. However, the threats from trapping and climate change interacted, causing a Gaspé population affected by climate change to become highly vulnerable to additional threats from trapping (Table 9: scenario B2 (Figure 16b) vs. FB2).

Irreplaceability/vulnerability analysis

Irreplaceability and vulnerability were graphed in terms of the 16 subregions (Figures 18-20). Highest priority areas (upper right quadrant) differ between species, and between threat processes for the same species (trapping, logging and climate change for the marten, and trapping, cycling, and climate change for the lynx). Western and northeastern Maine, northern New Brunswick, and northern Gaspé show highest priority under the marten trapping scenarios (Figure 18a), whereas northern New Brunswick, Cape Breton Island, and central Gaspé show highest priority under the logging scenarios (Figure 18b). All three areas in Maine show higher threat for the marten under trapping than under logging scenarios. Northeastern Maine and Cape Breton Island show highest priority under the climate change scenarios (Figure 19a).

The graphs for lynx identifies priority areas in northern Gaspé under the cycling scenarios (Figure 20a), in northern and central Gaspé under the trapping scenarios (Figure 20b), and in northern and Gaspé, northern New Brunswick, and western Maine under the climate change scenarios (Figure 19b). For comparison, highest priority areas for wolf include northern, northeastern, and western Maine (Carroll 2003).

TABLE 9 Percentage change in lynx population size between the PATCH scenarios described in Table 6.

					ME	NH	NY	So. PQ	NB	CBI	
					<i>Scenario</i>						
					A1 vs. C1	19.38	62.15	36.80	14.54	16.25	94.93
					A1 vs. B1	-14.76	3.27	0.99	7.97	-5.72	15.03
					A1 vs. A2	23.25	0.78	0.25	80.03	19.65	7.92
					C1 vs. C2	38.27	5.28	4.11	75.46	30.10	-9.68
					A2 vs. C2	35.16	63.87	39.24	-5.01	27.15	93.97
					B1 vs. B2	29.09	-3.04	-0.37	62.75	19.65	3.56
					A1(36) vs. C1(36)	20.57	38.00	18.82	11.28	17.75	51.18
					A1(36) vs. A2(36)	19.47	-0.31	0.06	79.53	14.79	0.54
R4	FB2	FB4	FL2	FR2	A1 vs. FA1	94.38	65.59	37.07	26.66	77.27	100.00
7918	4011	3266	1495	5424	B1 vs. FB1	90.43	69.05	37.44	34.15	65.60	100.00
2279	2108	2058	2096	2170	B2 vs. FB2	99.61	68.04	37.35	89.16	92.36	100.00
80	325	344	87	339	C1 vs. FC1	90.36	99.62	60.39	28.56	67.74	100.00
1413	1320	1248	1383	1494							
9876	10188	8436	7169	11412							
7411	4925	3712	2835	6079							
1688	0	0	0	0							
1237	0	0	0	0							

FIGURE 14 Comparison of predicted high value lynx habitat using the snowfall/deciduous forest model of Howing et al. (2005) and replacing AVHRR vegetation type data with vegetation type data from either MODIS or a detailed regional-scale vegetation layer prepared by the Nature Conservancy (TNC). The MODIS data appears to match the TNC data well in the U.S. but to overpredict lynx habitat in southeastern Canada. The border of the TNC vegetation data is shown in black; MODIS data only were available north of the St. Lawrence River.

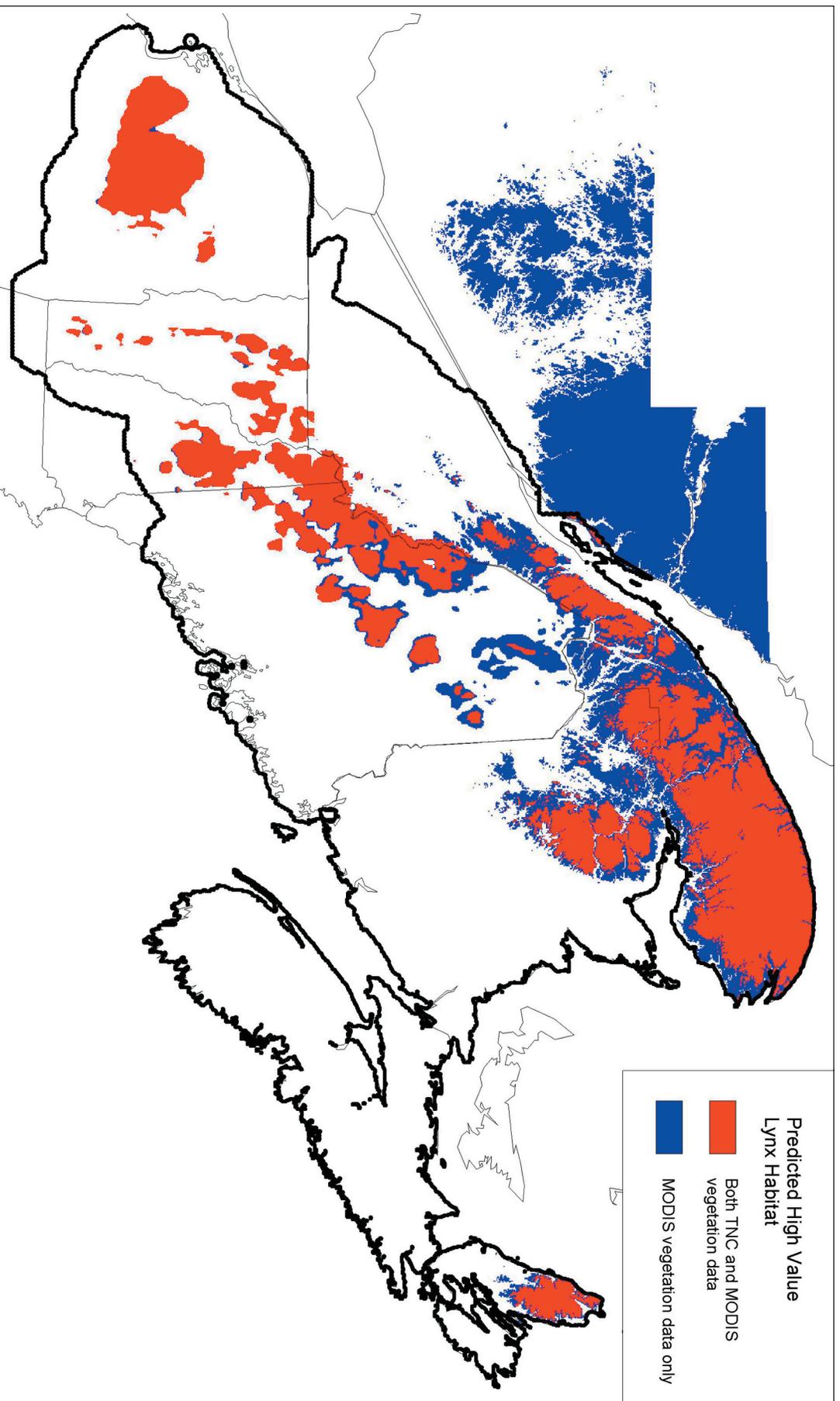


FIGURE 15 Response of lynx populations to cyclic variation in habitat quality: comparison of distribution of lynx under (a) mean environmental conditions (scenario A1, Table 5) and b) cycling of habitat suitability (scenario C1, Table 5). Legend shows percentage occupancy of habitat over time predicted by the PATCH model simulations.

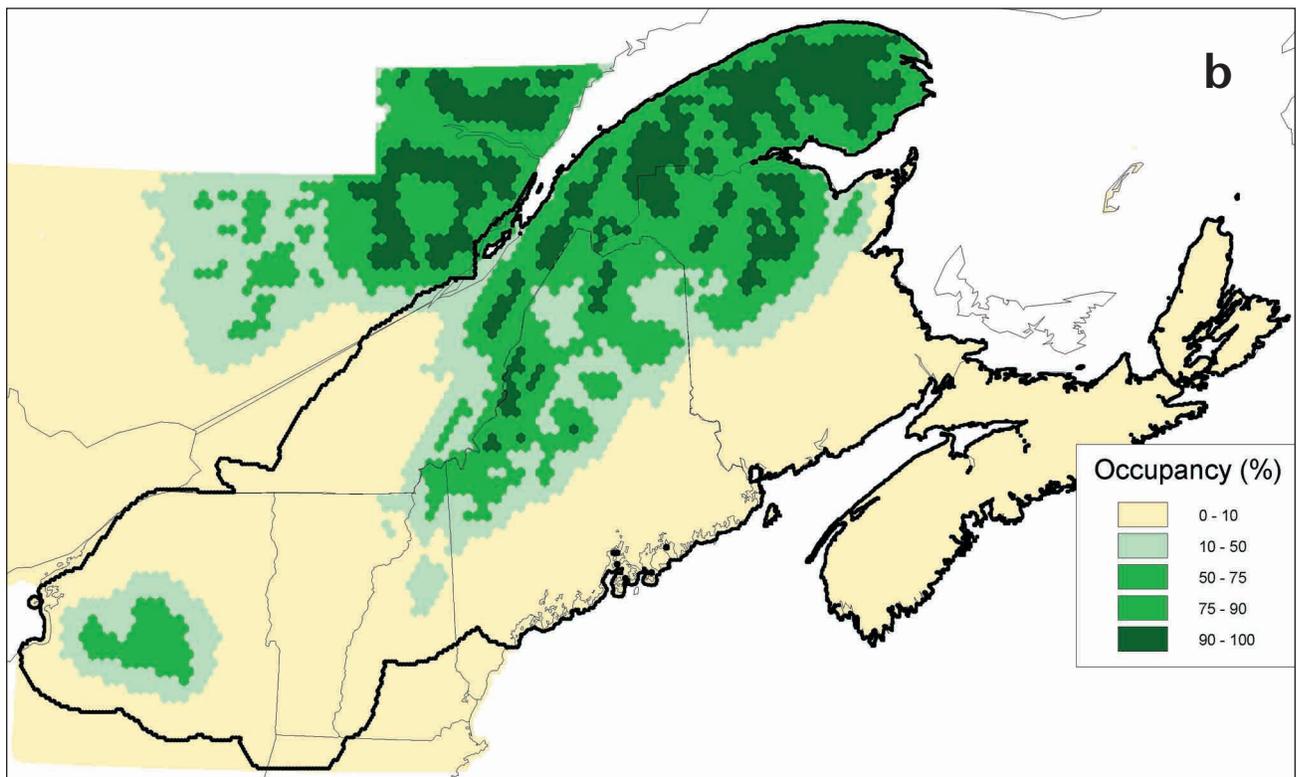
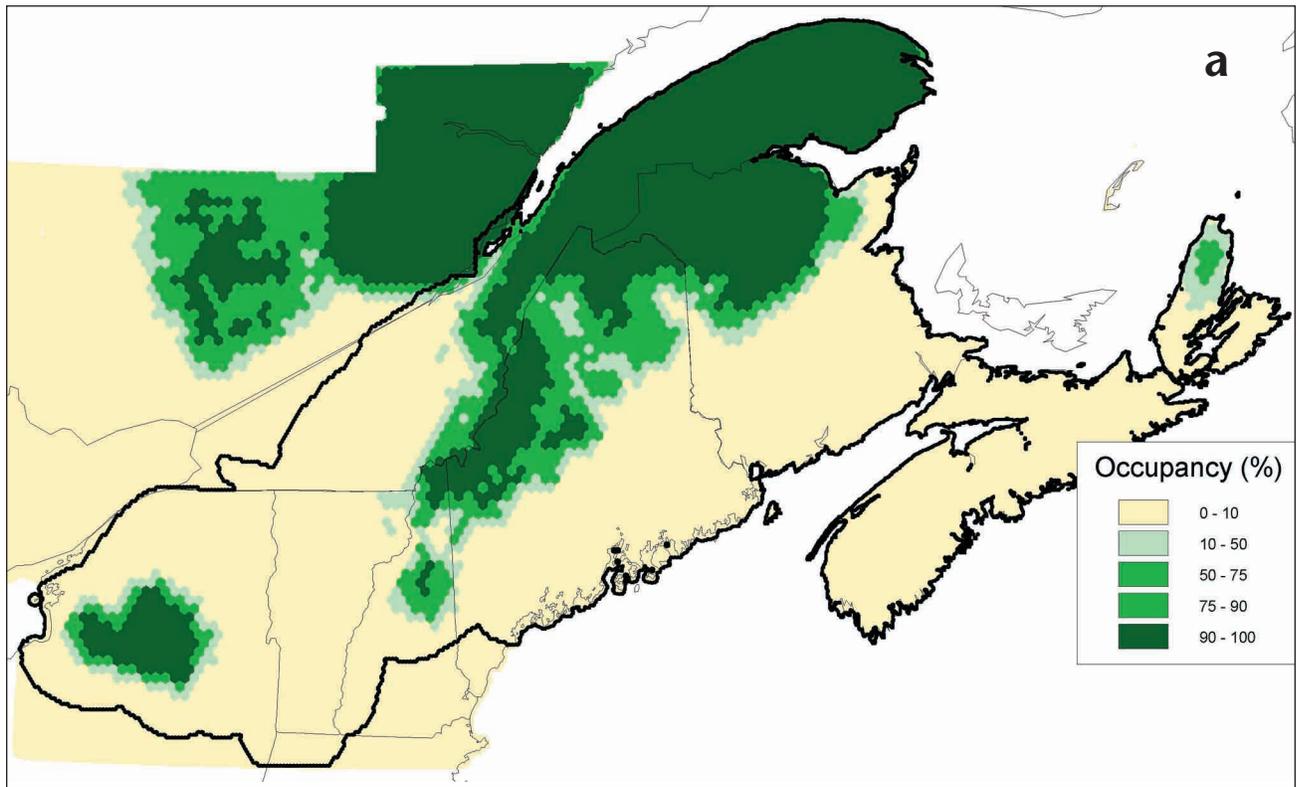


FIGURE 16 Response of lynx populations to increased trapping pressure: comparison of distribution of lynx under (a) scenario with cycling only in Gaspé (scenario B1, Table 5) and b) scenario with cycling only in Gaspé, and increased trapping mortality in Gaspé and central Québec (scenario B2, Table 5). Legend shows percentage occupancy of habitat over time predicted by the PATCH model simulations.

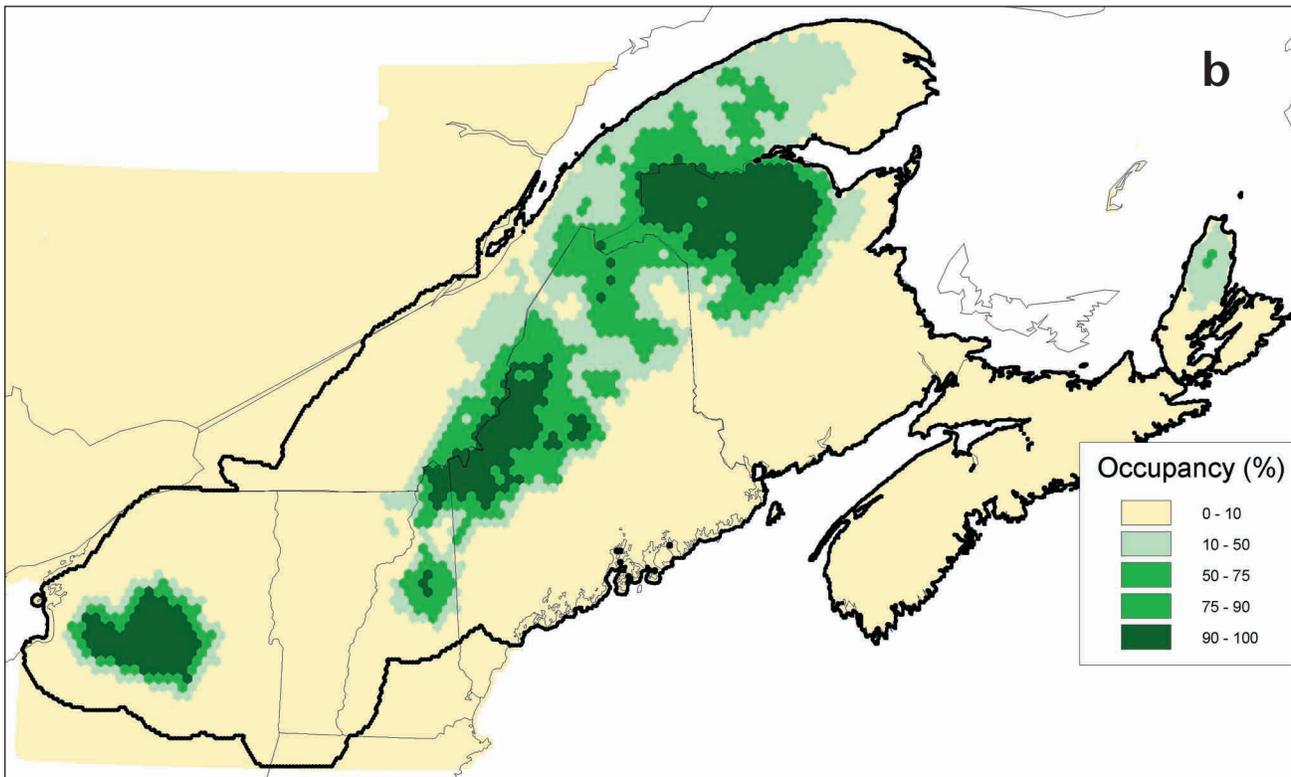
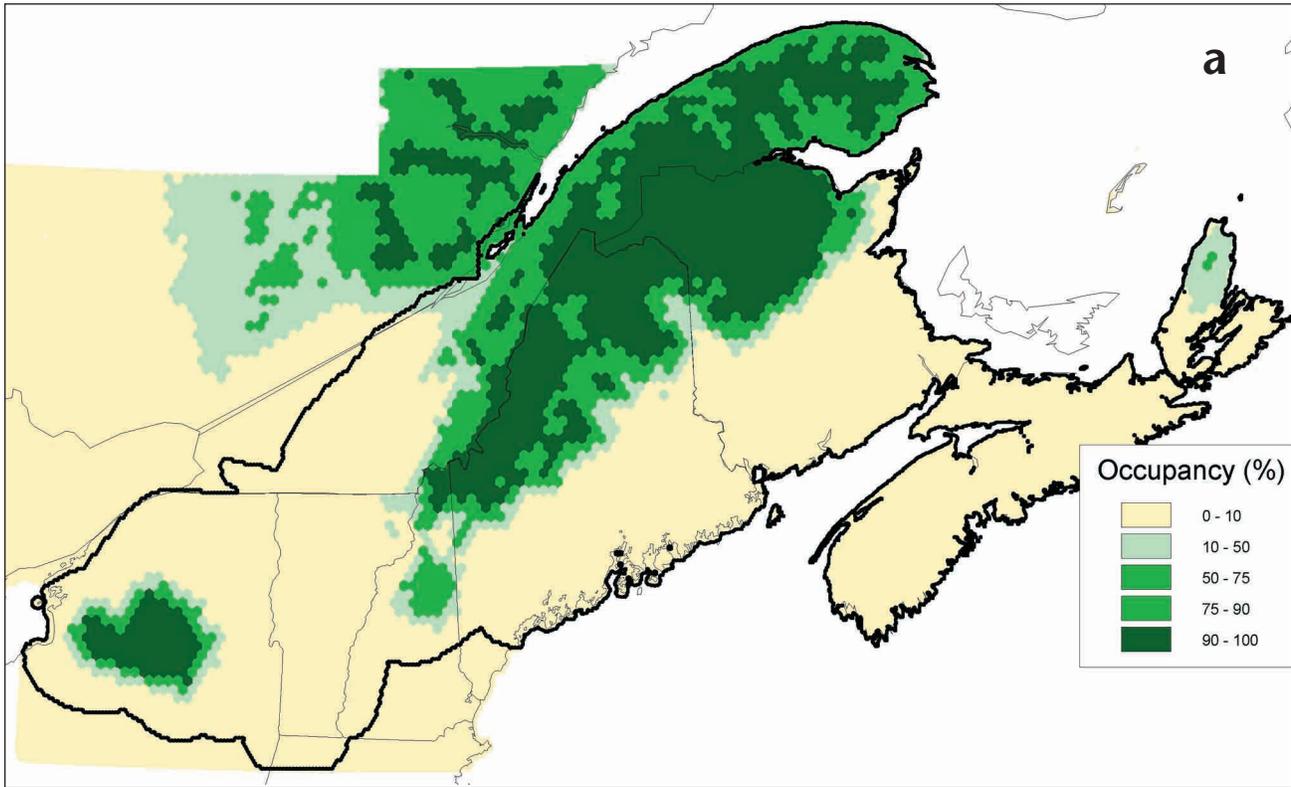


FIGURE 17 Response of lynx populations to climate change: comparison of distribution of lynx under (a) mean environmental conditions with predicted annual snowfall for 2055 (scenario FA1, Table 5) and b) predicted annual snowfall for 2055 with cycling only in Gaspé (scenario FB1, Table 5). Legend shows percentage occupancy of habitat over time predicted by the PATCH model simulations.

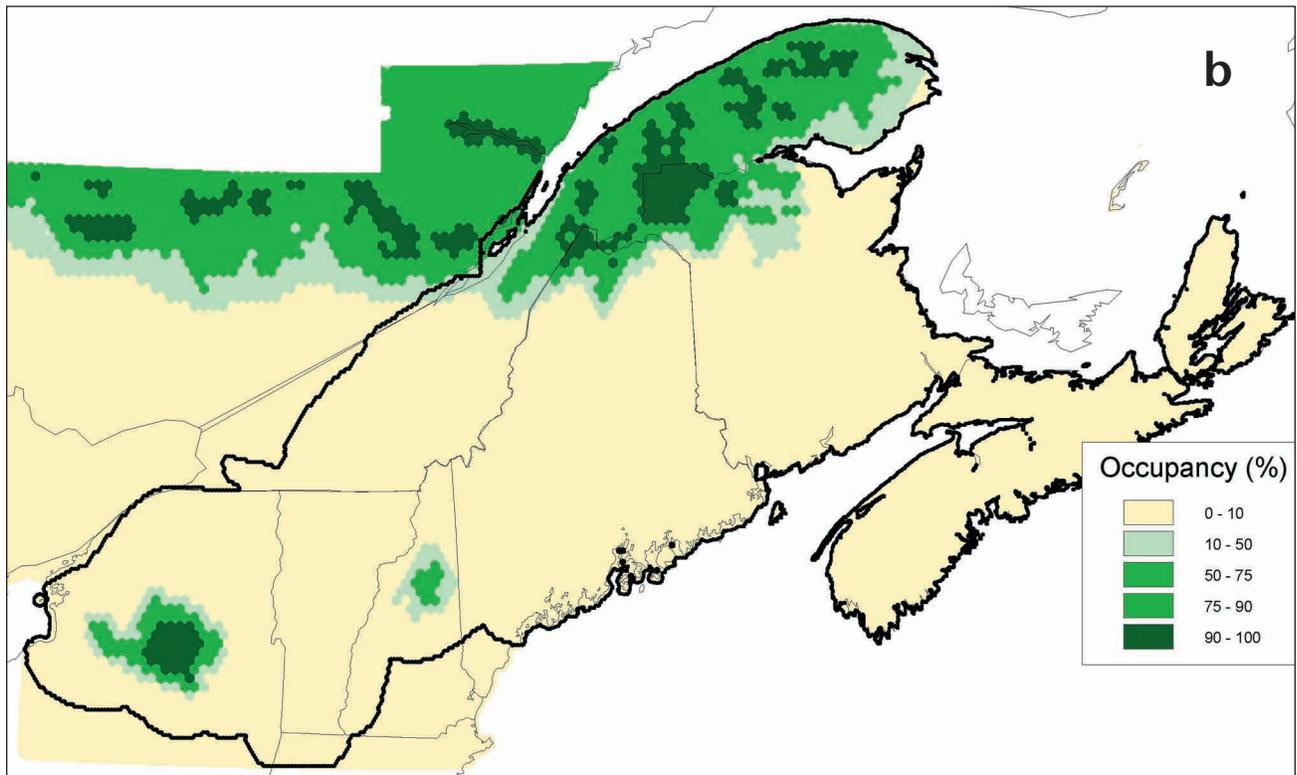
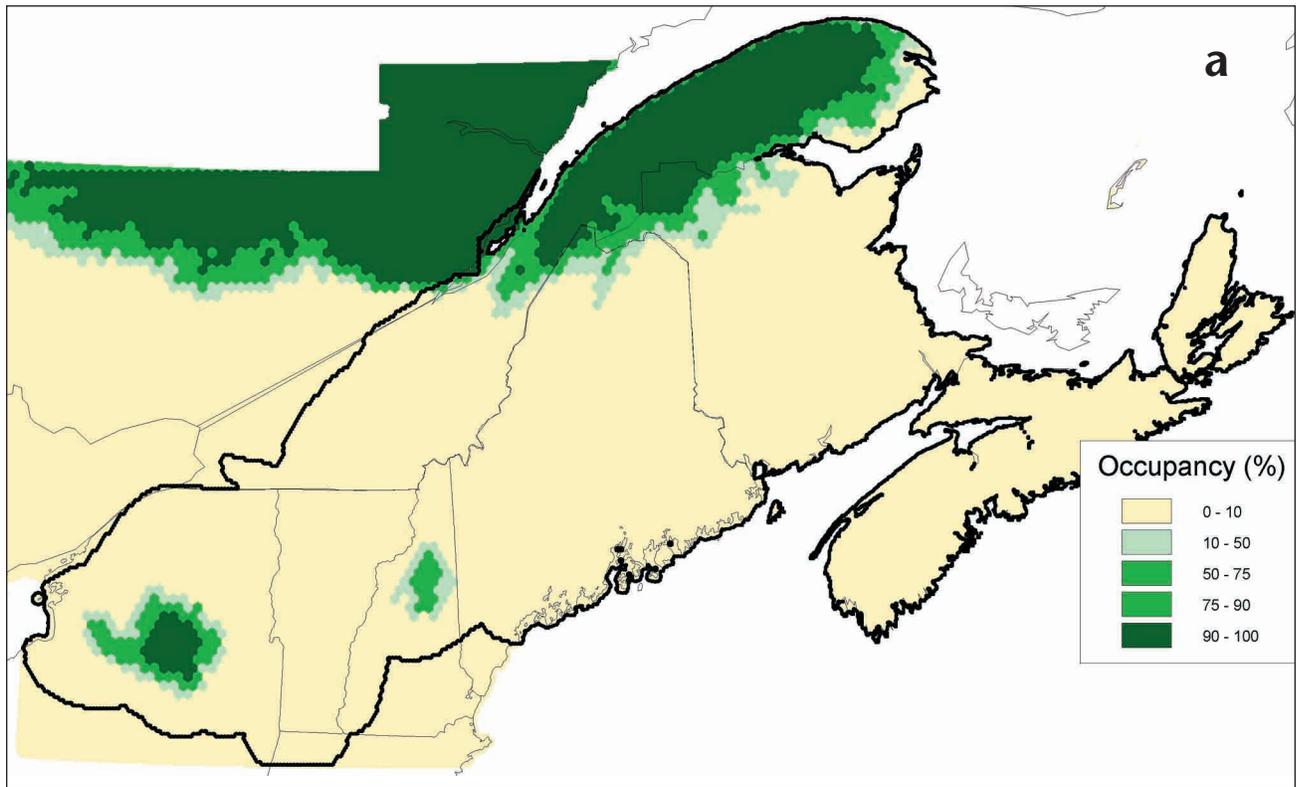


FIGURE 18 Irreplaceability and vulnerability graph for marten as influenced by (a) trapping pressure (base scenario 2 versus base scenario 4, Table 4, Figure 8) and (b) timber harvest (logging scenario 2 versus restoration scenario 2, Table 4, Figure 9).

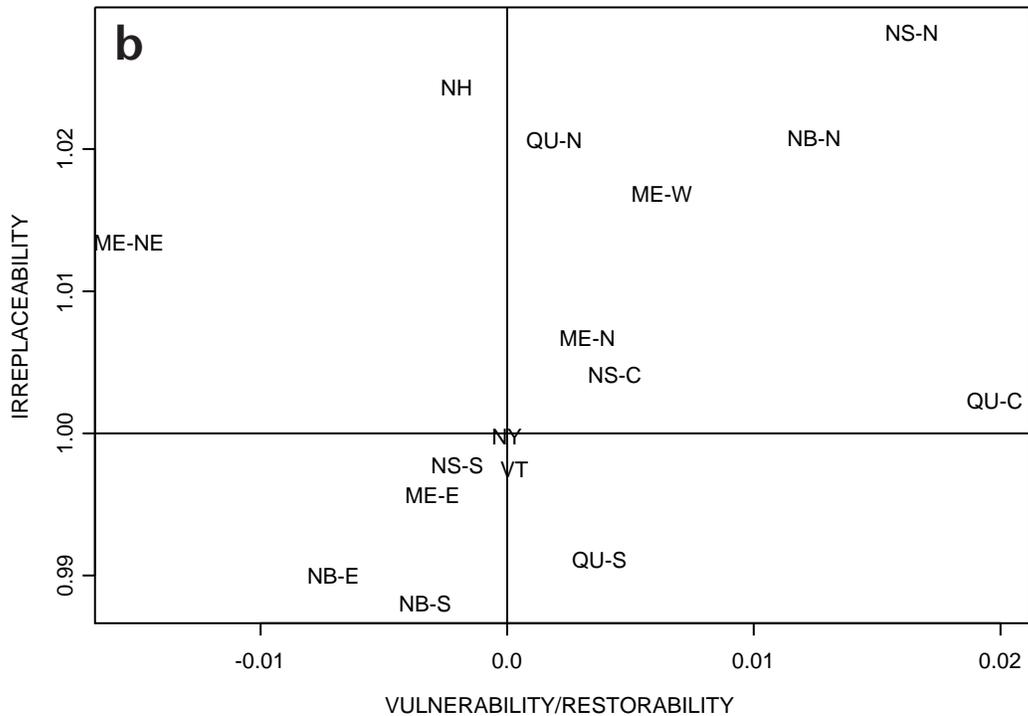
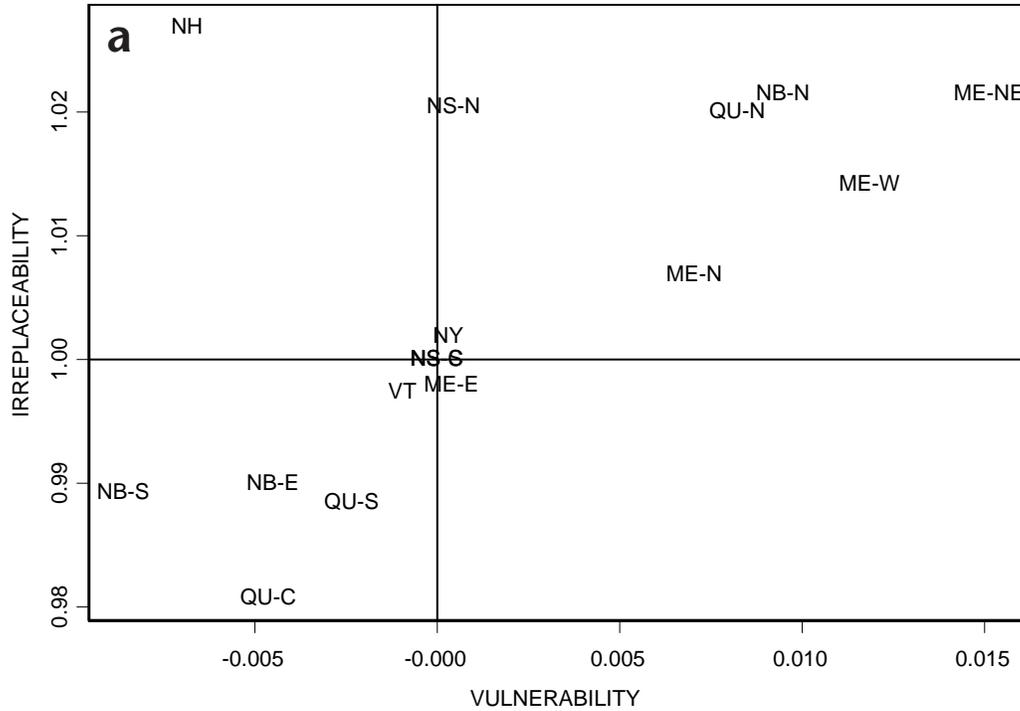


FIGURE 19 Irreplaceability and vulnerability graph for a) marten and b) lynx as influenced by climate change (marten: scenario B versus scenario FB2, Table 4, Figure 13a; lynx: scenario B1 versus scenario FB1, Table 5, Figure 17b).

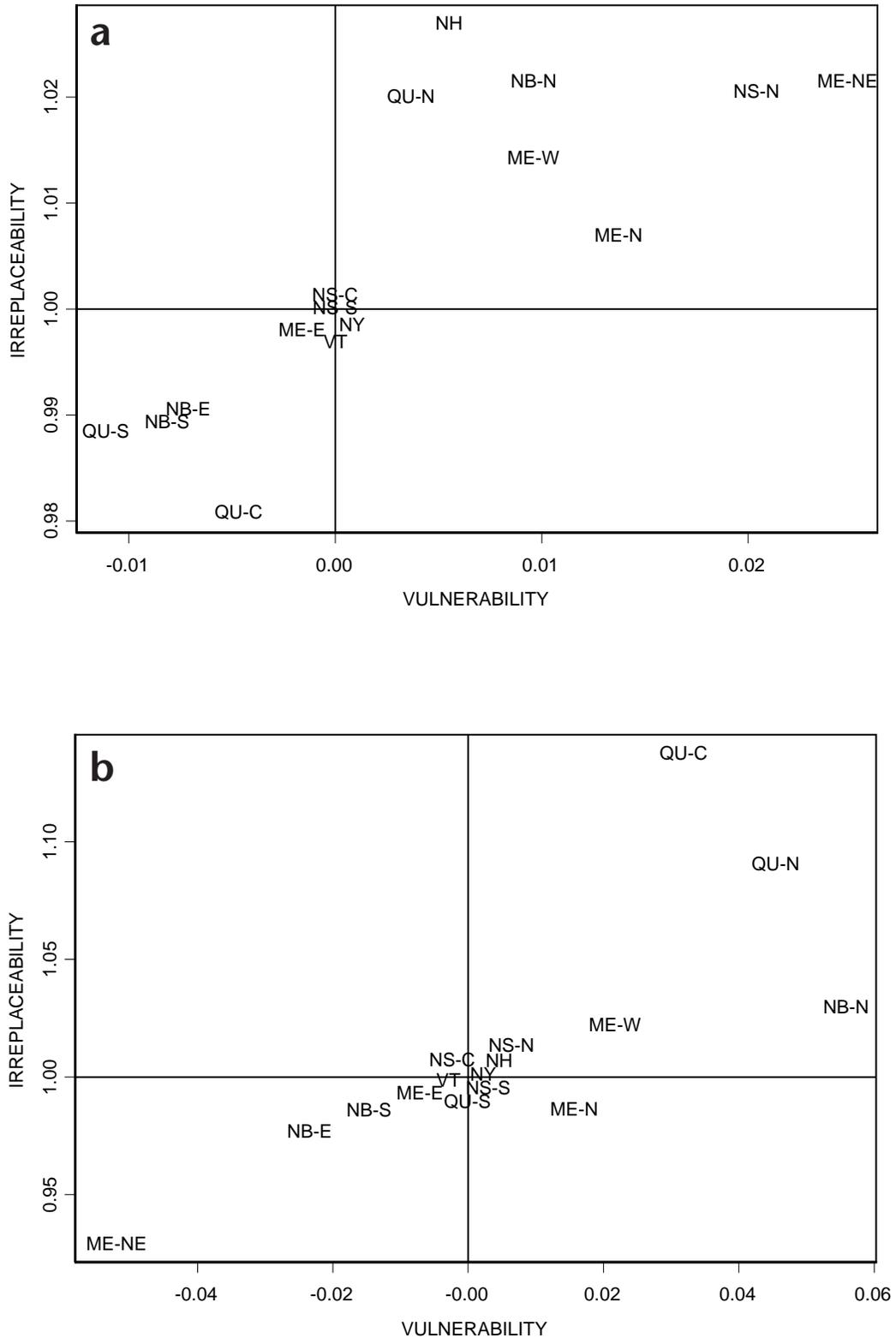
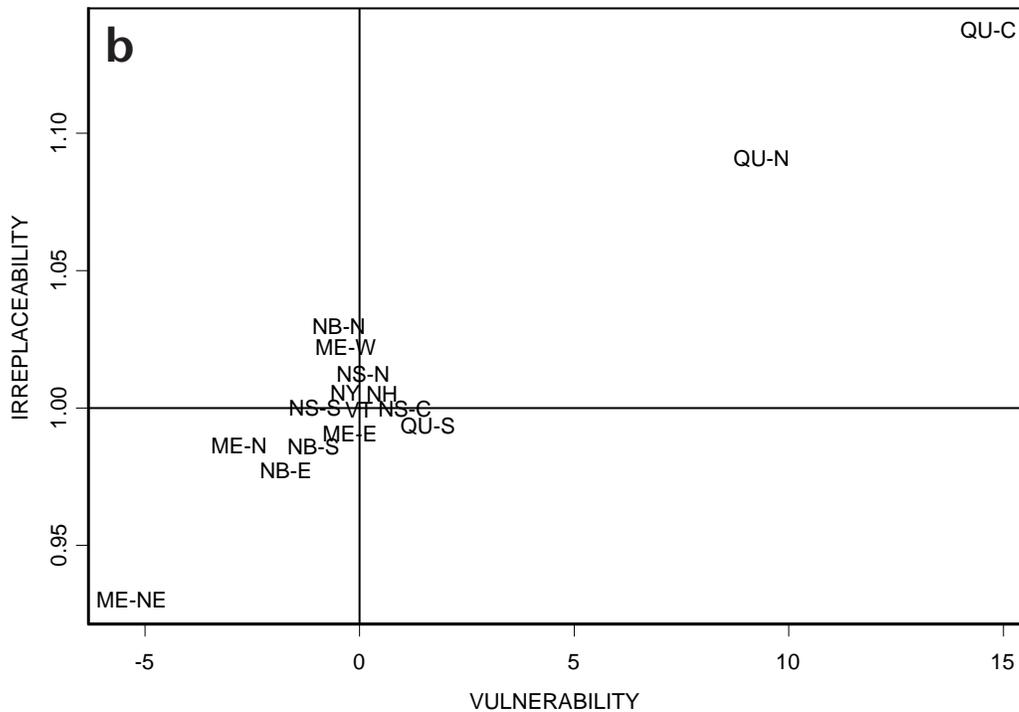
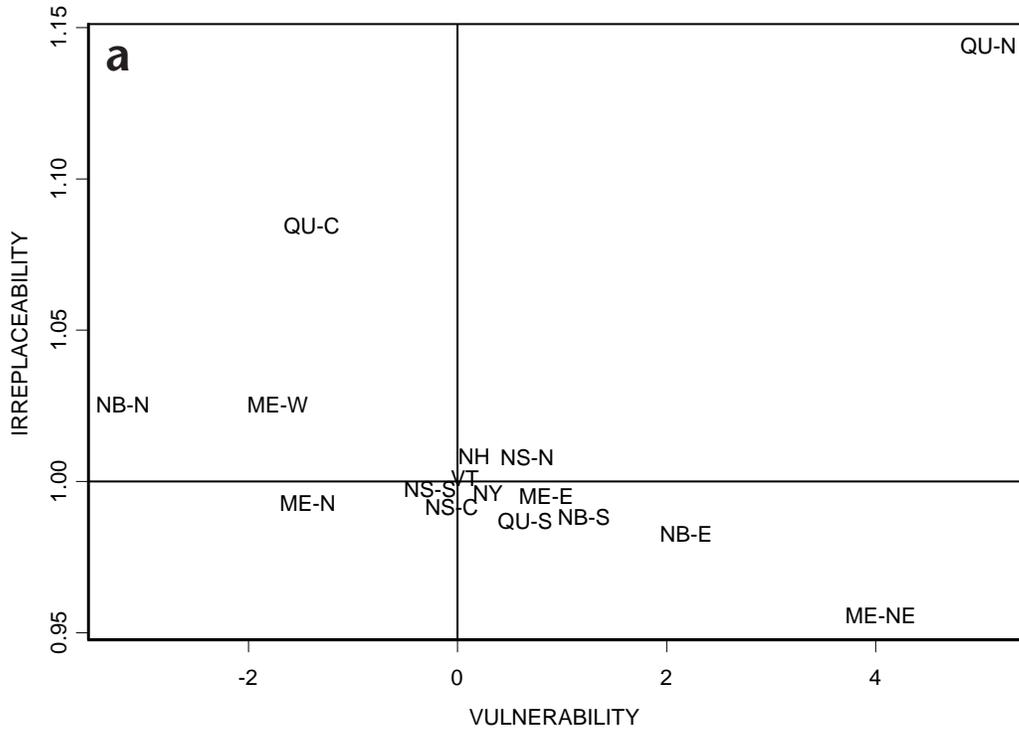


FIGURE 20 Irreplaceability and vulnerability graph for lynx as influenced by (a) population cycling (scenario A1 versus scenario C1, Table 5, Figure 13) and (b) trapping pressure (scenario B1 versus scenario B2, Table 5, Figure 15).



DISCUSSION

CARNIVORE CONSERVATION IN THE NORTHERN Appalachians faces fundamental challenges due to the expected impacts of climate change on species such as the lynx and marten, which are primarily associated with boreal regions. Habitat for these species at the southern limits of their range is already fragmented by climate and human-associated factors such as conversion of forest to farmland and urban areas. Climate change will strongly affect both regionally scarce species such as the lynx and relatively abundant species such as the marten.

Until recently, the effects of climate change on biodiversity were assessed using simple “climatic envelope” models that predicted changes in a species range without considering the dynamics of individuals and populations and the ability to disperse to new habitat. This study is thus the first comprehensive assessment of the how climate change will interact with other threats to affect carnivore population viability. Because of the small and semi-isolated carnivore populations of the region, climate change can interact with habitat conversion and direct exploitation (trapping) to form an “extinction vortex” (Gilpin and Soulé 1986). The results reported here help focus conservation action on policy changes and critical habitat areas which will be key to preventing the loss of these vulnerable species from large portions of the Northern Appalachians in the next century.

Contrasting contexts for carnivore conservation and management

Species recovery efforts that span national boundaries face challenges due to data inconsistencies and contrasting social and regulatory contexts. The three carnivore species - marten, lynx, and wolf - considered in this report and Carroll (2003) exemplify these challenges. In Canada, the conservation priority for wolves is often seen as low in the context of the species’ abundant boreal populations, whereas in the northeastern U.S. the species receives greater concern due to its extirpated status. Similarly, lynx are relatively abundant and commercially trapped in the Gaspé region of Québec, but threatened or extirpated elsewhere in the Northern Appalachians region. Marten are abundant and trapped in Québec, northern New Brunswick, and Maine, but managers in other jurisdic-

tions including Nova Scotia, southern New Brunswick, New Hampshire, Vermont, and New York may be faced with small or declining populations and failed reintroduction efforts. While management where a species is abundant will naturally differ from that where it is rare, it is important to recognize that these diverse management contexts are linked demographically and genetically by dispersal (Brown and Kodric-Brown 1977, Schwartz et al. 2003). Broad-scale analyses such as this one that encompass all components of the regional metapopulation, although necessarily less detailed than state/province-level efforts, may provide important insights as to the underlying drivers of species vulnerability that can make conservation policy more effective.

Limitations and strengths of models

The marten models reported here differ in scale from previous models of marten habitat selection in smaller landscapes (e.g. Chapin et al 1998). The weaknesses (lack of detailed habitat data) and strengths (incorporates entire metapopulation) inherent in regional models determine that certain questions are best answered at this scale, while others concerning habitat pattern and fragmentation are best addressed at finer scales. This study attempts to build on our knowledge from habitat suitability maps and demographic field studies by combining the two in spatially-explicit population models (SEPMs)(Dunning et al. 1995). The biological realism of complex SEPMs may come at the expense of increased sensitivity of the results to uncertainty in demographic, habitat, and movement data (Kareiva et al. 1996). We can place more confidence in the relative rankings of management options than in exact population numbers, and more confidence in the predicted carrying capacity or equilibrium distribution than in the predicted probability of rare events such as recolonization by natural dispersal (Carroll et al. 2003, McCarthy et al. 2003). Nonetheless, because SEPMs can assess habitat configuration in a population dynamic context, they provide novel insights into the prioritization of strategies for species restoration and allow comparison of the effects of several contrasting landscape scenarios.

Similarly, it is important to remain aware of both the limitations of the landscape change scenarios and the rele-

vant insights into regional population dynamics they may offer. Unlike the better validated PATCH models for the wolf and other large carnivores (Carroll et al. 2003), the marten and lynx scenarios should be seen as exploratory. Although I term the results from these simulations predictions (e.g., “predicted source habitat”), they are based on scenarios that attempt to discern general conclusions concerning the impact of regional-scale threats. The aphorism “all models are wrong, some models are useful” helps illustrate this point. For example, in Carroll (2003), I examined the results of current human population growth on wolf habitat by extending trends from census data for 25 years into the future. However, it is certain that unforeseen socioeconomic trends will result in actual human population distribution in 2025 differing from this scenario. Nonetheless, this model scenario is useful and informative because strong elements of current population trends will still be evident. Creating informative landscape change scenarios for the marten and lynx is more difficult than for the wolf. Given the challenges that the Nature Conservancy encountered in assembling a single regional vegetation layer, it is unlikely that a time series of past vegetation change could be assembled to predict future trends. Therefore, I created simplified landscape change scenarios based on the assumption that timber harvest in the near future would occur in the same general areas that have supported recent logging. To the extent that new logging occurs in different parts of the region than recent logging, or uses selective harvest methods with less impact on forest structure, these scenarios will be less relevant but still illustrative of general patterns. Any scenario that considers the effect of a transitory seral stage (such as regenerating forest) on long-term population viability is limited in this way.

The climate change scenarios are also limited by the coarse scale of available climate predictions. More importantly, I assume here that climate (e.g., snowfall) is a biologically limiting factor whose influence on marten and lynx populations will be similar in the ecosystems of 2055. As discussed below, field data supports the assumption that decreased snowfall impacts marten and lynx through decreased prey abundance and/or vulnerability, and decreased competitive advantage over sympatric carnivores (Krohn et al. 1995, Mowat et al. 2000). However, this relationship may change as competitor and prey species themselves each respond individually to climate change. However, the application of climate change predictions here is valuable as an initial exploration of the potential effects of decreased snowfall and

the interaction of climate change with other threat factors. By tying habitat change to population viability models, this analysis moves beyond the simple climatic envelope models typically used to assess threats from climate change, a step called for by previous studies (Schmitz et al 2003).

New insights from single species models

Marten The correlations between potential explanatory variables (e.g, gradients in snowfall, human impacts, and forest type) complicate efforts to identify a single best model to explain patterns of marten distribution. Based strictly on comparison of AIC values (Akaike 1973), a habitat effectiveness/snowfall model (Figure 7) would be preferred, but its low generality suggests that its high explanatory power may be due to spurious correlations. Previous field studies suggest that, unlike in the case of the wolf, direct human persecution (the inverse of habitat effectiveness) is less likely to be a proximal influence on marten abundance than is forest type or age (Chapin et al. 1998). While the importance of spatial refugia from trapping has been shown in Maine (Hodgman et al. 1997), it is unclear how closely trapping effort is correlated with road density. However, a plausible alternate hypothesis, given the explanatory power shown by habitat effectiveness in this study, would be that trapping effort *is* correlated with road density and thus the latter indirectly limits marten distribution. This may occur in some areas where the majority of trapping is by “longliners” (trappers who set high numbers of traps across a wide area, and must therefore position them close to roads for easy access)(W. Jakubas, pers. comm.).

Marten PATCH scenarios based on this hypothesis, although not explored here, could be expected to give similar results to those for a species such as the wolf that is strongly associated with low road density (Carroll 2003), with the bulk of the regional population located in western Maine, the Gaspé peninsula, and the Adirondacks.

Although not showing lowest AIC, the snowfall/conifer/mixed forest model selected for input to the PATCH simulations identifies two regional-scale factors as significant predictors of marten harvest which have strong mechanistic links to marten survival and fecundity. Snow causes marten, with their light foot loadings, to gain competitive advantage relative to sympatric carnivores such the fisher (Krohn et al. 1995). Arguably, fisher density would have been a more proximal limiting factor than

snowfall for use in predicting marten abundance (Krohn et al. 1995), but similar fisher harvest data was not available from New Brunswick and Québec. Unlike fishers, which seem to show variable responses to forest structure across their range, marten show a consistently strong association with older forest throughout North America (Powell et al. 2003). Use of older forest may be due to high canopy closure and/or the use for denning or foraging of the subnivean openings associated with coarse woody debris (Powell et al. 2003). Although marten show association with conifer over deciduous forest in other regions (Powell et al. 2003), field studies have shown lack of selection between these types in the northern Appalachians (D. Harrison, pers. comm.). The slight superiority of the model including conifer and mixed forest over one also including deciduous forest (Table 6) should therefore be interpreted cautiously.

One indication of the generality of the marten regression results is that a model based on data from trapped areas alone predicts (with a few exceptions) the levels of marten abundance in untrapped areas. However, compared to the marten trapping data, the regression model results shows higher suitability than expected on the Gaspé peninsula of Québec. This is plausible based on the relatively limited access in some parts of this area due to low road density and steep topography (and hence lower trapping effort). Unfortunately, both the static regression model and the dynamic PATCH model appear to have more difficulty in assessing the value of small isolated habitat areas such as the Adirondacks, Vermont, Fundy Park (New Brunswick), Cape Breton Island, and Tobetic (Nova Scotia), than they do in mapping habitat value within the mainland of the species' range in the Northern Appalachians. The model does not appear to correctly rate areas with failed or difficult reintroductions (southern Vermont and Fundy) and highly imperiled populations (Cape Breton Island) as lower suitability than areas with successful reintroductions (Tobetic) or less imperiled populations (Adirondacks). However, reintroductions may have failed due to other factors than habitat suitability, such as high densities of sympatric carnivore species (e.g., fisher) (Trombulak and Royer 2001).

The regression model may underpredict marten habitat suitability where wetland forest types dominate the landscape (e.g., Tobetic). This is due to inherent limitations of overstory cover as a predictor of marten habitat. Wetland forests may have more structure than expected by their sparse overstory cover. Conversely, areas of Cape Breton Island that have high overstory

cover may lack coarse woody debris (and hence have less value for marten) due to intensive site preparation ("crush and roll") after salvage harvest, which occurred extensively in the 1970s after a large spruce budworm outbreak (B. Locke, pers. comm.). It is encouraging that the regression model based on snow and older forest predicts the general regional pattern of source and sink habitat even before being adjusted for trapping intensity (base scenario 1, Table 4). This implies that habitat condition rather than trapping may be the overriding determinant of marten abundance except in peripheral populations. The addition of various trapping intensity scenarios (Table 4) to the analysis is nevertheless important for evaluating relative vulnerability to potential increased trapping levels. The irreplaceability/vulnerability analysis for marten (Figure 18) underscores the challenges of restoration efforts for marten in Cape Breton Island given the effects of logging there. The analysis also suggests the vulnerability of marten in northern New Brunswick, and to a lesser extent western Maine, to the interaction between effects of trapping and logging. In addition, the results of the climate change scenarios suggest that decreased snowfall will have high impact on marten, not only in small isolated populations such as Cape Breton Island, but also in areas such as northern Maine where they are relatively abundant under current conditions, but which lack mountainous refugia.

Lynx Although my static lynx model was derived from, and similar to, that developed by Hoving et al. (2005), it shows some contrasts in the distribution of suitable habitat. Because the PRISM snowfall data includes a lake effect (Daly et al. 1994), it predicts heavier snowfall and hence more suitable lynx habitat in the Tug Hills and southwestern Adirondacks that does Hoving et al. (2005). Annual snowfall may be a poorer surrogate for lynx habitat in these areas if snow crusting (and hence competitive advantage for sympatric carnivores such as bobcat [*Lynx rufus*]) is increased by frequent melt-thaw events (M. McCollough, pers. comm.).

Recent research on lynx genetics supports the conclusion that southern populations may be dependent on maintenance of connectivity with boreal populations (Schwartz et al. 2003). Although on a timescale of tens or hundreds of generations, the Northern Appalachians region may not be large enough in isolation to sustain a lynx population's genetic diversity and maintain evolutionary processes, on a timescale of generations, intraregional linkages between the Gaspé core population and

peripheral areas may be of greater importance to viability. However, what habitat types restrict or facilitate lynx movement is relatively unknown, and a more important isolating factor than linkage habitat per se may be reductions in available dispersers through weakening of core populations. The irreplaceability/vulnerability analysis for lynx (Figure 20) not surprisingly highlighted the Gaspé population as the highest priority for maintaining regional viability, but the model results suggest that, due to their vulnerability, conservation measures should also focus on peripheral populations.

Lynx populations in the southern portions of the study region appear to show non-linear responses to habitat area and connectivity. Simulations of western North American populations have suggested that the boreal zone is occupied consistently due to its high habitat value—and the most southerly areas are vacant for the opposite reason, but that intermediate areas along the southern periphery of the range are occupied because of a complex combination of site habitat value and proximity to sources of dispersers (Carroll et al. 2003). Although the extent of cycling in Northern Appalachians lynx populations is poorly known, there is evidence that it occurs at least in the core Gaspé population (D. Murray, pers. comm.) The PATCH scenarios (Tables 5 and 9) illustrate the complex manner in which cycling in this core population could affect peripheral populations. Lynx populations in Maine and New Brunswick were larger in scenarios where cycling was confined to the Gaspé population than when either none or all of the region experienced cycling (Table 9). Although Maine and New Brunswick lynx populations benefitted from dispersal from Gaspé during cyclic highs, this effect was erased by negative impacts when these areas also directly experienced population cycles, as these smaller populations were highly vulnerable to the impacts of cycling. This result contrasts with the relatively small impact of cycling in non-spatial lynx population models (Steury and Murray 2004). In addition, these peripheral areas were vulnerable to the indirect impacts of increased trapping pressure in the Gaspé (Table 9).

Even more dramatically than for the marten, climate change appears to have an overriding impact on lynx viability in the region, with distribution effectively contracting to the Gaspé peninsula. As for the marten, the results suggest areas such as Gaspé that hold robust lynx populations under current conditions will not be able to sustain current threat levels when coupled with the effects of climate change.

Comparisons between the three species

The marten regression model described here contains similar variables to a lynx regional habitat model (Hoving et al. 2005); snowfall and older conifer/mixed forest for the marten, and snowfall and lack of deciduous forest for the lynx. However, due to contrasts in the coefficients of the variables, the resulting model predictions differ greatly between the two species. In addition to the contrasts in distribution of suitable habitat, the additional parameters incorporated in the PATCH model (e.g., demography, home range size and dispersal ability) also produce contrasts between species. The PATCH results highlight contrasts between the three species in four major factors: the nature of threat processes, the scale of population processes, the level of environmental stochasticity, and the patterns of connectivity experienced by the species.

Nature of threat processes The three species differ in what constitutes high productivity habitat as well as what habitats confer highest survival. These two factors (fecundity and survival) tend to vary inversely for the wolf, with highest prey density in habitat also used by humans (Carroll 2003), resulting in a “conservation conundrum” (Mladenoff and Sickley 1999). This is not true for marten, for which older forest increases both fecundity and survival (Chapin et al. 1998). For lynx this relationship is poorly known, but may be driven largely by climatic and vegetation gradients rather than direct human impacts (Carroll et al. 2001, Hoving et al. 2004, 2005). This leads to contrasts in what constitutes refugia for each species, especially in a region of, unlike western North America, predominantly private ownership. For the wolf, the effects of habitat factors such as roads depend on management policy, and management reforms (e.g., protection within Québec parks) can have a rapid effect on population viability. For the 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. Changes in trapping policy can have rapid effects, while habitat improvement through forest regeneration is relatively slower and dependent on the rate of logging over time. Some evidence of an interaction between the effects of trapping pressure and habitat loss (e.g., as noted in Chapin et al. 1998) was shown in the PATCH model, and further analysis of how the spatial distribution of logging and of no-trapping refugia influence the impact of these processes may be informative. However, the ability of wildlife agencies to affect trapping

pressure through creation of single-species refugia may be limited where most harvest occurs as incidental take. For example, the northern Appalachians is one of the only areas where lynx are sympatric with high density populations of coyote (*Canis latrans*) (due in part to extirpation of wolves), and most lynx harvest in the region is in snares set for coyotes (H. Jolicoeur, pers. comm.). In this case, increased road development may result in more severe long-term impacts on vulnerable carnivore populations than if incidental trapping risk was low.

For all three 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. The 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 lynx or marten in the face of climate change. Moreover, unless steps are taken now to begin more precautionary and regionally-coordinated management of these species, they may also suffer range contraction in areas that are now considered the core of their regional range (Gaspé for the lynx, northern Maine for the marten). These results imply that reduction in trapping of vulnerable populations and habitat restoration in critical core areas and linkages may have a large effect in sustaining regional lynx and marten populations in the face of climate change.

Level of environmental stochasticity The PATCH results demonstrate the contrasting effects of environmental stochasticity on the vulnerability of the three species. Environmental stochasticity differs both in amplitude and temporal scale between the species, and this interacts with the spatial and temporal scale of the species population dynamics to affect vulnerability. While the impacts of varying habitat (cycles) on the lynx has long been known, the marten trapping data suggests variation of similar magnitude, but shorter cycle length, in the marten, perhaps due to alternate year mastings of trees such as beech (P. Jensen and W. Jakubas, in prep.). The wolf also experiences variation in prey abundance, but its “slower” life history pattern allows it to more easily buffer this variance. In addition to such cyclic variation, ongoing long-term trends in regional ecosystem processes in the Northern Appalachians suggest the value of dynamic models. These trends include climate change and its effect on snowfall, changes in the intensity of landuses such as timber harvest and trapping, the spread of competitor species such as coyote and fisher, and shifts in prey communities due to

expansion of the distribution of deer (*Odocoileus virginianus*), moose (*Alces alces*), and other species.

Spatial scale of population processes Territory size in the PATCH model varies from 4 km² (marten) to 500 km² (wolf), with similar variation in dispersal ability (marten: 4 km, wolf: >250 km). This leads to contrasts between the species in the relative importance of interregional (to north of the St. Lawrence River) versus intraregional fragmentation. PATCH thus assesses the scale of fragmentation from the perspective of the species, rather than as a characteristic of the landscape itself. The regional population structure of the marten is similar to that of the wolf (Carroll 2003) in that both New Hampshire and Vermont hold peripheral populations. In contrast to the wolf, the Adirondacks for marten and lynx are also a highly vulnerable peripheral population due to the stronger influence of climatic factors in limiting the two mesocarnivore species. While northern Maine is important for both marten and wolf, the marten shows a broader “mainland” of distribution, with New Brunswick and southern Québec as important as northern Maine. One would expect that marten populations would be less tightly linked across national boundaries than those of the wolf or lynx due to their finer scale of population dynamics. This also has implications for the viability of small, semi-isolated “island” populations, both those now extant and planned reintroductions. Although an isolated marten population could persist within a landscape too small to support wolves, the PATCH results suggest 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 when compared to larger populations (Tables 8-9). A striking policy implication emerging from the marten simulations is the need for more precautionary management of the isolated New York State marten population, which has emerged as vulnerable in a regional context by all analyses presented here. Even if this is in part due to the model’s underestimation of habitat in the Adirondacks, the recommendation would be supported by the relatively restricted distribution of Adirondack marten (NYDEC, unpublished data, J. Ray unpublished data).

Patterns of connectivity There is increasing interest in identifying linkage areas whose conservation can help sustain connectivity (e.g., dispersal) between carnivore populations. The PATCH model uses a variety of habitat and demographic data to predict births, deaths, and dispersal

of animals across a landscape. A less “data-hungry” alternative to tracking dispersal through such a population model is to identify linkages using a GIS method called “least cost path” (LCP) analysis which maps the lowest “cost” (in terms of potential mortality, etc.) route between two areas. There are important, but not necessarily incompatible, differences between the spatial population viability approach and a LCP approach such as was used to define the Adirondack-to-Algonquin (A2A) corridor (Quinby et al. 1999, 2000). First, a LCP analysis assumes that “source” populations (those where birth rate is higher than death rate) are known and fixed, whereas a spatial population viability model attempts to predict where sources and sinks are in the landscape. This is a potentially important difference because the LCP approach assumes that areas defined as sources will produce dispersing individuals, when in fact such pre-defined areas may in fact be sinks. Secondly, the LCP approach assumes that the first component of designing a protected areas network is the designation of linkages between core areas. Linkages may indeed in many cases be important to insure genetic exchange and long term population viability. However, before we invest major conservation resources in the creation of corridors, we should insure that such corridors will increase viability in core areas. Unfortunately, a LCP analysis alone has no capacity for addressing the impact of corridors on population viability. Identification and protection of linkages should be one component of a comprehensive planning process that 1) identifies source populations, 2) initiates conservation actions to increase their effective size of source populations via increases in protected area size and mitigation actions to reduce human-caused mortality in areas adjacent to protected areas and 3) identification of corridors that link source populations, preferably along routes that minimally rely on sink habitat. The LCP approach can be an effective and important component of this last phase, but should not be considered the only necessary component in the design of conservation networks.

Within this context, the PATCH model results identify several potential linkage areas that might be further explored with LCP analysis and finer-scale mapping and field assessment. PATCH results for the wolf suggest that at least four potential linkages currently exist for recolonization of the northeastern U.S. from north of the St. Lawrence River (Carroll 2003). However, the region appears to be at or near a threshold of potential dispersal, and successful dispersal may be unlikely under future landscape conditions unless wolf hunting and trapping

pressure diminishes in eastern Canada. Connectivity between potential wolf populations in Maine and the Adirondacks is tenuous and at high risk due to landscape change in Vermont and New Hampshire. The results of the lynx analysis emphasize the importance of a linkage from the regional core population in the Gaspé peninsula southward to northwestern Maine (Figure 21). The results of the marten analysis highlight the importance of linkages between the three regional core populations (in northern Maine, northern New Brunswick, and Gaspé) and between those cores and peripheral populations, especially in the White Mountains of New Hampshire (Figure 22). The linkage between New Brunswick and Nova Scotia, although holding little suitable habitat currently, may support occasional dispersers which may be critical over long term for maintenance of genetic viability in the isolated lynx and marten populations of Cape Breton Island. While there is some overlap between the geographic areas highlighted as linkages for the different species (for example, a linkage between northeastern Maine and central New Brunswick is important for both wolf (Figure 23) and marten), in other areas, linkage zones differ between species. In addition, conservation guidelines for preserving functional linkages will vary between species. For example, the wolf can persist in young forest landscapes if protected from hunting and illegal killing through road closures, whereas the marten needs a certain proportion of the landscape to contain older forest (Chapman et al. 1998). The scale of linkage necessary for each species will also differ, due to the contrast in home range size and dispersal ability between the marten, lynx and wolf. The contrasts in linkage needs between just these three carnivore species, a small subset of the region’s threatened species, reveals that identifying and protecting linkages is a complex question that requires a science-based approach rather than a rapid assessment based on human perceptions of landscape pattern.

The most important contribution of SEPMS to connectivity planning may not be their specific predictions, but rather the way in which they tightly link connectivity to its role in promoting population viability. The separation of connectivity from viability has led to potential misuse of the former concept in conservation planning. For example, conservation organizations increasingly use the term “corridor” to refer to regional landscapes that would, in traditional conservation planning terminology, be instead a planning landscape divided into components of cores, buffers, and corridors, each with distinct management regimes (Noss and Harris 1986). Use of corridors in

FIGURE 21 Potential linkages predicted by the PATCH model to be critical for persistence of the lynx metapopulation in the northeastern U.S. and maritime Canada, as well as a potential linkage to Cape Breton Island population.

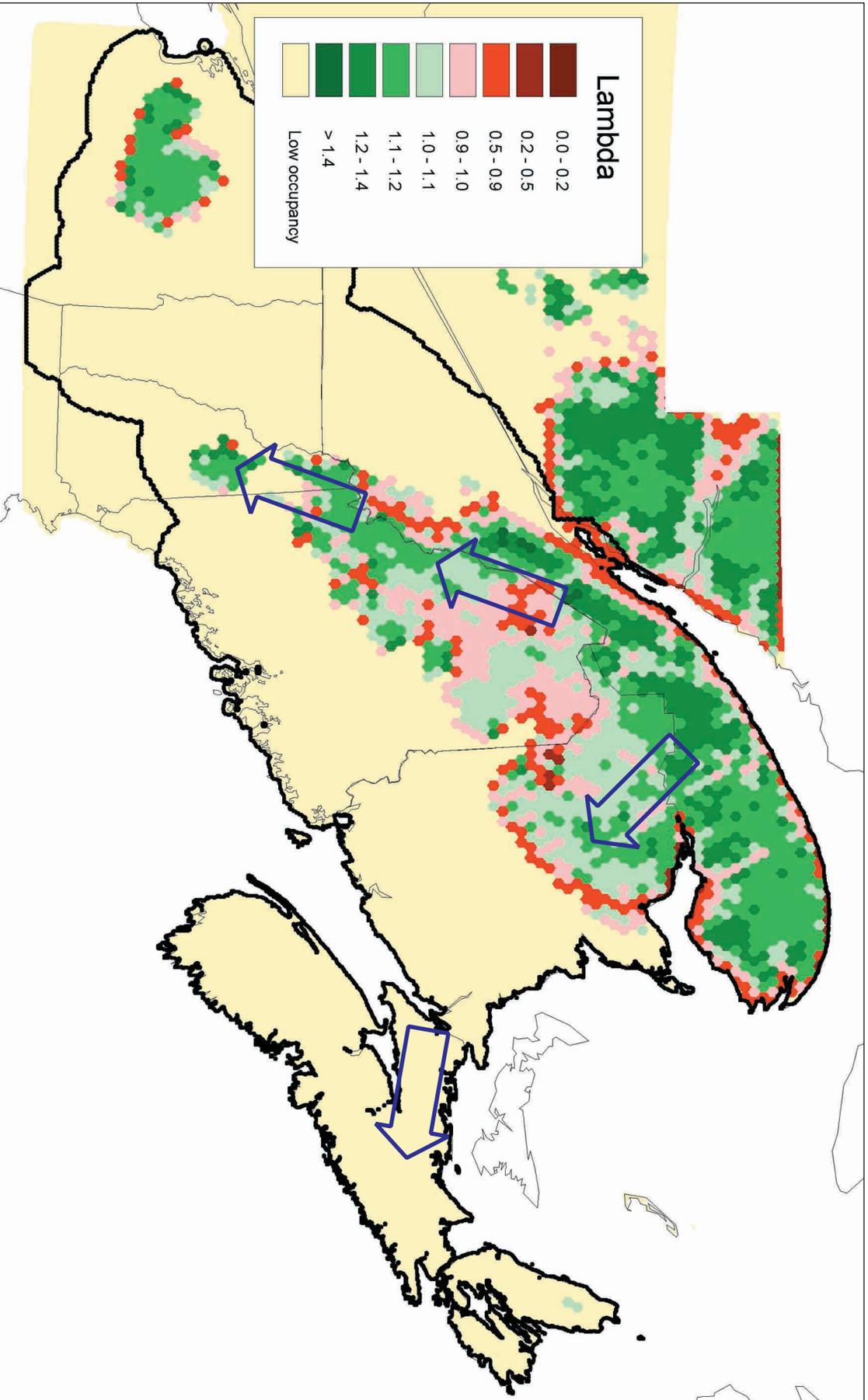


FIGURE 22 Potential linkages predicted by the PATCH model to be critical for persistence of the marten metapopulation in the northeastern U.S. and maritime Canada under an increased timber harvest scenario (Table 4), as well as a potential linkage to Cape Breton Island population.

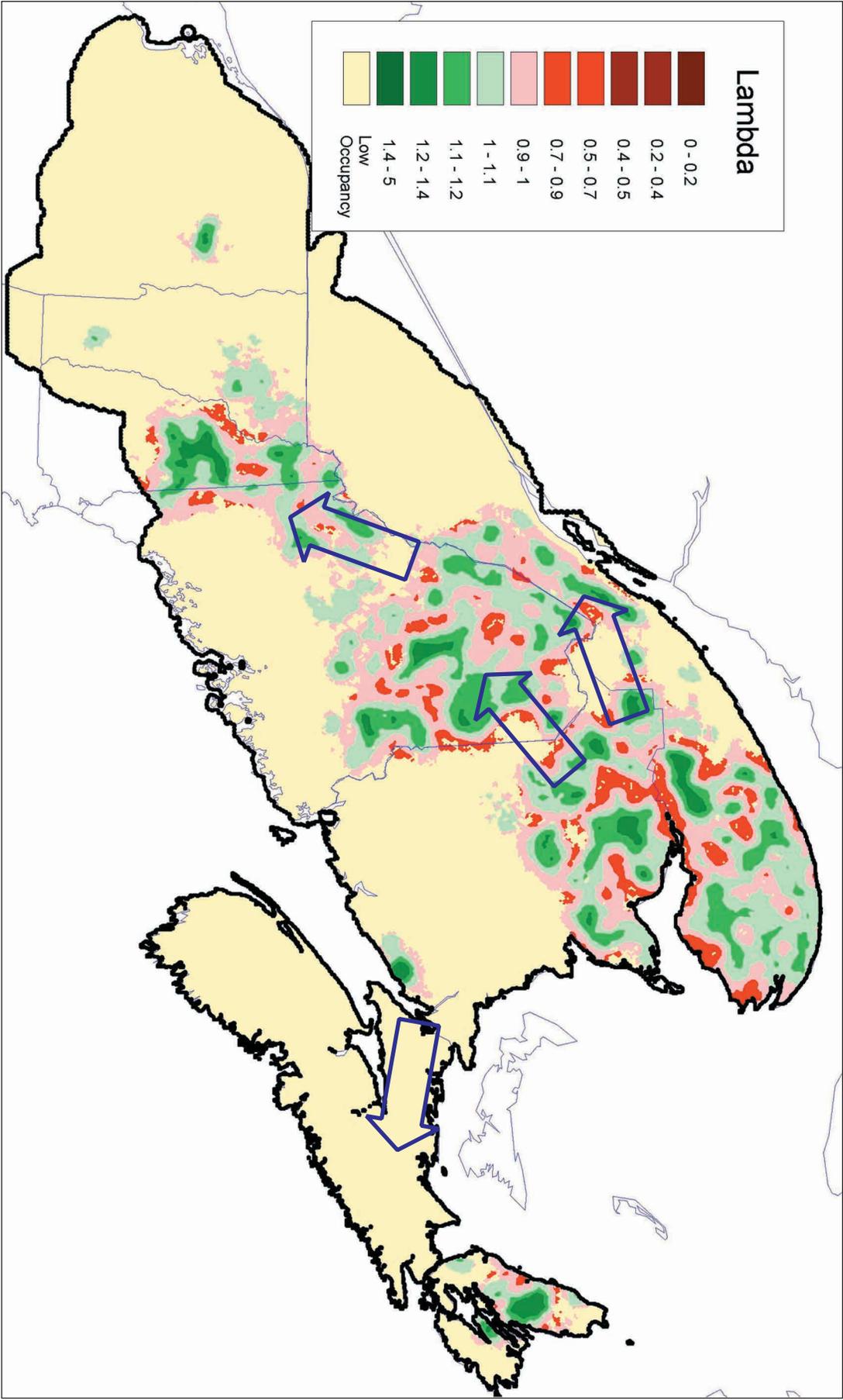
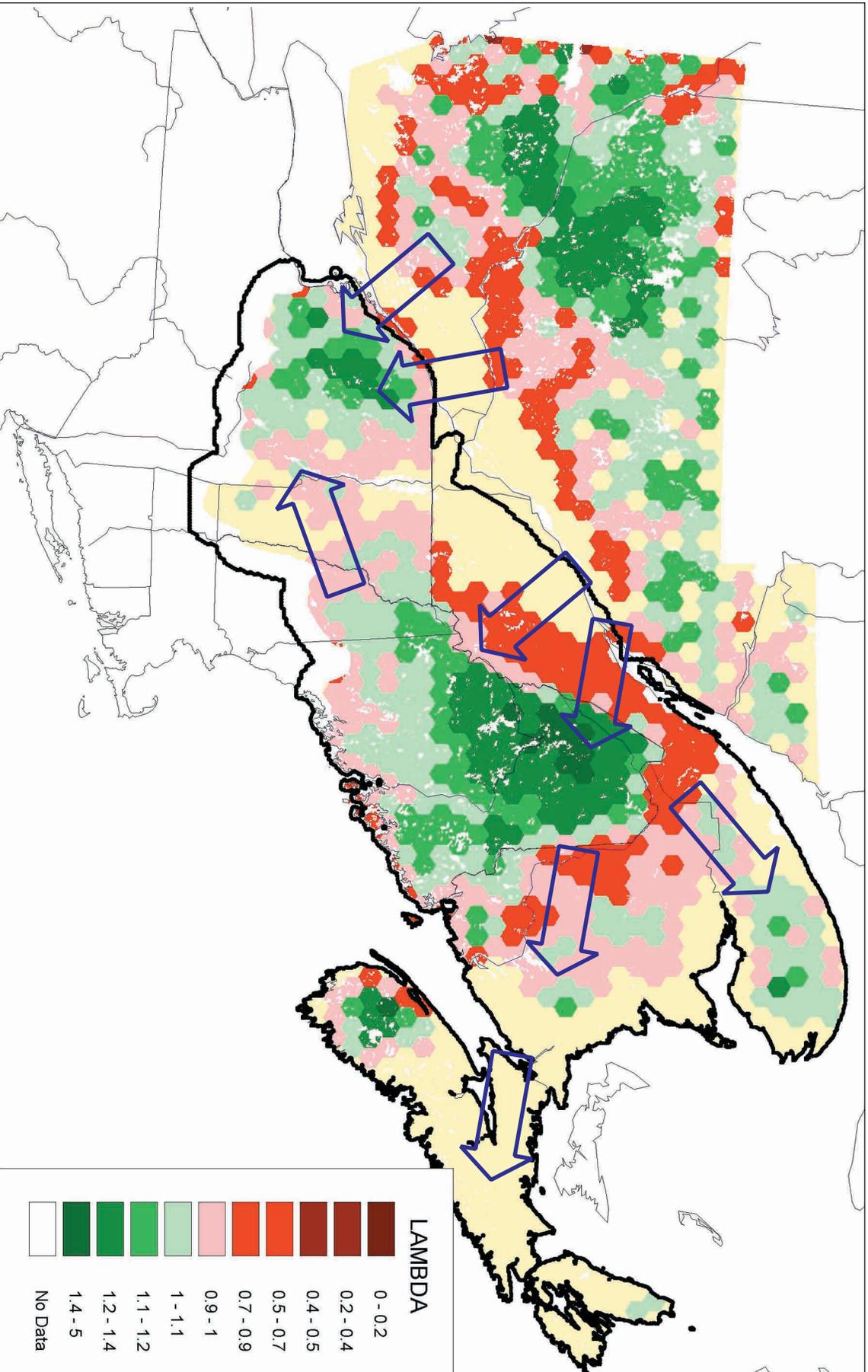


FIGURE 23 Potential linkages predicted by the PATCH model for recolonization by wolves of the northeastern U.S. and maritime Canada, as well as linkages between potential reestablished populations.



this broad sense tends to obscure the distinct roles played by the different components, e.g., strictly protected habitat that can sustain sources of species vulnerable to human-induced mortality versus less secure habitat (corridors in the narrow sense) that may sustain movement of these species. In this case, designation of the landscape as a “corridor”, which is assumed to require few restrictions on land use, may be a means of avoiding the harder challenges to slowing the loss of both core and connective habitat.

DUE TO THE LIMITED ABILITY OF REGIONAL-scale models to discern proximal limiting factors such as forest structure or prey density, as well as the additional limitations inherent in complex models such as SEPMs, the quantitative predictions from the PATCH scenarios should be interpreted cautiously. Nonetheless, both static and dynamic model results are highly relevant to carnivore conservation policy because they generate hypotheses concerning regional population dynamics and offer heuristic tools to begin considering how carnivore populations are linked across jurisdictions. Because marten, lynx, and

(potentially) wolf 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. This occurs at differing scales; the wolf suffers from the isolation of the Northern Appalachians from populations north of St. Lawrence River, the lynx from potential disconnection of the U.S. from the Gaspé population, and the marten from potential loss of contact between peripheral populations in New Hampshire, Vermont, and Nova Scotia from core populations in northern Maine/northern New Brunswick/Gaspé. In all three cases, however, conservation strategies must be binational and take into account the dynamic ecosystem context within which recovery will occur. The strong impact of climate change in our results imply, not that conservation action to address other threats will be useless, but on the contrary, that it is essential to move towards more precautionary management of populations that may today still appear robust.

ACKNOWLEDGMENTS

I WOULD LIKE TO THANK M. ANDERSON, P. Austin-Smith, P. Canac-Marquis, R. Cumberland, P. Doran, G. Forbes, D. Harrison, C. Hoving, W. Jakubas, H. Jolicoeur, G. Kehm, W. Krohn, P. Lee, C. Libby, B. Locke, R. Long, S. Lusk, M. McCollough, R. Noss, M. O'Brien, P. Paquet, D. Publicover, P. Quinby, J. Ray, C. Reining, T. Sutter, and M. Villemure for helpful suggestions and information received during the course of the study. This study was funded by the Wildlands Project, Richmond, VT.

REFERENCES

- Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 in B. N. Petrov and F. Csaki, eds. Second international symposium on information theory. Akademiai Kiado, Budapest.
- Brocke, R. H., K. A. Gustafson, and L. B. Fox. 1991. Restoration of large predators: potentials and problems. Pages 303-315 in D. J. Decker, M. E. Krasny, G. R. Goff, C. R. Smith, and D. W. Gross, eds. Challenges in the conservation of biological resources: a practitioner's guide. Westview Press, Boulder, CO.
- Brown, J. H., and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. *Ecology* 58:445-449.
- Carroll, C., W. J. Zielinski, and R. F. Noss. 1999. Using presence-absence data to build and test spatial habitat models for the fisher in the Klamath region, U. S. A. *Conservation Biology* 13:1344-1359.
- Carroll, C., R. F. Noss, and P. C. Paquet. 2001. Carnivores as focal species for conservation planning in the Rocky Mountain region. *Ecological Applications* 11:961-980.
- Carroll, C. 2003. Carnivore restoration in the northeastern U.S. and southeastern Canada: a regional-scale analysis of habitat and population viability for wolf, lynx, and marten. Progress report 1: wolf viability analysis. Unpublished report to The Wildlands Project, Richmond, VT.
- Carroll, C., R. F. Noss, P. C. Paquet and N. H. Schumaker. 2003. Use of population viability analysis and reserve selection algorithms in regional conservation plans. *Ecological Applications* 13:1773-1789.
- Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Sinauer, Boston, MA.
- Chapin, T. G., D. J. Harrison, and D. D. Katnik. 1998. Influence of landscape pattern on habitat use by American marten in an industrial forest. *Conservation Biology* 12: 1327-1337.
- Cihlar, J., L. St.-Laurent, and J. A. Dyer. 1991. Relation between the normalized difference vegetation index and ecological variables. *Remote Sensing of the Environment* 35:279-298.
- Crist, E. P., and R. C. Cicone. 1984. Application of the tasseled cap concept to simulated thematic mapper data. *Photogrammetric Engineering and Remote Sensing* 50:343-352.
- Daly, C., R. P. Neilson, and D. L. Phillips. 1994. A statistical-topographic model for mapping climatological precipitation over mountainous terrain. *Journal of Applied Meteorology* 33: 140-158.
- Dunning, J. B., Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* 5: 3-11.
- Gilpin, M E., and Soulé, M.E. 1986. Minimum viable populations: the processes of species extinction. Pages 19-34 in M. E. Soulé, editor. *Conservation Biology: The science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts.
- Harrison, D.J. and T.G. Chapin. 1998. Extent and connectivity of habitat for wolves in eastern North America. *Wildlife Society Bulletin* 26:767-775.
- Hepinstall, J. A., D. J. Harrison, and D. C. Payer. In prep. Predicting changes in habitat supply and potential abundance for American marten in Maine.
- Hodgman, T. P., D. J. Harrison, D. M. Phillips, and K. D. Elowe. 1997. Survival of American marten in an untrapped forest preserve in Maine. Pages 86-99 in Proulx, G., H. N. Bryant, and P. M. Woodard, eds. *Martes: taxonomy, ecology, techniques, and management*. Proc. 2nd Int. *Martes* Symp. Provincial Museum of Alberta, Edmonton, Alberta.
- Hoving, C. L. 2001. Historical occurrence and habitat ecology of Canada Lynx (*Lynx canadensis*) in eastern North America. M.S. Thesis, University of Maine, Orono, ME. 226 pp.
- Hoving, C. L., R. A. Joseph, and W. B. Krohn. 2003. Recent and historical distributions of Canada lynx in Maine and the northeast. *Northeastern naturalist* 10:363-382.
- Hoving, C. L., D. J. Harrison, W. B. Krohn, W. J. Jakubas, and M. A. McCollough. 2004. Canada lynx habitat and forest succession in northern Maine, United States. *Wildlife Biology* 10:285-294.
- Hoving, C. L., D. J. Harrison, W. B. Krohn, R. A. Joseph, and M. O'Brien. 2005. Broad-scale predictions of Canada lynx occurrence in eastern North America. *Journal of Wildlife Management* 00:00-00 (forthcoming).
- Kareiva, P., and U. Wennergren. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature* 373:299-302.
- Kareiva, P., D. Skelly, and M. Ruckelshaus. 1996. Reevaluating the use of models to predict the consequences of habitat loss and fragmentation. Pages 156-166 in S. T. A. Pickett, R.S. Ostfeld, M. Schachak, and G. E. Likens, editors. *The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity*. Chapman and Hall, New York, NY.
- Kiehl, J. T. and P. R. Gent. 2004. The Community Climate System Model, version 2. *Journal of Climate* 17:3666-3682.
- Krohn, W. B., K. D. Elowe, and R. B. Boone. 1995. Relations among fishers, snow, and martens: development and evaluation of two hypotheses. *Forestry Chronicle* 71: 97-105.
- Lambeck, R.J. 1997. Focal species: a multi-species umbrella for nature conservation. *Conservation Biology* 11:849-856.
- Litvaitis, J. A. 1993. Response of early successional vertebrates to historic changes in land use. *Conservation Biology* 7:966-873.
- Mace, R. D., J. S. Waller, T. L. Manley, K. Ake, and W. T. Wittinger. 1999. Landscape evaluation of grizzly bear habitat in western Montana. *Conservation Biology* 13:367-377.
- Margules, C.R., and R.L. Pressey. 2000. Systematic conservation planning. *Nature* 405:243-253.

- McCarthy, M. A., S. J. Andelman, and H. P. Possingham. 2003. Reliability of Relative Predictions in Population Viability Analysis. *Conservation Biology* 17: 982-989.
- Merrill, E. H., M. K. Bramble-Brodahl, R. W. Marris, and M. S. Boyce. 1993. Estimation of green herbaceous phytomass from Landsat MSS data in Yellowstone National Park. *Journal of Range Management* 46:151-157.
- Merrill, T., D. J. Mattson, R. G. Wright, and H. B. Quigley. 1999. Defining landscapes suitable for restoration of grizzly bears (*Ursus arctos*) in Idaho. *Biological Conservation* 87:231-248.
- Mladenoff, D. J., and T. A. Sickley. 1999. Assessing potential gray wolf restoration in the northeastern United States: a spatial prediction of favorable habitat and potential population levels. *Journal of Wildlife Management* 62:1-10.
- Mowat, G., K. G. Poole, and M. O'Donoghue. 2000. Ecology of lynx in northern Canada and Alaska. Pages 265-306 in L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, eds. *Ecology and conservation of lynx in the United States*. Univ. Press of Colorado, Boulder, CO. 480 pp.
- Noss, R. F., and L. D. Harris. 1986. Nodes, networks, and MUMs: preserving diversity at all scales. *Environmental Management* 10:299-309.
- Paquet, P. C., J. R. Strittholt, and N. L. Staus. 1999. Wolf reintroduction feasibility in the Adirondack Park. Unpublished report. Conservation Biology Institute, Corvallis, OR.
- Payer, D. C., and D. J. Harrison. 2003. Influence of forest structure on habitat use by American marten in an industrial forest. *Forest Ecology and Management* 179:145-156.
- Peterson, A. T., E. Martínez-Meyer, C. González-Salazar, and P. W. Hall. 2004. Modeled climate change effects on distributions of Canadian butterfly species. *Can. J. Zool.* 82:851-858.
- Possingham, H.P., I.R. Ball, and S. Andelman. 2000. Mathematical methods for identifying representative reserve networks. Pages 291-306 in S. Ferson and M. Burgman, editors. *Quantitative methods for conservation biology*. Springer-Verlag, New York.
- Powell, R. A., S. W. Buskirk, and W. J. Zielinski. 2003. Fisher and marten. Pages 635-649 in G. A. Feldhamer, B. C. Thompson, and J. A. Chapman, eds. *Wild mammals of North America*, 2nd edition. Johns Hopkins Univ. Press, Baltimore, MD.
- Pressey, R.L., and Taffs, K.H. 2001. Scheduling conservation action in production landscapes: priority areas in western New South Wales defined by irreplaceability and vulnerability to vegetation loss. *Biological Conservation* 100:355-376.
- Quinby, P., S. Trombulak, T. Lee, J. Lane, M. Henry, R. Long, and P. MacKay. 1999. Opportunities for Wildlife Habitat Connectivity between Algonquin Park, Ontario and the Adirondack Park, New York Unpublished report. Ancient Forest Exploration & Research, Powassan and Toronto, Ontario.
- Quinby, P., S. Trombulak, T. Lee, R. Long, P. MacKay, J. Lane, and M. Henry. 2000. Opportunities for wildlife habitat connectivity between Algonquin Provincial Park and the Adirondack Park. *Wild Earth* 10(2):75-80.
- Ray, J. C. Mesocarnivores of northeastern North America: status and conservation issues. WCS Working Papers No. 15, June 2000. Available for download from <http://www.wcs.org/science/>
- Ray, J. C., J. F. Organ, and M. F. O'Brien. 2002. Canada lynx (*Lynx canadensis*) in the northern Appalachians: current knowledge, research priorities, and a call for regional cooperation and action. Wildlife Conservation Society, Toronto, ON. 22 pp.
- Schmitz, O. J., E. Post, C. E. Burns, and K. M. Johnston. 2003. Ecosystem responses to global climate change: moving beyond color mapping. *Bioscience* 53:1199-1205.
- Schumaker, N. H. 1998. A user's guide to the PATCH model. EPA/600/R-98/135. U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon.
- Schwartz, M. K., L. S. Mills, Y. Ortega, L. F. Ruggiero, and F. W. Allendorf. 2003. Landscape location affects genetic variation of Canada lynx (*Lynx canadensis*). *Molecular Ecology* 12:1807-1816
- Schwarz, G. 1978. Estimating the dimension of a model. *Annals of Statistics* 6:461-464.
- Scott, J. M., F. Davis, B. Csuti, R. Noss, B. Butterfield, C. Groves, H. Anderson, S. Caicco, F. D'Erchia, T. C. Edwards, Jr., J. Ulliman, and R. G. Wright. 1993. Gap analysis: a geographic approach to the protection of biological diversity. *Wildlife Monographs* 123.
- Steuery, T. D., and D. L. Murray. 2004. Modeling the reintroduction of lynx to the southern periphery of its range. *Biological Conservation* 117: 127-141.
- Taper, M. L. 2004. Model identification from many candidates. Pages 488-501 in M. L. Taper and S. R. Lele, eds. *The nature of scientific evidence: statistical, philosophical, and empirical considerations*. University of Chicago Press, Chicago, IL.
- Trombulak, S.C., and K.J. Royar. 2001. Restoring the wild: species recovery and reintroduction. Pages 157-181 in C. McGrory Klyza, ed. *Rewilding the Northeast: A New Wilderness Paradigm*. University Press of New England. Hanover, NH.
- Vogelmann, J. E., S. M. Howard, L. Yang, C. R. Larson, B. K. Wylie, and N. Van Driel. 2001. Completion of the 1990s National Land Cover Data Set for the conterminous United States from Landsat Thematic Mapper data and ancillary data sources. *Photogrammetric Engineering and Remote Sensing* 67:650-662.
- Wharton, S. W., and M. F. Myers. 1997. MTPE EOS data products handbook: Vol. 1. Pub. 902, NASA Goddard Space Flight Center, Greenbelt, MD. 266 pp.
- White, J. D., S. W. Running, R. Nemani, R. E. Keane, and K. C. Ryan. 1997. Measurement and remote sensing of LAI in Rocky Mountain montane ecosystems. *Canadian Journal of Forest Research* 27:1714-1727.
- Wilson, P. J., S. Grewal, I. D. Lawford, J. N. M. Heal, A. G. Granacki, D. Pennock, J. B. Theberge, M. T. Theberge, D. R. Voigt, W. Waddell, R. E. Chambers, P. C. Paquet, G. Goulet, D. Cluff, and B. N. White. 2000. DNA profiles of the eastern Canadian wolf and the red wolf provide evidence for a common evolutionary history independent of the gray wolf. *Canadian Journal of Zoology* 78:1-11.