WILDLANDS PROJECT

SPECIAL PAPER **NO. 5**

Bridging the gap between conservation science, practice, and policy

Impacts of Landscape Change on Wolf Viability in the Northeastern U.S. and Southeastern Canada

Implications for Wolf Recovery

By Carlos Carroll, Ph.D.

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.

WILDLANDS PROJECT

P.O. Box 455
Richmond, VT 05477
802/434-4077
info@wildlandsproject.org
www.wildlandsproject.org

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Design and layout by Todd Cummings

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Carlos Carroll is a research ecologist with the Klamath Center for Conservation Research (P.O. Box 104, Orleans, CA 95556; carlos@sisqtel.net). 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, the conservation and restoration of wolves in the Rocky Mountains of Canada and the U.S., northern Mexico, and the Pacific states.

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PREFACE

The Wildlands Project is pleased to release this research report on the potential for wolf recovery in the northeastern U.S. and southeastern Canada. The analysis, prepared by Dr. Carlos Carroll, offers the best current scientific thinking about the means and prospects for wolf restoration in the region at a time when political events affecting the wolf's future are heating up. This month (October 2003) the Wildlands Project joined a lawsuit with Defenders of Wildlife and several other plaintiffs to challenge the legality of the Fish and Wildlife Service's final rule on reclassifying the gray wolf (*Canis lupus*) under the Endangered Species Act (ESA). As the lead agency charged with implementing the ESA, the U.S. Fish and Wildlife Service has an obligation to use the best available science—not politics—to protect America's imperiled wildlife. We hope this report advances scientific understanding of wolf recovery issues and will be helpful to policymakers in the U.S. and Canada, agency and academic wolf biologists, and the conservation community.

The U.S. Fish and Wildlife Service has an obligation to use the best available science—not politics—to protect America's imperiled wildlife.

BACKGROUND

In July 2000, the U.S. Fish and Wildlife Service (FWS) issued a draft rule to reclassify gray wolves under the Endangered Species Act. The agency proposed to establish four "Distinct Population Segments" in the contiguous United States and Mexico, downlist the wolf to Threatened status in three of the four recovery areas, and delist wolves entirely outside the Distinct Population Segments. (Mexican wolves in the Southwest would retain Endangered status given the early stage of reintroduction efforts.) The agency received roughly 16,000 comments on the proposed rule, noting in its analysis of public feedback that most citizens opposed delisting, and that the "overwhelming preponderance of responses support U.S. Fish and Wildlife Service recovery and reintroduction efforts…."

In spring 2003, the Fish and Wildlife Service released its final rule on gray wolf classification, which differed dramatically from the proposed rule. The northeastern and Great Lakes planning regions were combined into an Eastern Distinct Population Segment comprising 21 states, from Minnesota and Wisconsin (where wolves are present) to Rhode Island and New Jersey (unlikely terrain for wolves in any scenario). Northeastern wolf restoration was essentially abandoned: the FWS stated that "Our recovery goal for restoring gray wolves in the eastern U.S. is being achieved by the expanding wolf populations in Minnesota, Wisconsin, and Michigan" and it had "no plans to restore gray wolves elsewhere in the Eastern United States." As a result, millions of acres of suitable habitat in northern Maine and New England were written off for wolf recovery.

SCIENCE INFORMING POLICY

The fate of wolf recovery efforts in the northeastern U.S. and other areas of historic wolf range are not simply a matter of law, however. While the courts will decide if agency actions to downlist and eventually eliminate Endangered Species Act protections for gray wolves are legal, citizens and communities are actively debating wolf restoration, and scientists are publishing provocative research describing the vital ecological role that wolves and other "top carnivores" play in healthy ecosystems.

The Wildlands Project commissioned this analysis of wolf recovery potential in the northeastern U.S. and southern Canada. Dr. Carlos Carroll is one of the leading scientists applying dynamic population modeling to conservation questions. The population modeling techniques pioneered by Dr. Carroll can predict how wildlife populations may expand or shrink over time based on habitat quality, security from threats, and predicted land-use change. Land-use change is extrapolated from past trends for a given region, such as development, human population growth, and road-building patterns. Such models can be extremely useful for determining conservation priorities. Dr. Carroll's report offers some dramatic results; among the findings, it:

- Confirms earlier studies that identified habitat in northern Maine and the Adirondack/Tug Hill Plateau region of upstate New York capable of supporting a robust regional wolf population.

- Suggests that the possibility of Canadian wolves dispersing into the U.S. in sufficient numbers to reestablish a viable population is extremely unlikely under current landscape conditions because of landscape fragmentation, and hunting and trapping pressure in Ontario and Quebec. It will likely be impossible by 2025 because development patterns are severing the few existing landscape connections.

- Predicts that an active reintroduction program is highly likely to be successful in establishing a viable wolf population in Maine and northern New England, in both current and future landscape conditions.

- Predicts that Canadian wolf populations south of the St. Lawrence River would potentially be more dependent on reintroduced U.S. wolf populations than vice versa. A high level of interdependence between wolf subpopulations in the Northern Appalachians ecoregion is likely, making transboundary conservation critical to long-term wolf recovery.

Dr. Carroll's analysis informs a spirited debate about regional conservation priorities: Should effort be focused on protecting wildlife linkages and reducing wolf mortality in southern Canada, which would allow dispersing animals from source populations north of the St. Lawrence to establish new territories in the U.S.? Or should federal and state agencies implement an active reintroduction program similar to the Yellowstone wolf recovery program, focusing on the excellent potential wolf habitat in Maine? The answer is clear: *both* will be necessary for the long-term viability of wolves in northern New England and New York, but in the near term, a reintroduction program offers the only realistic hope of restoring a robust, ecologically effective population of wolves to the region.

In short, if wolves are to come home now, a century after people systematically eliminated them from the landscape, we will have to help them. The Wildlands Project believes we have an ecological and moral mandate to do so.

Leanne Klyza Linck, Executive Director

EXECUTIVE SUMMARY

The major conclusions from this analysis of wolf habitat and potential population viability in the Northern Appalachians region are:

- MAINE: A wolf population of around 1000 animals could inhabit northern and central Maine and would have high viability in both current and future regional landscapes.

- ADIRONDACKS: A smaller subpopulation of around 300-400 wolves could inhabit the Adirondacks but would have higher vulnerability to landscape change (increased development). Habitat outside the Blue Line, to the west of the Park, would be critical to this population's viability.

- MARITIME PROVINCES: Wolves could potentially persist in areas of central New Brunswick and along the Québec/Maine border, but would be dependent on dispersal from the Maine population. Smaller areas of potential habitat exist on the Gaspé peninsula (Québec) and in southern Nova Scotia.

- LANDSCAPE CONNECTIVITY: At least four potential routes currently exist for recolonization of the northeastern U.S. from north of the St. Lawrence River. However, the region appears to be at or near a threshold of potential dispersal. 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.

- REINTRODUCTION: Reintroducing wolves to either Maine or the Adirondacks has a high likelihood of initial success. However, a reintroduction to Maine would more rapidly reestablish wolf populations in neighboring states and provinces.

- CONSERVATION PRIORITIES: The relatively low potential for rapid natural recolonization of northern Maine, the trend towards increasing isolation of the area from sources of dispersers in Canada, the high potential for success of a reintroduction effort there, and the large effect of a reestablished Maine population on facilitating wolf recovery in neighboring jurisdictions support the use of active reintroduction as a tool for species recovery. If reintroduction is excluded as an option, successful natural recolonization may depend on the creation of strong transboundary initiatives for habitat protection and regulatory reform. These initiatives are in fact a necessary component of any long-term regional wolf conservation strategy, because they will facilitate protection or restoration of landscape linkages between Maine and the Laurentides and Adirondacks. While a Maine wolf population would be viable in isolation on an ecological time scale, restoring connectivity between the northeastern U.S. and the Laurentides region to a level that would allow occasional dispersal events is important for avoiding inbreeding depression and preserving the evolutionary potential of the eastern wolf.

A NOTE ON METHODS: The simulation models used in the analysis are sensitive to biological details, such as wolf dispersal behavior, which cannot be estimated with precision. However, the qualitative guidelines suggested by the model results, such as the relative rankings of alternate recovery strategies for wolves, appear to be similar across a range of plausible parameter values. There is more uncertainty in model predictions of population size, and most uncertainty in the predicted probability of rare events such as recolonization.

INTRODUCTION

Mammalian carnivores are of interest for conservation both in their own right and for what they may indicate concerning emergent landscape characteristics such as connectivity (Noss et al. 1996, Lambeck 1997, Carroll et al. 2001a). In the area of the northeastern U.S. and southeastern Canada known as the Northern Appalachians/Acadia 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 is the foundation for an analysis of recovery potential in the region for the eastern gray wolf (*Canis lupus,* or *Canis lycaon* after Wilson et al. [2000]). The second phase of this study will analyze viability for lynx (*Lynx canadensis*) and American marten (*Martes americana*). 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 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. 2001a, Carroll et al. 2003b).

The research described in this report is the foundation for an analysis of recovery potential in the region for the eastern gray wolf.

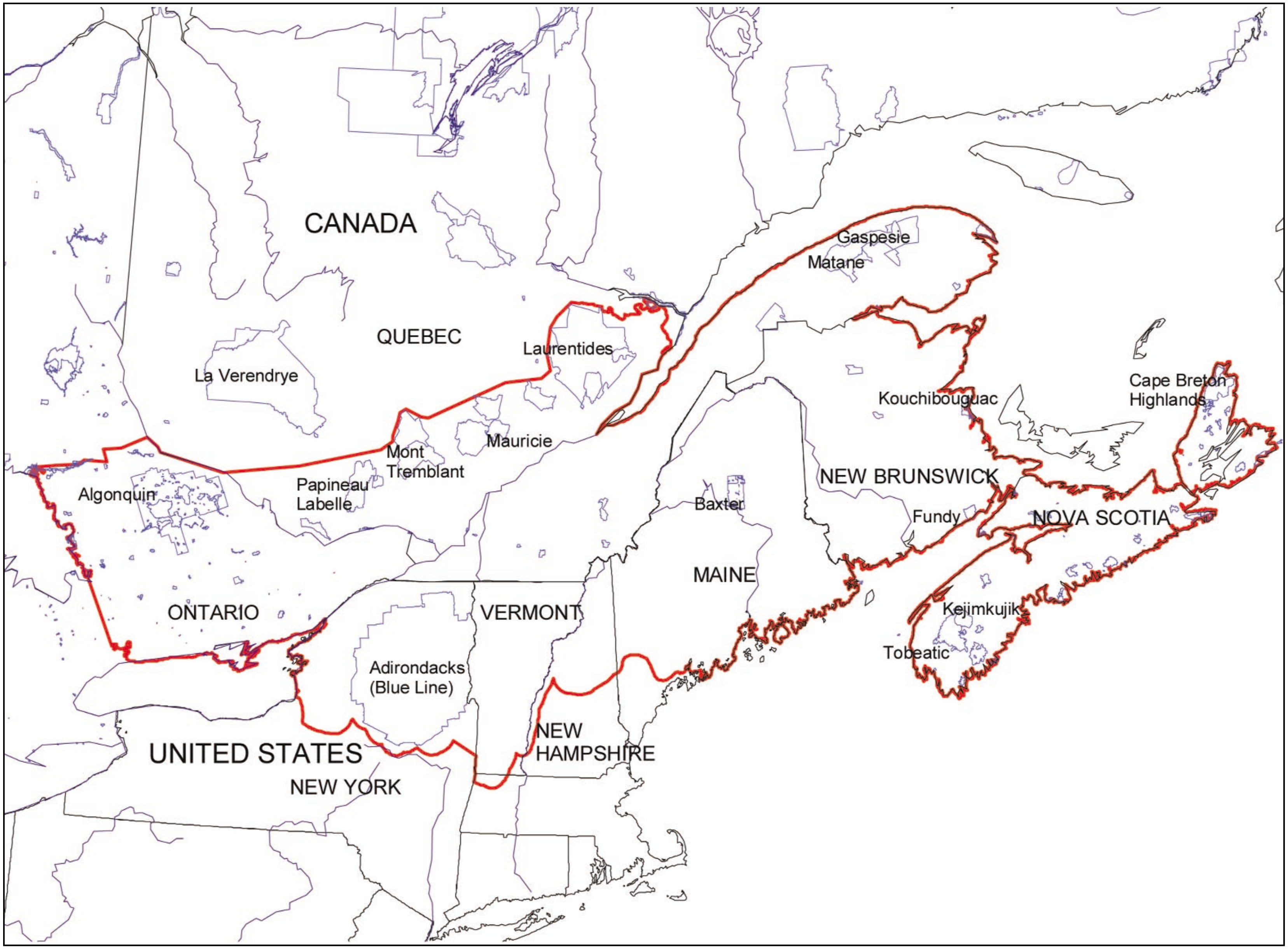
The analysis adapts techniques developed in carnivore restoration projects in the Rocky Mountain region (Carroll et al. 2001a, 2001b, 2003a, 2003b), but also builds upon earlier carnivore habitat analyses for the northeastern U.S. (e.g., Harrison and Chapin 1998, Quinby et al. 1999, Mladenoff and Sickley 1999). When completed in 2004, the multi-carnivore restoration analysis will form a key component of the Wildlands Project's development of a proposed wildlands network for the Northern Appalachians/Southern Canadian Shield region. The study's results will also hopefully 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.

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 wolf has larger home ranges than the lynx and marten, and is likely not currently extant in the Northern Appalachians/Acadia ecoregion. Therefore, our 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 do not summarize results such as population estimates for these peripheral areas but rather examine their effects on wolf populations that might inhabit the Northern Appalachians/Acadia ecoregion.

The model used in this study, PATCH (Schumaker 1998), is an example of a spatially-explicit population model (SEPM) (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. 2003b). 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 meas-

Figure 1 Map of the study area in southeastern Canada and the northeastern United States. The study area boundary is shown in red. Major parks and wildlife reserves are outlined in blue.



ured 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 (Caswell 2001). The model scales the matrix values based on the hexagon scores, with lower scores translating into higher mortality rates and lower reproductive output. The simulations incorporate demographic stochasticity using a random number generator, and may be conducted with or without environmental stochasticity.

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.

Habitat effectiveness—a metric combining road density, local human population density, and interpolated human population density—was used to predict mortality risk.

In the first step of the modeling process, I developed regional-scale models that relate GIS habitat data to the relative fecundity and survival rates shown by wolves in different habitats. In the second step, I incorporated these static habitat models into the PATCH model. Because predictions from such complex simulation models may be sensitive to uncertainty in poorly-known parameters such as dispersal distances (Kareiva et al. 1996), I performed sensitivity analyses to determine uncertainty associated with model predictions.

Habitat effectiveness, a metric combining road density, local human population density, and interpolated human population density, was used to predict mortality risk (Merrill et al. 1999). Habitat rankings were calibrated to specific demographic values based on field studies from areas showing similar habitat quality (e.g. road density) to habitat classes in the PATCH input layers (Ballard et al. 1987, Fuller 1989, Pletscher et al. 1997). However, these field studies were mainly from the western U.S. and Canada and the northcentral U.S., rather than from eastern Canada. Because the response of eastern wolves (including the putative species *Canis lycaon* [Wilson et al. 2000]) to human impacts may differ from that shown by western wolves (Paquet et al. 1999), I explored the sensitivity of model results to assumptions as to how wolf survival varies in response to human impacts such as road density.

The wolf fecundity model was based on estimates of deer (*Odocoileus virginianus*) and moose (*Alces alces*) abundance (Fuller 1989) collected by game agencies throughout the region (Breton and Potvin 1997, St-Onge et al. 1998, Mladenoff and Sickley 1999, FAPAQ unpublished data, NBDNR unpublished data). However, I was not able to obtain comparable data for Nova Scotia or Ontario. Therefore, I developed separate multiple linear regression models to predict deer and moose density based on a variety of regional-scale variables derived from the MODIS satellite imagery (Wharton and Myers 1997), latitude, and topography. Alternate models were compared using AIC and BIC statistics (Akaike 1973, Schwarz 1978). Predicted ungulate density values were then discounted in areas of rugged terrain to account for reduced prey accessibility, by the formula $y = \text{DEPU} * 0.931377^{x}$, where x = slope in degrees (Paquet et al. 1996).

I used a version of PATCH that had been modified to better reflect wolf demography by allowing territory holders to be social rather than solitary (Carroll et al. 2003a). This social structure adds demographic resilience because individuals from the same pack can rapidly replace territory holders (alpha females) that die, and it strongly influences movement rates and patterns. Fecundity is assumed to be independent of pack size because no general relationship between the two factors has been documented (Ballard et al. 1987). As pack size increases, individual wolves in PATCH have a greater tendency to disperse and search for new available breeding sites. Probability of leaving a pack is a quadratically increasing function, with high dispersal probabilities as pack size approaches the theoretical maximum. Setting the theoretical maximum at 24 adults resulted in observed maximum pack sizes of 10 adults, with a mean pack size of 5-6 adults, which is consistent with field data from eastern Canada (Messier 1985, Forbes and Theberge 1995). The size of hexagons or pack territories used in the PATCH model was 500 km^2. Considering that this hexagon size includes interstitial areas between packs, it is similar to that of wolf packs in the moose/deer prey systems of the northern portion of our study region (Messier 1985, Villemure 2003) but larger than territory sizes observed in deer ecosystems (Forbes and Theberge 1995, Jolicoeur and Henault 2002). The mean annual fecundity rate for wolves of greater than 2 years old in the most productive habitat class was set at 3.21 female offspring per breeding female (of which there is at most one per pack). Mean annual survival rates in the most secure habitat class were 0.96 for adults, 0.86 for subadults, and 0.46 for pups (Carroll et al. 2003a). However, these rates varied annually due to environmental stochasticity. I modeled environmental stochasticity by drawing the maximum Leslie matrix values from a truncated normal distribution with coefficients of variation of 30% for fecundity, 40% for pup mortality, and 30% for adult mortality (Ballard et al. 1987, Fuller 1989).

Five sets of alternate scenarios were examined in the PATCH simulations. These assessed the effects on wolf viability of 1) regional landscape change, 2) changes in model assumptions as to mortality risk in Canada, 3) changes in model assumptions as to mortality risk in the U.S., 4) reintroduction of wolves to either Maine or the Adirondacks and 5) changes in model assumptions concerning the dispersal ability of wolves.

The landscape change scenarios used here estimated potential change in human-associated impact factors (e.g., roads and human population) by proportionately increasing road density, except within protected areas, and increasing human population based on current trends derived from a time series of human census data. Census data were available for the period 1990-2000 (U.S.) or 1990-1996 (Canada) (U.S. Census Bureau 1991), Statistics Canada 1997). I predicted human population growth from 2000 to 2025 based on growth rates from 1990 to 1996/2000. Road density was predicted to grow at 1% per year.

After deriving the habitat effectiveness layer from data on roads and human population centers, I offset this base habitat effectiveness value to account for differences in human lethality between jurisdictions. For example, in the United States the Endangered Species Act nominally protects wolves from deliberate killing by humans (Nowak 1978). In contrast, hunting and trapping of wolves is permitted on most public and private lands in Canada. Wolves cannot be hunted in most Canadian national parks and in a few provincial parks such as Algonquin (Ontario) (Forbes and Theberge 1996). Most provincial wildlife reserves within Québec were opened to trapping of wolves in 1984 (Potvin 1987). I offset habitat effectiveness values using the formula $y = 1 - ((1 - H) * z)$, where H is habitat effectiveness and z is the offset factor. An offset of 0.50 was used in strictly protected areas where no hunting or trapping of wolves or other game animals is permitted. These areas form less than 4% of the study region (WWF unpublished data, TNC unpublished data). Offsets of either 0.70, 0.85, or 1.00 (no offset) were used in other areas within the United States. The offset factor on non-park lands in Canada was varied between 1.00 (no offset), 1.25, and 1.50 to assess the effect of different assumptions concerning the effect of contrasts in wolf management policies between the two nations.

> In the United States the Endangered Species Act nominally protects wolves from deliberate killing by humans. In contrast, hunting and trapping of wolves is permitted on most public and private lands in Canada.

I chose two alternate potential reintroduction sites, one each in northwestern Maine and the western Adirondacks, based on preliminary results as to which areas exhibited the highest long-term potential occupancy rates in PATCH. Each reintroduction site was 2500 km^2

in size and consisted of 5 pack territories. I approximated the standard reintroduction protocol (Bangs and Fritts 1996) by introducing five breeding-age females in the first year and setting survival for the first five years at close to 100% under the assumption that new animals would be released to replace mortality among the initial releases.

Although some data on maximum dispersal distance exist from western North America and the northcentral U.S. (Mech et al. 1995, Wydeven et al. 1995, USFWS, unpublished data), it is uncertain how applicable these data are to eastern wolves. It is also difficult to directly translate net dispersal distances measured in the field into PATCH parameters. The maximum dispersal parameter in PATCH is based on the summed distance of all movements, not the net displacement from start to finish of the dispersal. Therefore I varied maximum dispersal distance between 250 and 1500 km to assess the effects on model predictions of uncertainty in this parameter.

I report both equilibrium predictions, the capacity for an area to support the species over 200 years (i.e. equilibrium carrying capacity), as well as transient population dynamics. Carrying capacity was estimated based on simulations which began with all suitable habitat occupied by wolves. Population estimates are assumed to be in winter before birth of pups, when pack size is at its yearly minimum. Simulations to estimate recolonization rates began with wolves occupying only those territories lying north of the St. Lawrence River. I performed 500 replicate simulations of 200 years each for each model scenario predicting equilibrium carrying capacity. For scenarios predicting the likelihood of natural recolonization or the success of active reintroduction, I performed 1000 simulations of 200 years each to more precisely estimate colonization or extinction probability.

Prey density is highest in low-elevation areas in southern Maine, and the Connecticut, St. Lawrence and Champlain valleys, and lowest in the northern portions of the study area.

RESULTS

PREY DENSITY MODEL

The linear regression model predicting deer density took the form deer / km^2 = 0.1830 - 0.0044* ELEVLAT - 0.0008*JEVI + 0.5924*MWET - 0.0214MWET^2 - 5.8919*FOREST +0.409*JBRT (n=107, $p < 0.01$, $R^2 = 0.571$ for the multivariate model). The linear regression model predicting moose density took the form moose / km^2 = 0.8166 + 0.0001486* ELEVLAT - 0.00008619*JEVI + 0.1096*FOREST +0.03738*JWET (n=107, $p < 0.01$, $R^2 = 0.456$ for the multivariate model), where ELEVLAT is elevation (m) adjusted for the effects of latitude, JEVI is MODIS July Enhanced Vegetation Index (Wharton and Myers 1997), MWET and JWET are MODIS March and July tasseled-cap wetness (Crist and Cicone 1984), JBRT is MODIS July tasseled-cap brightness and FOREST is percent MODIS land cover type in forest.

Prey density is highest in low-elevation areas in southern Maine, and the Connecticut, St. Lawrence and Champlain valleys, and lowest in the northern portions of the study area (Figure 2). It tends to vary inversely with habitat effectiveness (security), which is highest to the north of the St. Lawrence valley, in northern Maine, the Adirondacks, and in the Gaspé peninsula (Figure 3).

PREDICTED EQUILIBRIUM DISTRIBUTION AND POPULATION SIZE

PATCH simulations for equilibrium distribution of wolves, under current landscape conditions and a scenario with moderate Canadian and U.S. mortality risk and moderate dispersal ability (the baseline parameters), predict that wolves could inhabit most of northern and central Maine, the western Adirondacks, and portions of western and central New Brunswick, with small isolated populations in the Gaspé peninsula and southern Nova Scotia (Figure 4). The approximate number of wolves that could potentially inhabit the region's states and provinces under current conditions and base parameters ranges from 1200 in Maine, 400-500 each in New York, New Brunswick, and Québec south of the St. Lawrence, to 100-200 each in Nova Scotia, Vermont, and New Hampshire (Table 1).

Table 1. Wolf population estimates for states and provinces under the PATCH model, moderate Canadian mortality risk scenario. These estimates represent the carrying capacity, or the long-term potential of the habitat to support wolves, given landscape conditions in either 2000 or 2025. Southern Québec is defined as that portion of the province south of the St. Lawrence River.

	Population Size*		Percent Reduction	Sensitivity to Dispersal Parameters (% Variation)	
Year	**2000**	**2025**	**2000-2025**	**2000**	**2025**
Maine	1170	1030	11.97	0.68	0.78
New Hampshire	110	68	38.18	5.45	8.82
New York	460	338	26.52	1.71	1.18
Vermont	168	50	70.24	11.90	24.00
Southern Québec	450	252	44.00	11.11	8.73
New Brunswick	486	230	52.67	16.08	22.61
Nova Scotia	158	112	29.11	2.53	0

*750 km dispersal scenario

PREDICTED DEMOGRAPHIC STRUCTURE

Most of northern Maine is predicted to be source habitat for wolves under current landscape conditions and baseline parameters (Figure 4). This source habitat is fringed on all sides in southern Maine, western New Brunswick, and Québec by territories that constitute sink habitat. Areas in Québec adjacent to the Maine border are strong sink habitat (high numbers of wolf mortalities). Source habitat is found in central New Brunswick, and is connected to habitat in Maine via occupied sink habitat under this scenario (Figure 4). The western Adirondacks and adjacent areas to the west constitute a smaller block of source habitat, which is also surrounded by sink habitat, for example in the eastern higher-elevation portions of the Adirondacks (Figure 4). A small linkage zone of occupied sink habitat connects Maine with the Adirondacks via New Hampshire and Vermont. In Québec north of the St. Lawrence River, occupied habitat along the southern margin of wolf range is sink habitat, sustained by source habitat lying further to the north. Most of the smaller wildlife reserves in the area constitute sink habitat, whereas Algonquin Park and its buffer zone are predicted to support a source population surrounded by strong sinks.

EFFECTS OF LANDSCAPE CHANGE

Predicted landscape change over the period 2000 to 2025 has a relatively strong effect on potential equilibrium wolf distribution or carrying capacity, but this impact varies between jurisdictions (Table 1, Figure 7). Smaller populations, such as those in Vermont and New Hampshire, that are sustained by dispersal form adjacent source areas, experience the largest reductions in population size (Table 1). The New Brunswick and southern Québec populations, although large under current conditions, are also highly vulnerable to landscape change due to their dependence on dispersal from Maine. While the Adirondack population suffers a reduction in carrying capacity from 2000 to 2025 of approximately 27%, the larger and more secure Maine population experiences a reduction of 12%. Under future conditions, there is no longer a linkage zone of occupied habitat connecting Maine with the Adirondack population (Figure 7 versus Figure 4).

Predicted landscape change over the period 2000 to 2025 has a relatively strong effect on potential equilibrium wolf distribution or carrying capacity, but this impact varies between jurisdictions.

EFFECTS OF VARYING MORTALITY RISK IN CANADA

Varying mortality risk in the Canadian portion of the study area between the low and high mortality scenarios causes a 64-83% reduction in equilibrium carrying capacity in southeastern Canada (Figure 5 versus Figure 6), but causes less than a 10% reduction within the larger subpopulations in the northeast U.S. (Table 2). A slight reduction in the size of the Maine population when Canadian mortality risk is low is likely due to increased dispersal from Maine into Canada under those conditions. Increasing mortality risk in Canada has a strong negative effect on the predicted probability of natural recolonization of the northeast U.S. (Table 3). Recolonization probability is somewhat higher for the Adirondacks than for Maine under moderate Canadian mortality parameters. However, for both states, under current landscape conditions, probability is near zero under the high Canadian mortality parameters and high under the low mortality parameters (Table 3). Dispersal sources in Canada retreat northward under higher mortality assumptions (Figure 6 versus Figure 4) and the intervening landscape (St. Lawrence valley) becomes more hostile to wolves.

Table 2. Wolf population estimates for states and provinces under the PATCH model, under contrasting Canadian mortality risk scenarios. These estimates represent the carrying capacity, or the long-term potential of the habitat to support wolves, given landscape conditions in either 2000 or 2025.

	2000			2025		
	Low	Med	High	Low	Med	High
Maine	1196	1170	1148	974	1030	1004
New Hampshire	118	110	104	54	68	62
New York	498	460	456	262	338	340
Vermont	202	168	158	30	50	44
Southern Québec	742	450	276	362	252	134
New Brunswick	768	486	268	368	230	106
Nova Scotia	418	158	98	164	112	78

Table 3. Maximum occupancy of wolf habitat in the northeastern U.S. as predicted by the PATCH model under contrasting parameter sets. Values represent the percentages out of 1000 PATCH simulations of 200 years each. Simulations began with wolves occupying only areas north of the St. Lawrence Valley.

Maine

Mortality	Low		Medium			High	
Dispersal (km)	**750**	**1500**	**250**	**750**	**1500**	**750**	**1500**
2000	62.88	90.52	0.20	2.09	10.35	0	0.28
2025	0.96	2.62	0	0.10	0	0	0

New York State

Mortality	Low		Medium			High	
Dispersal (km)	**750**	**1500**	**250**	**750**	**1500**	**750**	**1500**
2000	98.65	98.71	5.15	54.01	86.87	0.32	4.72
2025	26.72	61.59	0.10	0.72	5.97	0	0.02

EFFECTS OF VARYING MORTALITY RISK IN THE U.S.

Varying mortality risk in the U.S. portion of the study area between the low and high mortality scenarios (with mortality risk in Canada held constant) causes a large (45-95%) reduction in equilibrium carrying capacity in the Adirondacks, New Hampshire and Vermont, and 17-28% reduction in Maine. Reductions in southeastern Québec and New Brunswick (23-53%) are intermediate between these extremes (Table 4, Figure 8 versus Figure 4). Effects of variation in mortality assumptions are greater under future landscape conditions (Table 4).

Table 4. Wolf population estimates for states and provinces under the PATCH model, under contrasting U.S. mortality risk scenarios. These estimates represent the carrying capacity, or the long-term potential of the habitat to support wolves, given landscape conditions in either 2000 or 2025.

	2000			2025		
	Low	**Med**	**High**	**Low**	**Med**	**High**
Maine	1260	1170	1046	1172	1030	844
New Hampshire	144	110	72	118	68	32
New York	582	460	318	498	338	182
Vermont	292	168	52	204	50	10
Southern Québec	524	450	402	310	252	212
New Brunswick	560	486	418	316	230	148
Nova Scotia	166	158	158	114	112	112
TOTAL	**3528**	**3002**	**2466**	**2732**	**2080**	**1540**

EFFECTS OF VARYING DISPERSAL PARAMETER ON PROBABILITY OF NATURAL COLONIZATION AND CARRYING CAPACITY

The probability of colonization of the northeast U.S. and Maritime Provinces by dispersal from areas north of the St. Lawrence River varies greatly in response to alternate dispersal parameters (Table 3, Figures 9-11). For example, under the moderate mortality scenario, with current landscape conditions, the probability of the Adirondacks being recolonized goes from 5% (250 km) to 87% (1500 km). However, the areas most likely to be recolonized remain constant, with the Adirondacks having a somewhat higher probability than northern Maine (Figures 9-11). Under future landscape conditions, recolonization probabilities for all dispersal parameters go to near zero except for the Adirondacks under the low Canadian mortality scenario (Table 3, Figure 12). In contrast to the above, an increase in the maximum dispersal parameter from 250 to 1500 km in the equilibrium simulations (which begin with all habitat occupied) has a relatively small effect on carrying capacity (Table 1). Population estimates under the different dispersal parameters vary by 11-16% in areas (southern Québec, New Brunswick, and Vermont) peripheral to the large source population in Maine. Population estimates for Maine and the Adirondacks vary by less than 2% under varying dispersal parameters.

Reintroduction of wolves to Maine has a less than 1% failure (extinction) rate in all cases, including parameter sets representing combinations of three mortality scenarios, three alternate dispersal distances, and both current and future landscape conditions.

REINTRODUCTION SCENARIOS

Reintroduction of wolves to Maine has a less than 1% failure (extinction) rate in all cases, including parameter sets representing combinations of three mortality scenarios, three alternate dispersal distances, and both current and future landscape conditions. A reintroduction to the Adirondacks has similarly high success, with failure rates ranging from < 1% under the most favorable parameters to 5.22% for the high mortality scenario under future landscape conditions. However, growth of a reintroduced Adirondack population to other areas is slower than if wolves were reintroduced to Maine (Figure 14 versus Figure 13). Regional wolf populations eventually attain 75-80% of their equilibrium carrying capacity through dispersal from a Maine population, but only 17-21% of carrying capacity through dispersal from a reintroduced Adirondack population (Table 5).

Table 5. Wolf population estimates for the overall study region (excluding Ontario and Québec north of the St. Lawrence river) under the PATCH model, under contrasting U.S. mortality risk scenarios. These scenarios begin with reintroduction of 5 breeding pairs to either Maine or New York, and assess population size after 200 years.

	2000			2025		
	Low	Med	High	Low	Med	High
Maine	3302	2420	1848	2226	1508	1158
New York	2880	624	320	990	356	198

DISCUSSION

The results from this study suggest that a wolf population inhabiting northern and central Maine would have high viability in both current and future regional landscapes. A smaller subpopulation might exist in the western Adirondacks but would have higher vulnerability to landscape change. In Canada's Maritime Provinces, wolves could potentially persist in areas of central New Brunswick and southern Québec but would likely be dependent on dispersal from the Maine population. Smaller habitat areas exist on the Gaspé peninsula (Québec) and in southern Nova Scotia, but these are unlikely to be recolonized naturally. At least four potential routes currently exist for recolonization of the northeastern U.S.

from north of the St. Lawrence River. However, successful dispersal may be unlikely under future conditions unless hunting and trapping pressure diminishes on wolf populations north of the St. Lawrence valley.

LIMITATIONS AND STRENGTHS OF THE ANALYSIS

Complex spatial viability models such as PATCH (Schumaker 1998) may be more biologically realistic than simpler tools, but this may come at the expense of increased sensitivity of the results to lack of detailed demographic, habitat, and movement data (Kareiva et al. 1996). Therefore, it is important to assess which conservation questions can be answered with relative confidence despite model uncertainty. For example, 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 (Carroll et al. 2003b).

The habitat data input to the PATCH simulations are composed of two data layers: one representing fecundity (prey availability), and one representing survival (human-associated mortality). The use of roads and human population (Merrill et al 1999) as a surrogate for mortality risk is likely to be robust in this landscape, where most wolf mortality is associated with access by hunters and trappers (Vucetich and Paquet 2000, Villemure 2003). However, the effect of contrasts in hunting regulations between jurisdictions is uncertain, and thus treated in the sensitivity analysis below. The relationship of wolf fecundity to prey availability is also likely to be robust across different ecosystems (Fuller 1989). The prey abundance data (Figure 2) reveals the strong elevational and latitudinal gradients in prey productivity in the region. In this context they highlight the inverse correlation between prey productivity and habitat security. Protected areas at high elevation (the Adirondacks) or higher latitude (the Laurentides reserves) generally support lower prey densities than do more productive habitats. However the latter areas are usually dedicated to human uses and thus less suitable for wolves. Where the secure and productive zones overlap, as in central Maine (Mladenoff and Sickley 1999) or the western Adirondacks, they form potential key areas for wolf recovery if managed correctly (Mladenoff et al. 1997).

> The results from this study suggest that a wolf population inhabiting northern and central Maine would have high viability in both current and future regional landscapes. A smaller subpopulation might exist in the western Adirondacks but would have higher vulnerability to landscape change.

The model's predictions of recolonization success are quite sensitive to variation in the dispersal parameter (Table 3). Sensitivity to dispersal parameters is commonly identified as a weakness of spatially-explicit population models (Kareiva et al. 1996). However, experience applying such models to several regions of the western U.S. and Canada (Carroll et al. 2003a, Carroll et al. 2003b) suggest that the PATCH model rarely show high sensitivity to dispersal parameters when applied to real landscapes. Subpopulations are usually close enough that any biologically-realistic dispersal parameter is sufficient to connect them, or so distant that they are never connected by effective dispersal. The current study's high sensitivity to the dispersal parameter suggests that the region may be at or near the connectivity threshold for wolves. The model's predictions of equilibrium occupancy or carrying capacity are relatively robust to changes in the dispersal parameters (Table 1). Therefore, estimates of how many wolves might eventually inhabit the northeastern U.S. may be useful guides for conservation planning. Model conclusions are also fairly robust in their relative ranking of wolf subpopulations as to long-term viability and their assessment of the effects of policy changes in one jurisdiction on overall regional population viability. This makes the results useful for priority-setting for restoration efforts (Carroll et al. 2003a).

A recent study of the genetics of eastern wolves suggests that they may merit status as a distinct species (*Canis lycaon*), which is more closely related to red wolves (*Canis rufus*) and coyotes (*Canis latrans*) than to the western gray wolf (*Canis lupus*) (Wilson et al. 2000).

Genetic relatedness between eastern wolves and coyotes might lead to high levels of interspecific hybridization if the founding wolf population was small in number compared to the sympatric coyote population (Paquet et al. 1999, D. Harrison pers. comm.). The PATCH model does not incorporate information on genetics, so this study cannot address any additional factors affecting eastern wolf recovery that might arise from this taxonomic revision. Almost all of the our study area falls within the zone of distribution of the putative *C. lycaon* (Villemure 2003). *C. lycaon* is usually characterized as the 'Algonquin' wolf ecotype, whose relatively small size is adapted to prey systems dominated by white-tailed deer (Jolicoeur and Henault 2002). However, in some portions of our study area such as northern Maine, moose form a significant component of the potential prey base for wolves. Deer range has also expanded northward since European settlement in response to landscape change (Parker 1995). If, as seems likely, moose formed an important source of prey for pre-settlement wolf populations in the region, moose may have been preyed upon by either a second subspecies of wolf that coexisted with *C. lycaon* or a larger-bodied ecotype of *C. lycaon*. This highlights the fact that regional wolf recovery would occur in the context of historical and ongoing trends in the region's ecosystems brought about as the ranges of other species of carnivores and prey respond to climate change and forest loss and regrowth. These trends will impact wolves very differently than they will impact mesocarnivores such as the lynx or marten.

Increasing mortality risk in Canadian landscapes not only makes dispersal routes across the St. Lawrence valley more hostile, it also causes source habitat in Québec and Ontario to retreat farther northward.

NATURAL RECOLONIZATION

Although conclusions about actual recolonization probability are limited by the model's sensitivity to the dispersal parameter (Table 3), the results do suggest the strong influence of wolf management policy in Canada on the probability of natural recolonization of the northeastern U.S. (Table 3). We can assess the plausibility of alternate scenarios for mortality risk in Canada by comparing model predictions (Figures 5-7) with the current limits to wolf distribution north of the St. Lawrence valley (Harrison and Chapin 1998). This suggests that the low mortality scenario for Canada is probably unrealistic under current conditions, although it is helpful for showing the potential effects of a change in wolf management regulations in eastern Canada. Changes in Canadian wildlife regulations have a dramatic effect on U.S. colonization potential (Table 3), but a small effect on the subsequent viability and size of U.S. populations (Table 2). Increasing mortality risk in Canadian landscapes not only makes dispersal routes across the St. Lawrence valley more hostile, it also causes source habitat in Québec and Ontario to retreat farther northward. This is because the reserves on the north side of the St. Lawrence valley, with the exception of Algonquin Park and its buffer zone, are not large enough to maintain secure source habitat (Forbes and Theberge 1996, Villemure 2003). Without enlargement or regulatory changes in these reserves, maintenance of source habitat depends on the de facto reserve status of roadless areas to their north which are being reduced over time by the northward expansion of timber extraction. Spatially-explicit models such as PATCH reveal how this ongoing landscape change interacts with potential policy alternatives to affect population viability. This in turn suggests guidelines for the size of reserves that may be necessary to maintain viable populations in the region (Carroll et al. 2003b).

REINTRODUCTION

The high predicted success rates for reintroduction of wolves to either Maine or the Adirondacks support exploration of the use of active reintroduction as a tool for species recovery. Restoring wolves to Maine is a higher priority than recovery effort in New York State because a Maine population would be more resilient to future landscape change (Table 1) and would be of greater benefit to the overall region because it would be large enough to support peripheral sink populations in neighboring states and provinces (Table 5). This high level of interdependence between wolf subpopulations in the northern Appalachians ecoregion is an important insight from the models. The northeastern U.S. depends on Canada for initial wolf dispersers, but not for ongoing demographic rescue (Brown and Kodric-Brown 1977). However, portions of Canada, such as central New Brunswick, may depend on U.S. wolf populations for demographic rescue. Canadian wolf populations south of the St. Lawrence River would potentially be more dependent on reintroduced U.S. wolf populations than vice versa. Genetic issues, which are not incorporated in the PATCH model, may make occasional dispersal events between the northeastern U.S. and the Laurentides region important for avoiding inbreeding depression. However, the level of dispersal necessary for avoidance of inbreeding is much less than that necessary for demographic rescue (Mills and Allendorf 1996).

Restoring wolves to Maine is a higher priority than recovery effort in New York State because a Maine population would be...large enough to support peripheral sink populations in neighboring states and provinces.

COMPARISON WITH RESULTS FROM PREVIOUS STUDIES

Wolf recovery in the northeastern U.S. has been the subject of several previous studies, with two (Harrison and Chapin 1998, Mladenoff and Sickley 1999) using spatial habitat models to address the issue. My results agree with these earlier studies concerning where wolves might be located in the northeastern states. In addition, the PATCH population estimates are similar to those from a static logistic regression model (Mladenoff and Sickley 1999). The comparable results achieved by these quite different type of models lends confidence to the parameters used in the PATCH simulations. A similar study in Colorado found good agreement between wolf population estimates from a static resource selection function model and the PATCH model (Carroll et al. 2003a).

Although all studies have predicted high recovery potential in northern Maine, they have disagreed as to prospects for wolf recovery in the Adirondack region. Wydeven et al. (1998) suggested that no plausible dispersal corridor existed to the Adirondacks from Canadian wolf populations. In contrast, Quinby et al. (1999) identified a linkage from Algonquin Park to the Adirondacks (the “A2A” corridor). However, although a route along the Frontenac Axis was identified as the best remaining linkage between the two areas, it was not compared with linkages known to be used by wolves in other areas. Paquet et al. (1999) concluded that although a small wolf population could potentially inhabit the Adirondacks, it would have low long-term viability due to its small size and ongoing landscape change there.

The PATCH model results suggest at least four potential linkages between Canada and the northeastern U.S. (Figure 11). Two linkages to Maine, originating to the east and to the west of Québec City, have been highlighted previously (Harrison and Chapin 1998, Wydeven 1998). The A2A linkage (Quinby et al. 1999) also is used in the PATCH simulations. A second linkage between Papineau-Labelle reserve and the northern Adirondacks is also used. Recolonization probability is higher for the Adirondacks than for northern Maine in the PATCH simulations (Table 3). However, it is probably unwise to give much weight to the exact recolonization probabilities, as dispersal in PATCH does not accurately mimic the patterns of long-distance dispersal (e.g., directionality, tortuosity) shown by wolves. The conclusion that the Adirondacks are more likely to be recolonized than is northern Maine may be an artifact of how dispersal mortality is treated in the PATCH model. Because there is no explicit dispersal mortality except at the end of each yearly time step (Schumaker 1998), the likelihood of a disperser traversing a short but highly hostile landscape may be overestimated. We can have more confidence in the fact that the model predicts that dispersal probability will drop dramatically under future landscape conditions, unless protective regulations or buffer zones are established in southern Canada. Dispersal from protected wolf populations in the Laurentides region is currently primarily northward into forested habitat where vacant wolf territories have been created by trapping, rather than southward into the agricultural landscape of the St. Lawrence valley (Villemure 2003, H. Jolicoeur pers. comm.). Therefore trapping not only blocks southerly dispersers (Villemure and Jolicoeur in press) but also relieves dispersal pressure.

CONSERVATION IMPLICATIONS

My results suggest that, although the concerns of Paquet et al. (1999) as to the viability of an Adirondack wolf population are justified, proper management and land use policy could likely sustain a population there. The effects of landscape change are twice as severe in the Adirondacks as in northern Maine, due both to the landscape trends themselves and to the inherent vulnerability of the smaller wolf population. Habitat outside the Blue Line, to the west of the Park, would be critical to this population's viability. Fortunately, recent conservation acquisitions in areas such as the Tug Hills may support these steps.

> A focus on connectivity at this broader scale is important because wolves appear to be able to travel through a wide range of landscapes but may not readily settle in areas that lack other wolves.

Restoring connectivity between Maine and the Adirondacks appears problematic due to the pace of landscape change in Vermont and New Hampshire. The few wolf packs that might inhabit the latter two states under current conditions are even more vulnerable than those in New York State, as they are peripheral populations dependent on connectivity with the core population in Maine. However, preserving linkage habitat in Vermont and New Hampshire is important because of the necessity over the long-term of maintaining genetic interchange between regional subpopulations. The PATCH results (e.g., Figure 4) identify broad linkage zones of potentially inhabited habitat rather than narrow corridors that may permit travel but not residence by wolves. I believe that a focus on connectivity at this broader scale is important because wolves appear to be able to travel through a wide range of landscapes but may not readily settle in areas that lack other wolves (Mech and Boitani 2003). Preservation of "stepping stone" areas that may support resident wolves may facilitate effective dispersal between disjunct populations whereas a narrow travel corridor would not.

The effects of landscape change in the northern Appalachians match patterns predicted over the same period in regions of the western U.S. (Carroll et al. 2003a, Carroll et al. 2003b). The potential core populations in Maine and the Adirondacks show levels of threat similar to those of large core populations in the west such as the Greater Yellowstone Ecosystem (Noss et al. 2002). Peripheral northeastern populations show the higher threat levels characteristic of small core and peripheral populations in the west such as in Colorado (Carroll et al. 2003a). Wolf recovery in Maine should be a facet of a larger multi-jurisdictional planning effort that would protect linkages between northern Maine and areas such as central New Brunswick. Because the principle of redundancy is important in species conservation, a secondary recovery effort in the Adirondacks may be worthwhile. Smaller potential recovery areas in the Gaspé peninsula and Nova Scotia that are unlikely to be recolonized by natural dispersal would be lower priorities for restoration.

Protected areas currently form only about 6% of the study region (WWF unpublished data, TNC unpublished data). Current *de facto* refugia on the northern edge of the study region are likely to lose their value as they are roaded in the course of timber harvest. For wolf populations to persist in the region, a larger percentage of the landscape must have low mortality risk due to low human access (road density [Thiel 1985]) and/or low hunting and trapping pressure (Carroll et al. 2003a). This can be achieved by protected area expansion, regulatory reform (e.g., trapping restrictions), or a combination of the two. Strategically-placed buffer zones can greatly enhance the effectiveness of small protected areas for wolves (Forbes and Theberge 1996, Vucetich and Paquet 2000, Villemure 2003), as seen by the relatively high viability of the Algonquin Park population in the simulations. Because wolves, unlike mesocarnivores such as the marten, do not require mature forest structure, any regulatory changes will immediately benefit wolf population viability.

The relatively low potential for natural recolonization of northern Maine, the trend towards increasing isolation of the area from sources of dispersers in Canada, the high potential for success of an active reintroduction there, and the large effect of a reestablished Maine population on facilitating wolf recovery in neighboring jurisdictions, supports exploration of the use of active reintroduction as a tool for species recovery. Even though wolves may occasionally disperse across the St. Lawrence valley (Villemure and Jolicoeur in press), and possibly reach Maine, achievement of a large viable population there might be slow and uncertain due to factors known as Allee effects (e.g., scarcity of mates) that lower the growth rate of small founder populations. If active reintroduction is excluded as an option, successful natural recolonization may depend on the creation of strong transboundary initiatives for habitat protection and regulatory reform. These initiatives are in fact a necessary component of any long-term regional wolf conservation strategy, because they will facilitate protection or recreation of landscape linkages between Maine and the Laurentides and Adirondacks.

The completion of this study in early 2004 will allow comparisons between the needs of the gray wolf as outlined above and those of other carnivore species in the region. As was the case for the wolf, this second phase will build on past studies of regional habitat potential for the lynx and American marten, but add insights on viability from the PATCH model. This will allow the design of conservation networks, through the reserve selection software SITES (Possingham et al. 2000), that provide optimal combinations of habitat for ensuring the long-term viability of the region's native carnivore species.

For wolf populations to persist in the region, a larger percentage of the landscape must have low mortality risk due to low human access and/or low hunting and trapping pressure. This can be achieved by protected area expansion, regulatory reform or a combination of the two.

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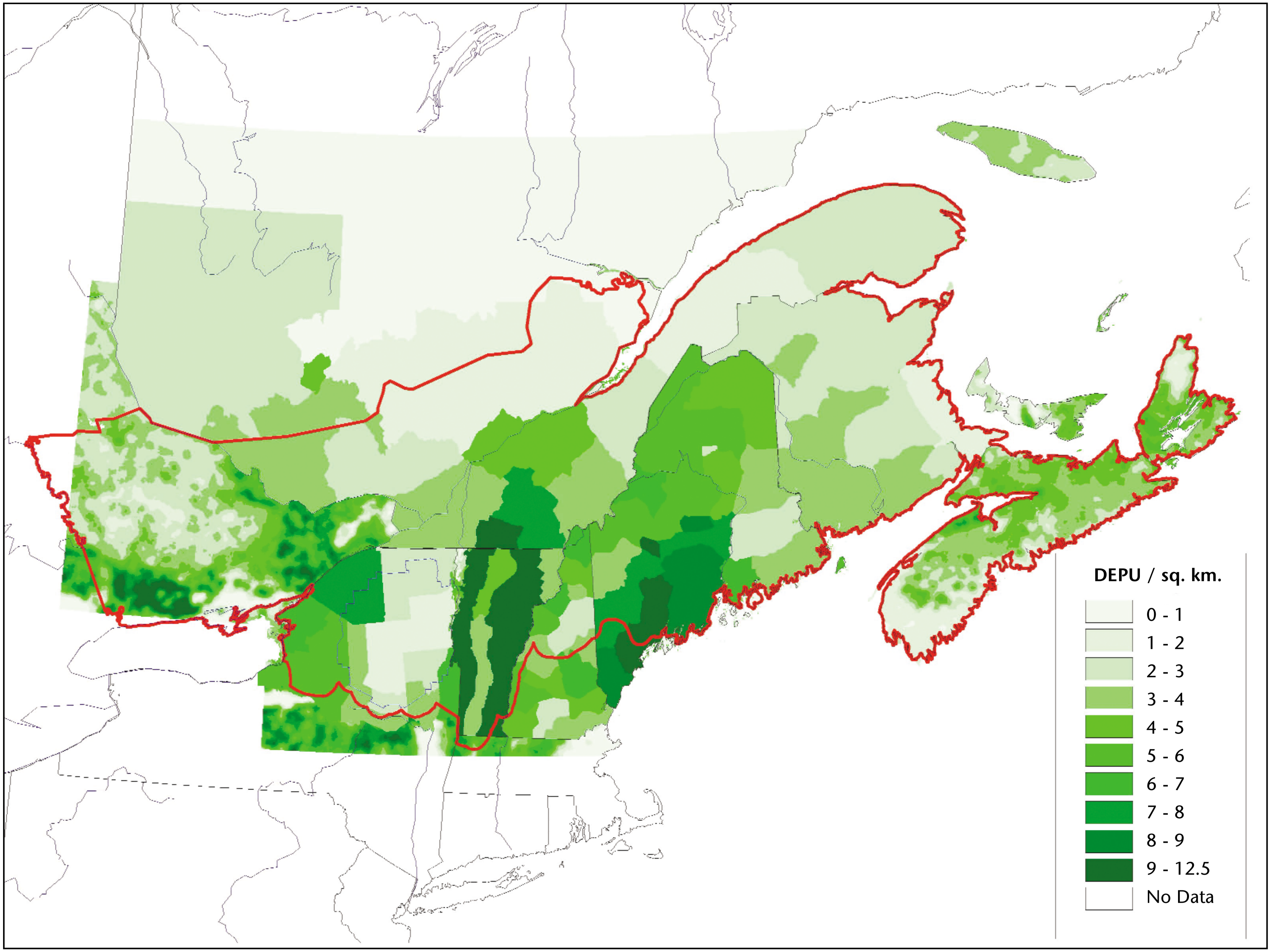
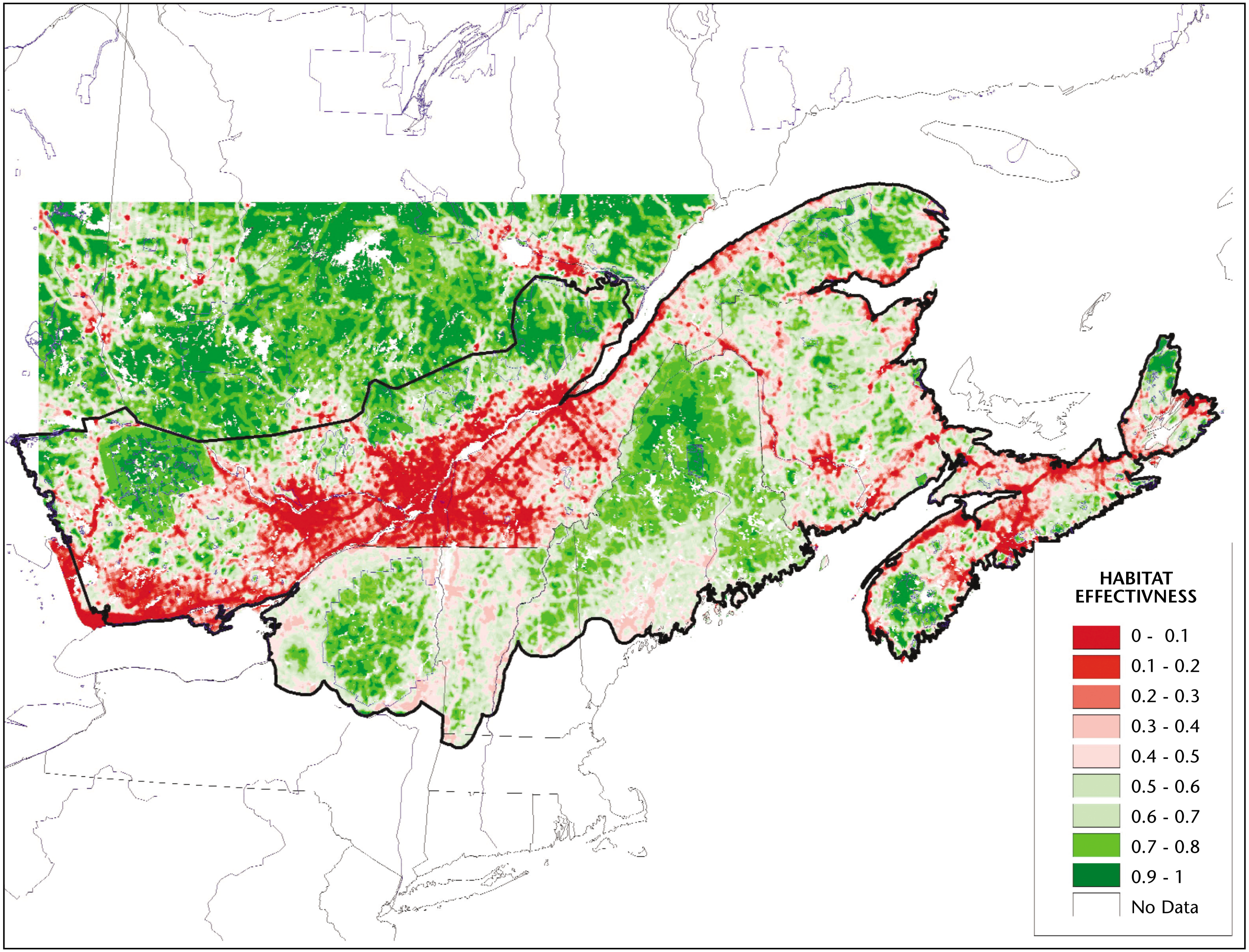


Figure 2 Prey abundance data used in the wolf PATCH simulations. DEPU, or deer-equivalent prey units, is a metric for expressing prey density in multi-prey systems (Mladenoff and Sickley).

Figure 3 Habitat effectiveness (Merrill et al. 1999) under current conditions (2000) for large carnivores in southeastern Canada and the northeastern United States under the moderate Canadian mortality risk scenario (see text). Secure areas (green) are characterized by low road density and human population density.



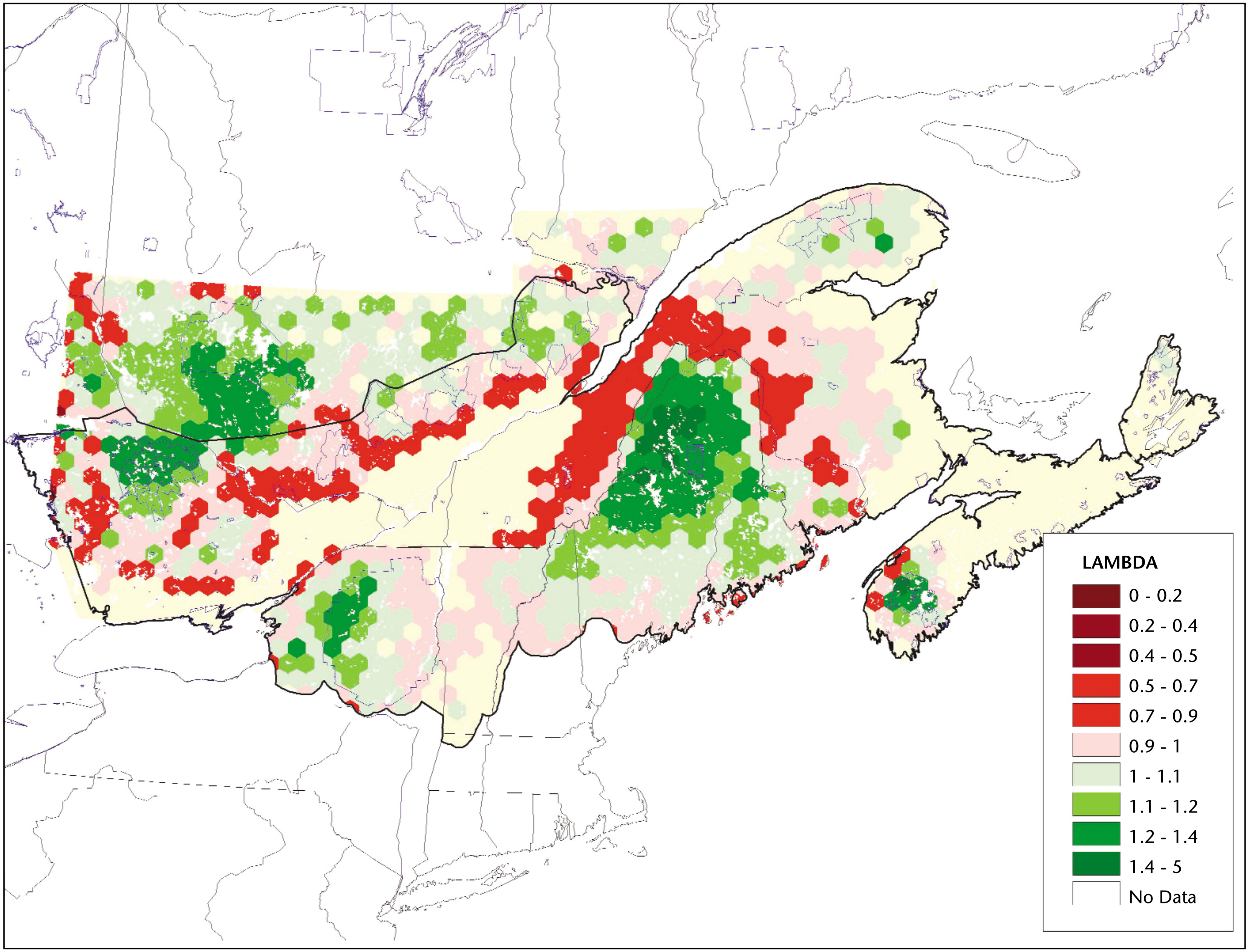
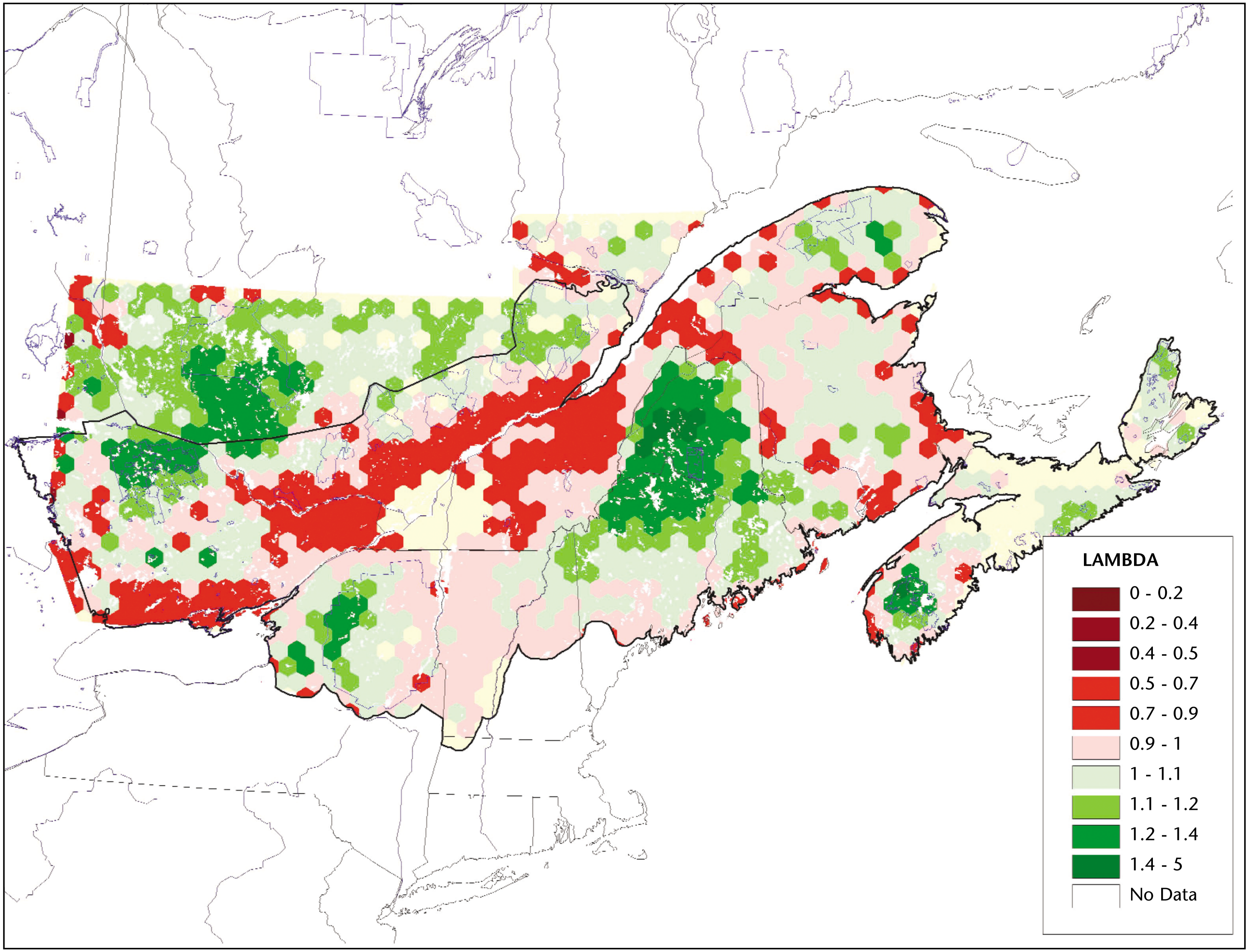


Figure 4 Demographic potential of wolves under current landscape conditions and the moderate Canadian mortality risk scenario (see text). Legend shows population growth rate (lambda) values predicted by the PATCH model simulations. Areas in green are population sources, whereas areas in red are sinks. Areas with less than 50% probability of occupancy are shown in yellow.

Figure 5 Demographic potential of wolves under current landscape conditions and the low Canadian mortality risk scenario.



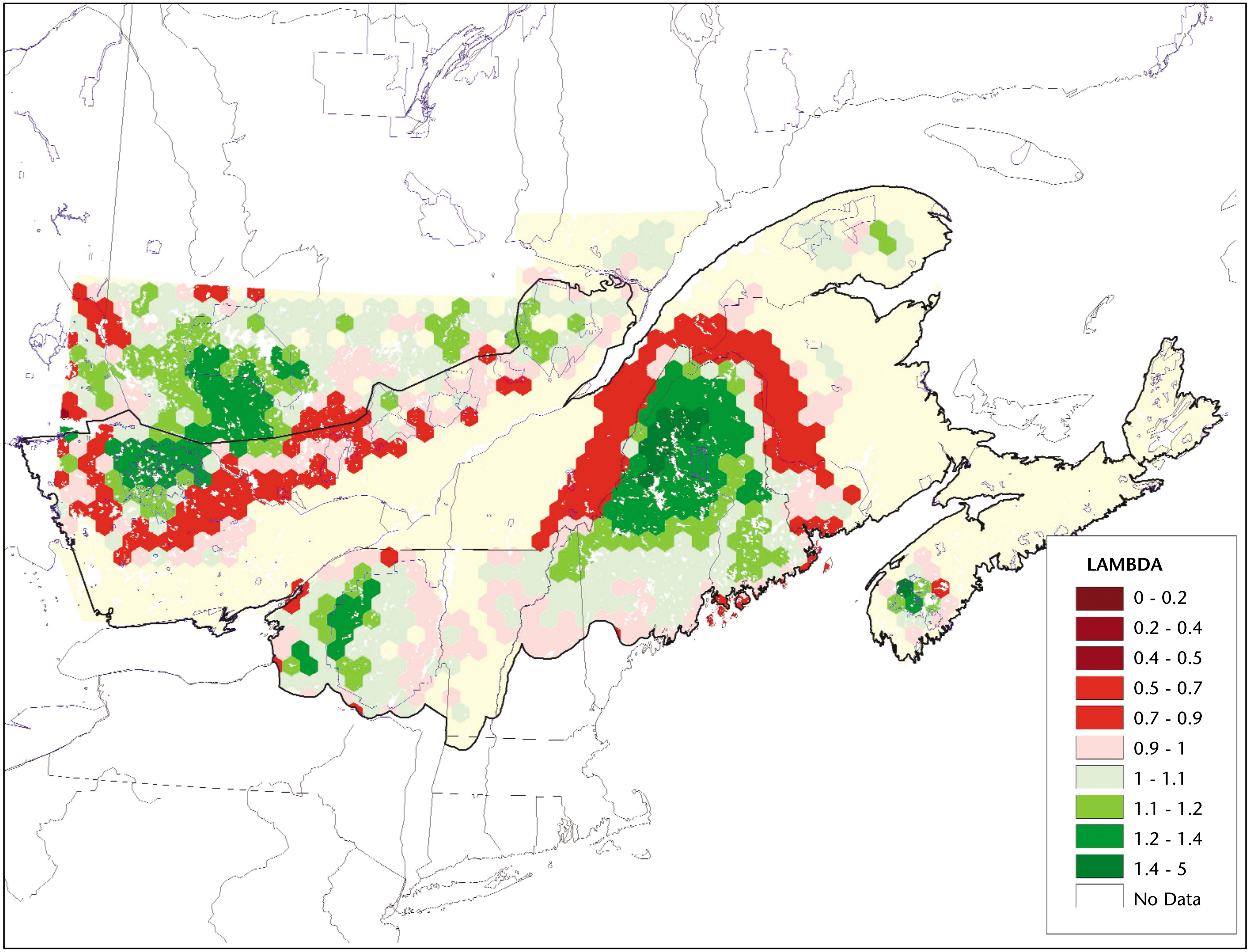
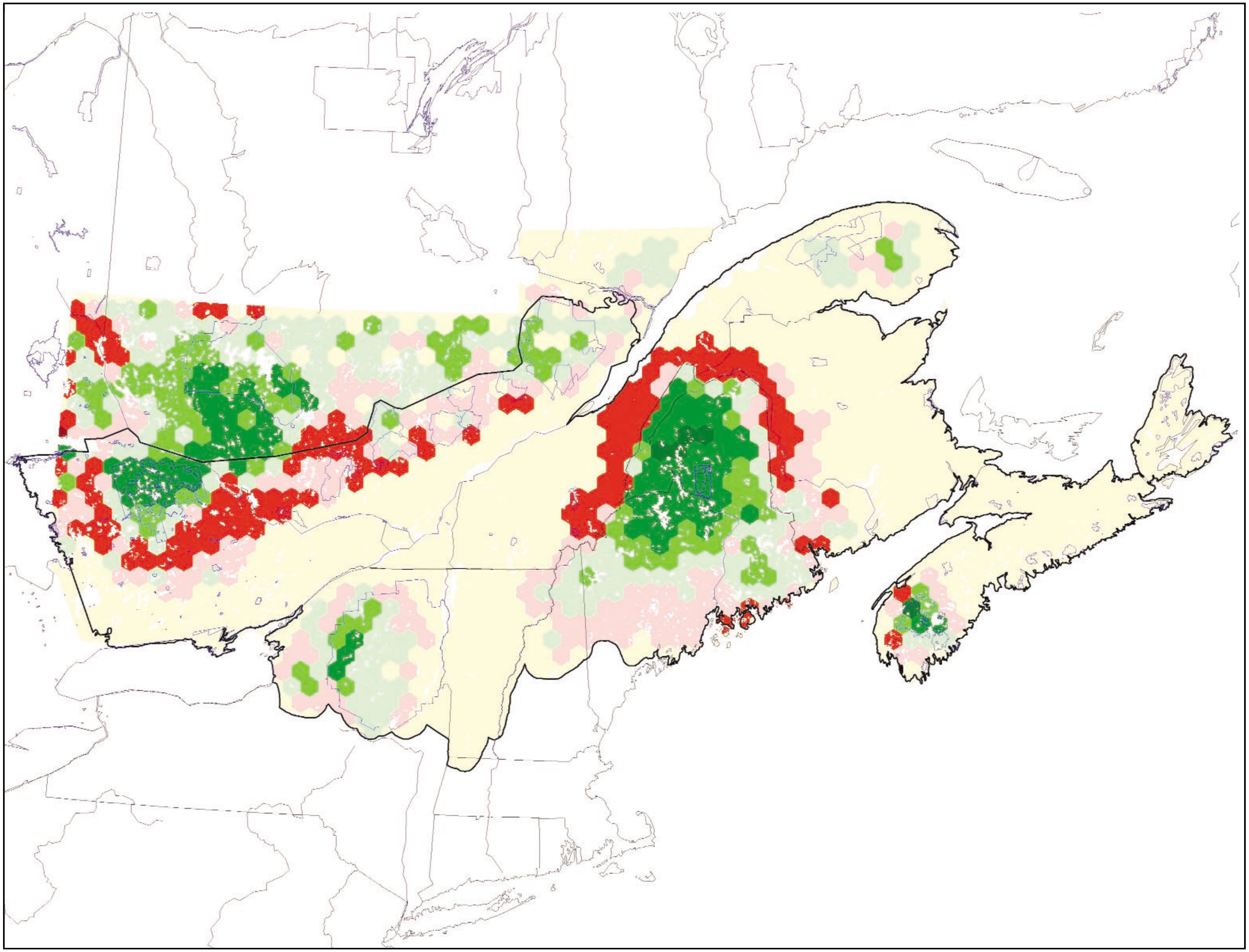


Figure 6 Demographic potential of wolves under current landscape conditions and the high Canadian mortality risk scenario.

Figure 7 Demographic potential of wolves under future (2025) landscape conditions and the moderate Canadian mortality risk scenario.



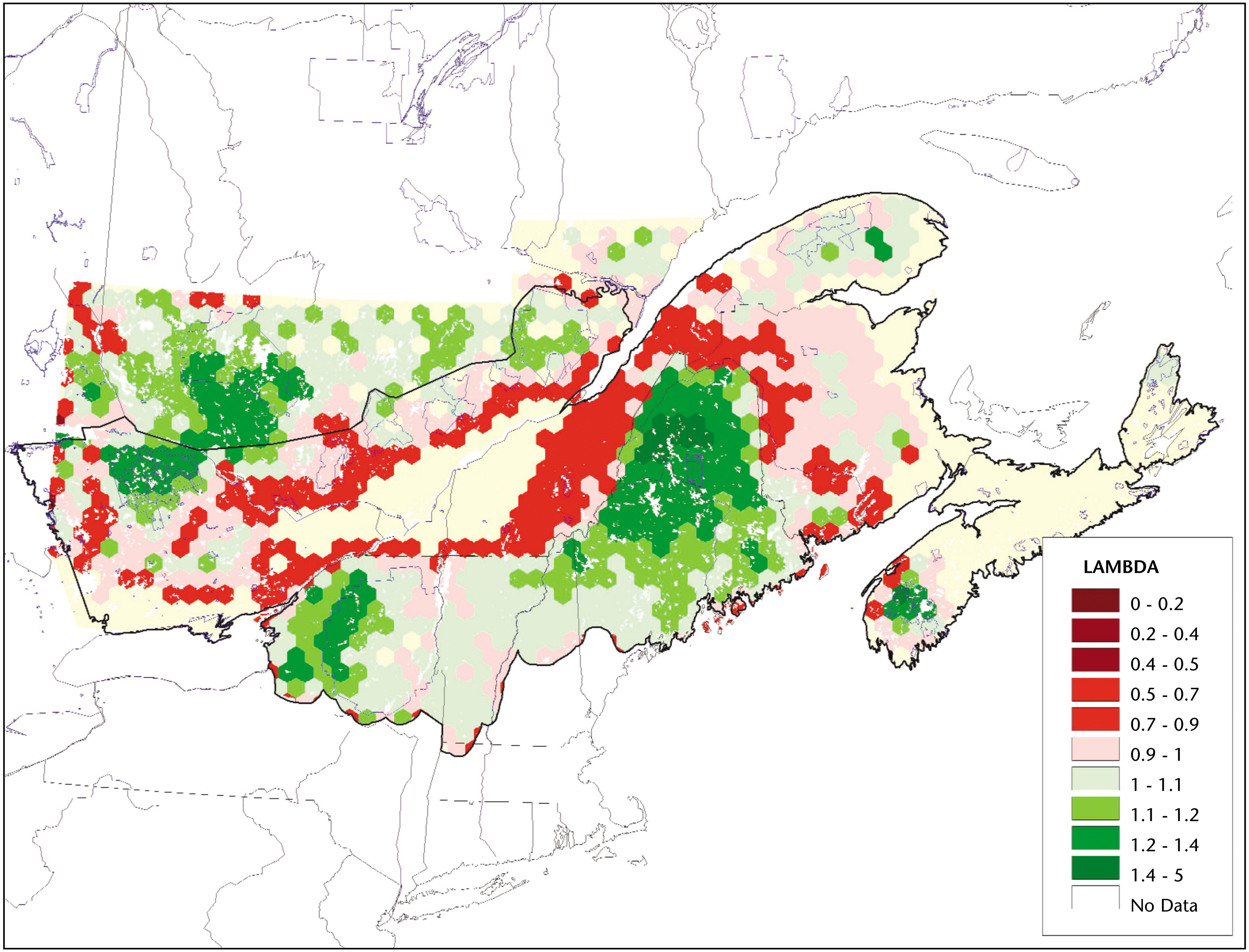
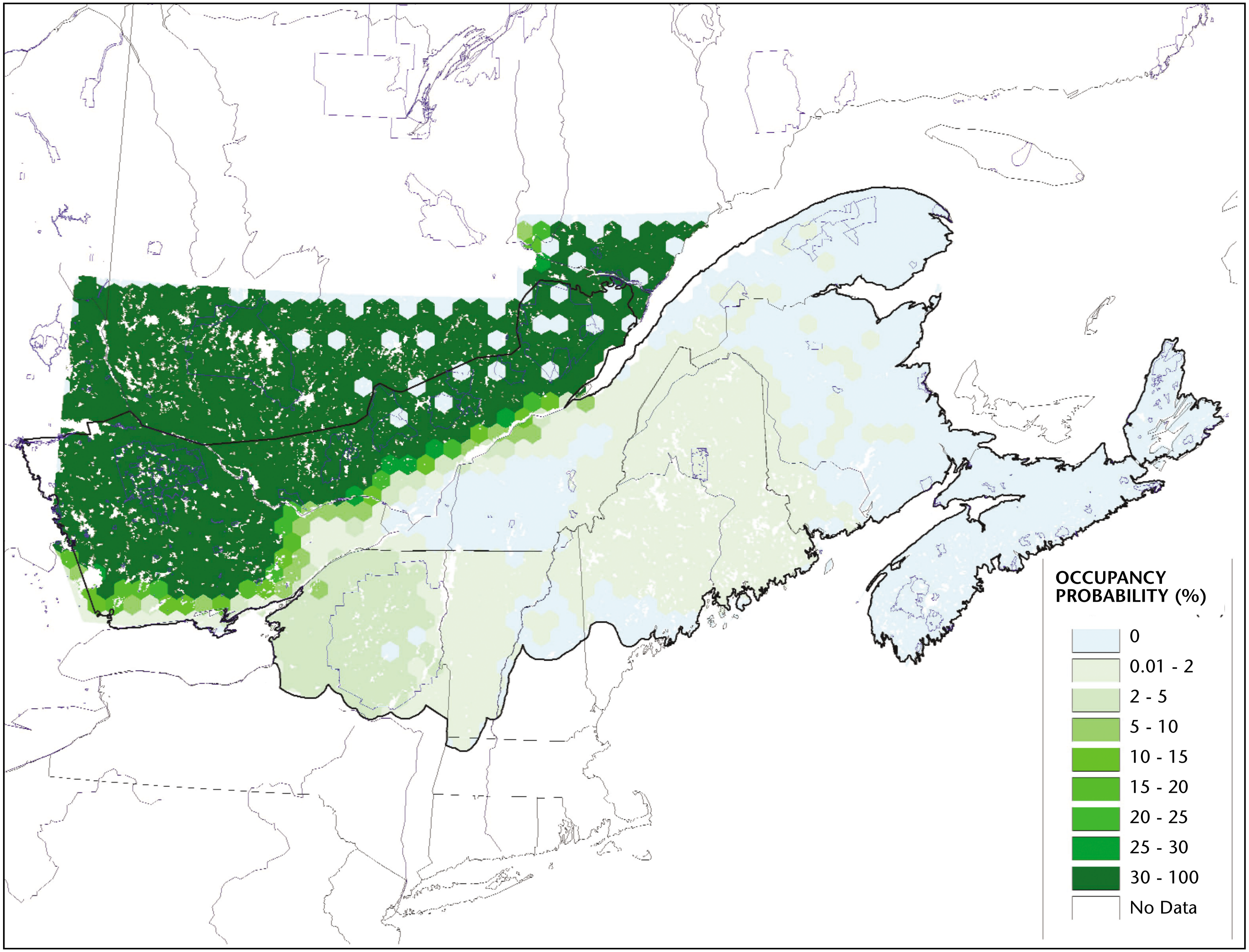


Figure 8 Demographic potential of wolves under current landscape conditions, the baseline (moderate) Canadian mortality risk scenario, and the low U. S. mortality risk scenario.

Figure 9 Predicted potential for recolonization by wolves of the northeastern U. S. and maritime Canada under current landscape conditions and the moderate Canadian mortality risk scenario, assuming a 250 km per year maximum dispersal distance (see text).



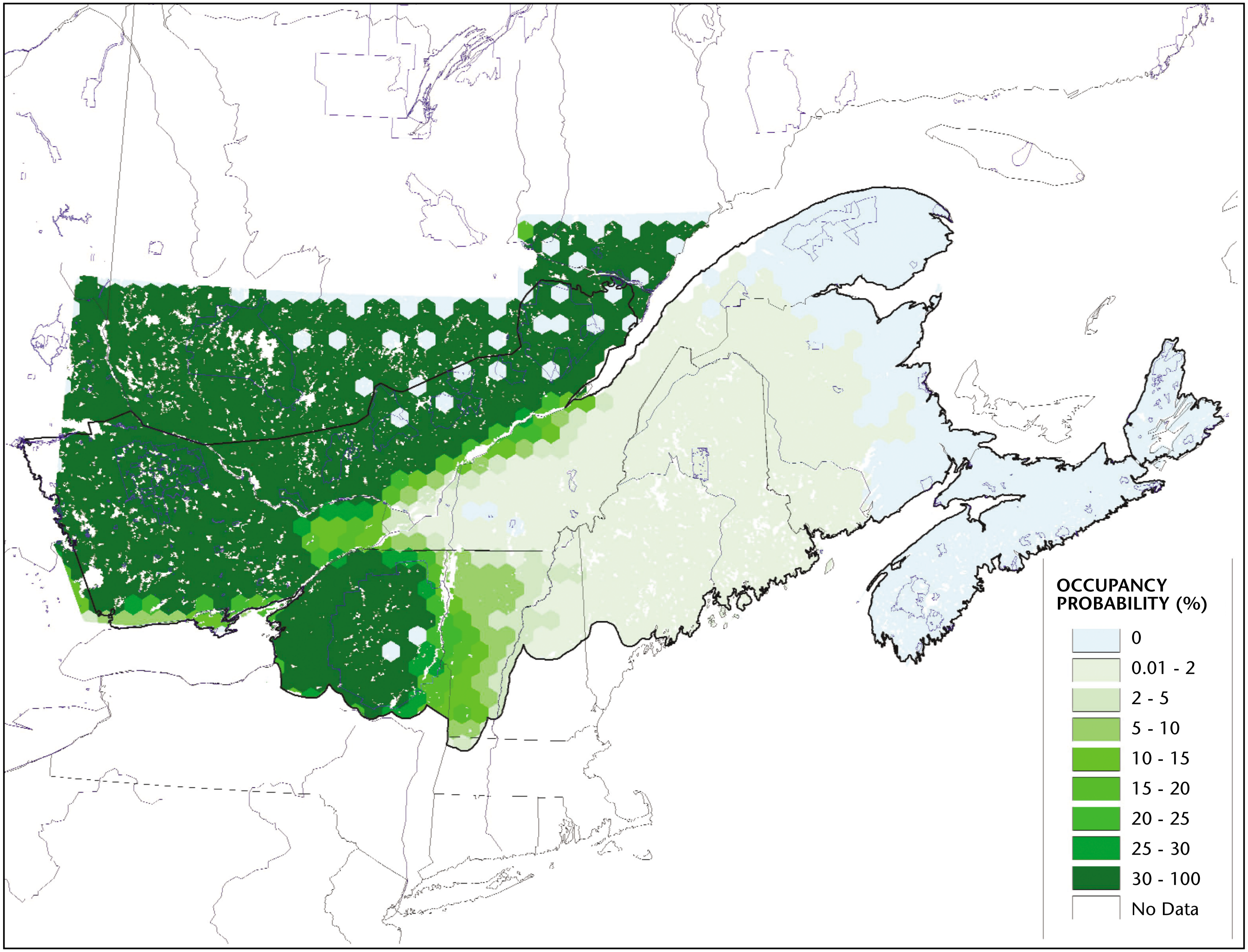
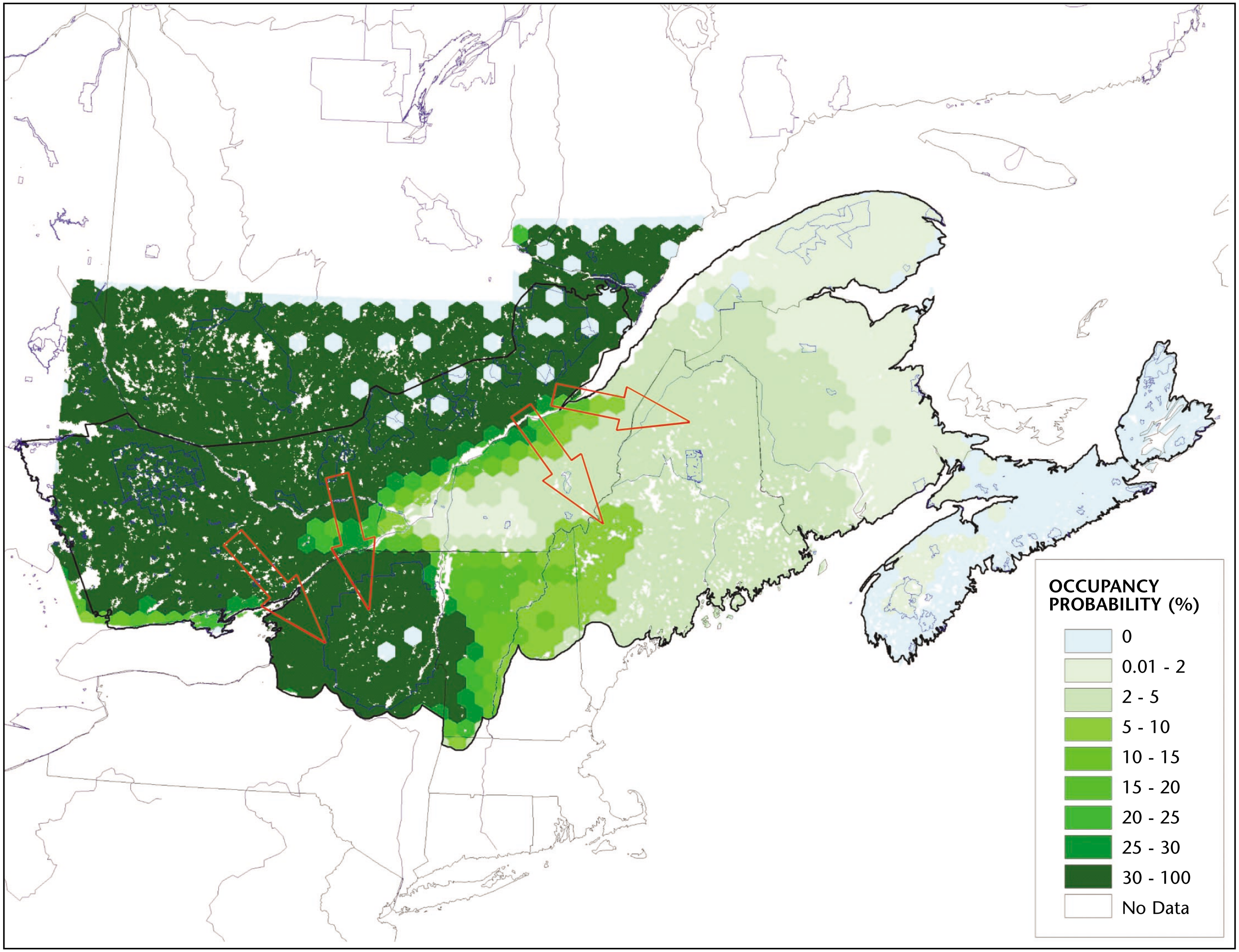


Figure 10 Predicted potential for recolonization by wolves of the northeastern U. S. and maritime Canada under current landscape conditions and the moderate Canadian mortality risk scenario, assuming a 750 km per year maximum dispersal distance (see text).

Figure 11 Predicted potential for recolonization by wolves of the northeastern U. S. and maritime Canada under current landscape conditions and the moderate Canadian mortality risk scenario, assuming a 1500 km per year maximum dispersal distance (see text). Highest probability linkages are shown in red.



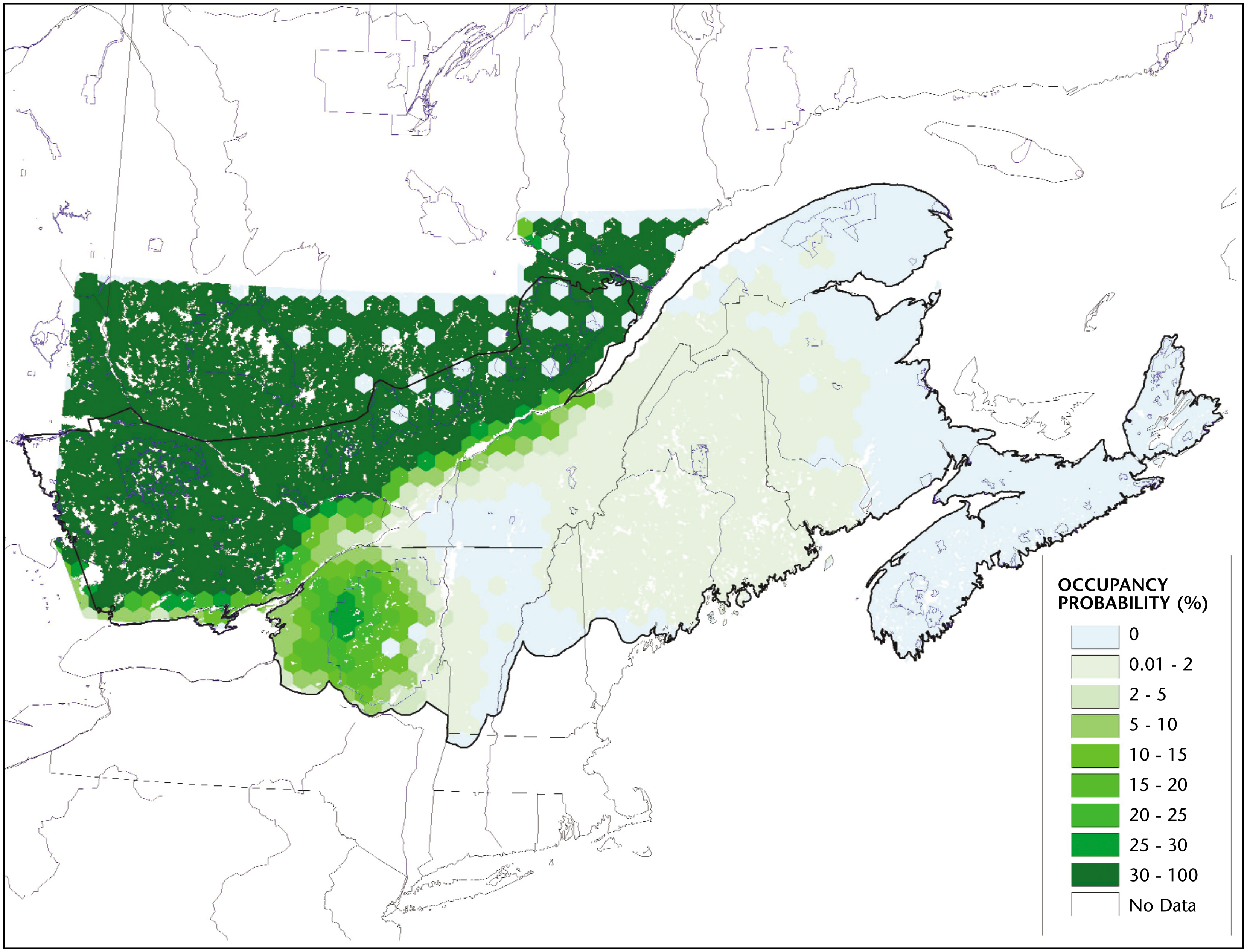
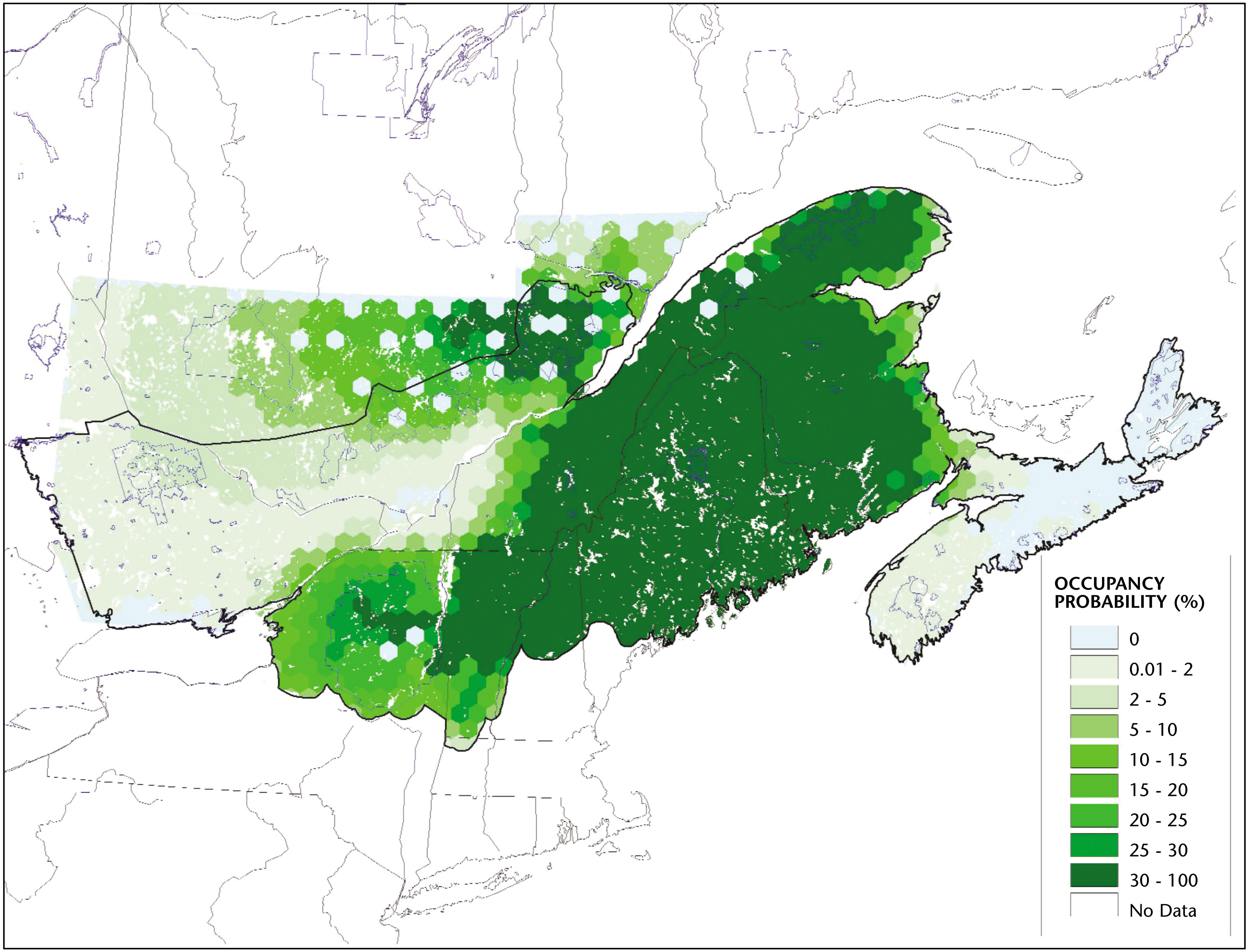


Figure 12 Predicted potential for recolonization by wolves of the northeastern U. S. and maritime Canada under future landscape conditions and the low Canadian mortality risk scenario, assuming a 750 km per year maximum dispersal distance. All other mortality parameter sets tested showed near zero recolonization probability under future landscape conditions.

Figure 13 Predicted potential for wolf dispersal from an initial reintroduction site in northern Maine to other areas of the northeastern U. S. and southeastern Canada under current landscape conditions and the baseline parameters (moderate Canadian and U. S. mortality risk scenario, 750 km per year maximum dispersal distance).



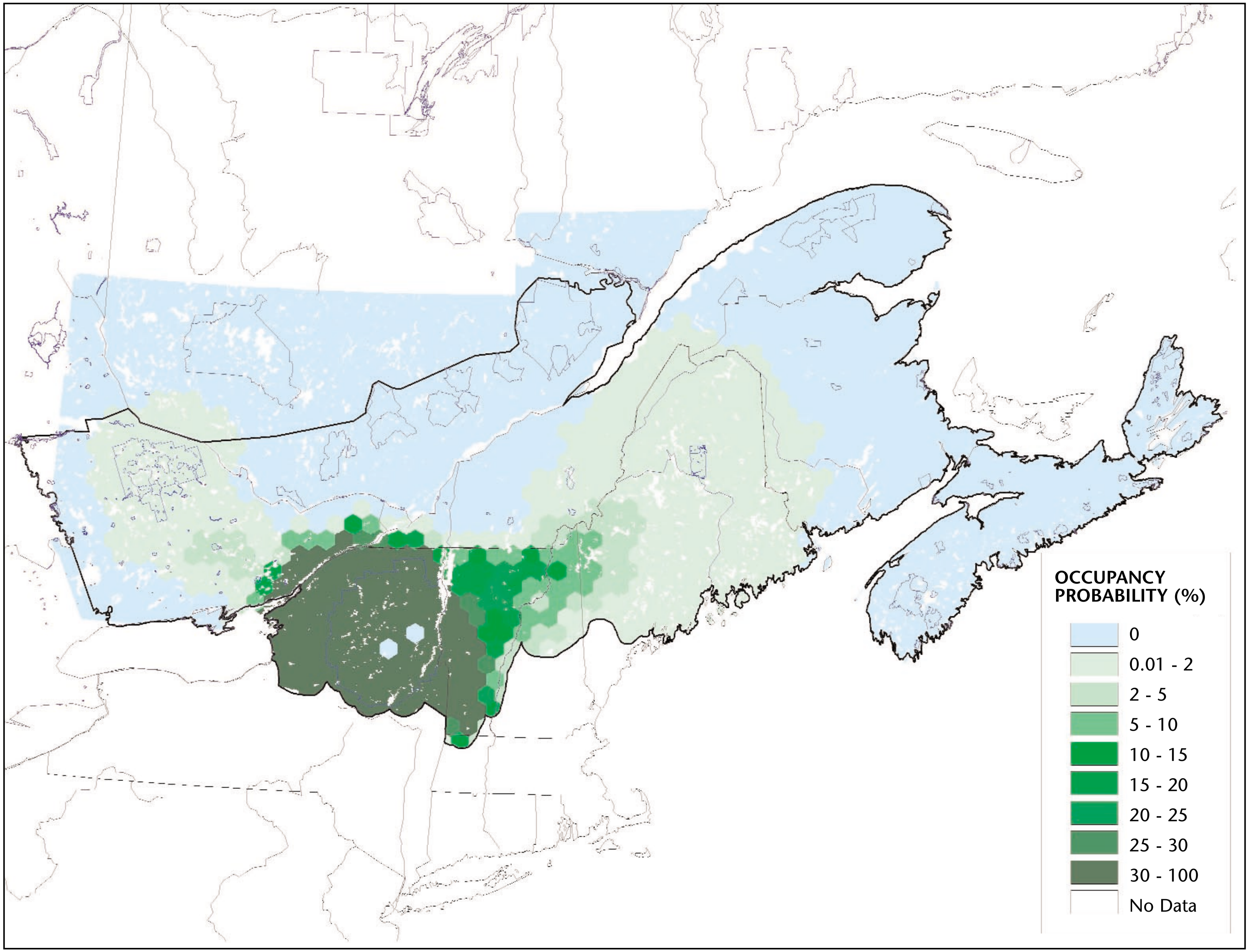


Figure 14 Predicted potential for wolf dispersal from an initial reintroduction site in the Adirondacks to other areas of the northeastern U. S. and southeastern Canada under current landscape conditions and the baseline parameters (moderate Canadian and U. S. mortality risk scenario, 750 km per year maximum dispersal distance).

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