HISTORICAL OCCURRENCE AND HABITAT ECOLOGY OF CANADA LYNX (*LYNX CANADENSIS*) IN EASTERN NORTH AMERICA

By

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(*LYNX CANADENSIS*) IN EASTERN NORTH AMERICA

By Christopher L. Hoving

Thesis Co-Advisors: Dr. Daniel J. Harrison and Dr. William B. Krohn

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
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The contiguous USA population of Canada lynx (*Lynx canadensis*) has been listed as threatened under the federal Endangered Species Act. Past literature and policy decisions have frequently inferred that forest management degrades habitat for lynx in the southern part of their range, but the specific affects of different forms of forest management, as well as potential impacts of climate change on lynx in the eastern USA and Canada have not been investigated. Further, the historic distribution and current status of lynx in Maine has been unclear, and was challenged during the listing process in 1998 by the state agency responsible for lynx management in Maine.

The past and present occurrence and distribution of lynx in Maine was documented by searching museum records, periodicals, books, and newspapers for evidence that lynx occurred historically in Maine. Recent records were available from track surveys by the Maine Department of Inland Fisheries and Wildlife (MDIFW) and interviews conducted by the US Fish and Wildlife Service. Based on 118 records of 509 lynx, this species has been distributed throughout much of Maine, 1833-1999. Records of 39 kittens representing a minimum of 21 litters suggest that a breeding population has existed in Maine. The spatial distribution of Canada lynx observations

contracted in the late-1800s through early-1900s, and many biologists and respected naturalists noted a decline in lynx abundance that coincided with a range expansion by bobcats (*L. rufus*) circa 1900.

Studies of lynx have concentrated on stand-scale habitat associations, however, broad-scale associations are also important. Biologists from the northeastern USA and Canada provided spatially-explicit data on 1,150 lynx, 1985-1999. Snowfall, road density, bobcat harvest, deciduous forest, and coniferous forest at random locations were compared to lynx observations using logistic regression. Models were compared using Akaike's Information Criterion (AIC). A model incorporating snowfall and deciduous forest had a low (good) AIC and best predicted a reserved dataset of 278 points (CCR = 0.94). Lynx were predicted to occur on the Gaspé, northern Maine, northern New Brunswick, and Cape Breton Island. Climate warming could potentially constrict future lynx distributions in northeastern North America.

Winter track surveys were conducted by the MDIFW, 1994-1999. One kilometer transect segments where snowshoe hares (*Lepus americanus*) were abundant were compared to segments where hares were absent using logistic regression. Models changed through time as hare densities changed. Hares were positively associated with late regeneration and forested wetlands, and negatively associated with recent clearcuts and partial harvests.

Lynx presence or absence on track surveys from northwestern Maine were compared using logistic regression. Within northwestern Maine, lynx were positively associated with late regeneration, and negatively associated with forested wetlands, recent clearcuts and partial harvests within an area of 100 km^2. Lynx in Maine were more closely associated with young forest than mature forest; over-mature forest was functionally absent from the landscape. In conclusion, in eastern North America lynx habitat consists of areas of deep snow (> 268 cm) with relatively little

deciduous forest; within deep snow areas in northwestern Maine, lynx are most likely to occur in complexes of regenerating forest, where snowshoe hare are likely to be abundant.

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Craig McLaughlon and Walter Jakubas made available the original datasheets from the MDIFW track surveys, 1994-1999, and Matthew Hoyt, Amanda Paradis, and Sean Chisholm

helped digitize the transect routes. Jennifer and Adam Vashon contributed capture points of lynx collected during a radio-telemetry study in northern Maine.

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FOREWORD

The US Fish and Wildlife Service (USFWS), after years of litigation, listed the Canada lynx (*Lynx canadensis*) as threatened under the federal Endangered Species Act in March 2000 (USFWS 2000). In 1994, a group of environmental organizations petitioned the USFWS to list the Canada lynx as endangered in the contiguous United States. Later that year, the USFWS decided that human activity did not endanger the lynx. Several environmental organizations responded in 1996 by suing the USFWS. US District Judge Gladys Kessler, the federal judge hearing the case stated that:

> "… the agency ignores the findings of its own biologists that forest clearing and current timber management represents ongoing threats to the already greatly diminished lynx populations and that such threats will only continue absent imposition of legal protections under the Endangered Species Act."

Later that same year the USFWS stated that listing of the lynx was "…warranted, but precluded by work on other higher priority species…" (US Dept. of the Interior 1997). That decision was also legally challenged by environmental groups, and the USFWS responded by proposing to list the Canada lynx as threatened in the contiguous USA. On March 24, 2000 the contiguous USA population of Canada lynx was listed as threatened under the federal Endangered Species Act (USFWS 2000).

Ruggiero et al. (2000) compiled a review of scientific knowledge about Canada lynx ecology and conservation in the United States, but conclusions were based primarily on studies from the western USA (Brittell et al. 1989, Koehler 1990, Apps 2000, McKelvey et al. 2000, Squires and Laurion 2000). What little is known of lynx in the eastern United States has come from a study on Cape Breton Island in Nova Scotia (Parker et al. 1983) and the reintroduction attempt in New York in the 1990s (Brocke et al. 1991). However, the lynx introduced to New York did not establish

a breeding population, and the highlands of Cape Breton Island, in terms of climate and geology, are unlike any other region of the eastern USA. Aubry et al. (2000a) stated that both broad-scale and intensive studies in the northeastern USA were necessary to address critical knowledge gaps.

McKelvey et al. (2000) addressed association of lynx with general vegetation zones in the eastern United States as part of a geographic scale analysis. When the contiguous United States were considered as a single entity, lynx were associated with northern forests with a conifer component (McKelvey et al. 2000). This particular broad-scale study was an important step towards understanding distributional ecology of Canada lynx; however, a thorough understanding of factors influencing patterns of occurrence of lynx will require studies that encompass multiple spatial and temporal scales.

Ecological processes occur at a variety of scales, and lynx likely respond to habitat conditions at multiple scales. Many organisms appear to perceive habitat in a hierarchical manner (Kotliar and Wiens 1990). At a regional spatial scale, a dispersing organism must choose where to cease dispersal. At finer scales, an organism must choose where in a region to establish a home range, and where in the home range to concentrate activities, such as foraging, reproduction, and resting (Johnson 1980). Ecological processes also operate across temporal scales. McKelvey et al. (2000) evaluated historical harvests of lynx in the United States to determine whether population cycles lagged or were synchronous with cycles in Canada. Those authors did not directly address changes longer than the 10-year cycle of lynx. A comprehensive understanding of habitat must account for several spatial and temporal scales.

The chosen scale of an ecological study should have meaningful biological significance (Goodwin and Fahrig 1998). Two important ecological units at which lynx perceive their environment are the dispersal distance and home range. Because lynx disperse unusually far for an animal of their size, one important scale to consider is a multi-state or international spatial

extent. The mean dispersal distance of 91 tagged or radio-collared lynx in the Northwest Territories of Canada was 163 km +/- 209 km (range: 17 km – 930 km) (Poole 1997). Two lynx dispersed over 900 km. At a regional scale the state of Maine is within 930 km of extant populations of lynx occurring along the Ontario/Quebec border to James Bay, the Gaspé Peninsula, and Cape Breton Island. The St. Lawrence Seaway and the Bay of Fundy probably act as barriers to lynx dispersal, similar to their effect on wolves (*Canis lupus*) (Wydeven et al. 1998).

Lynx home range sizes vary from 9.9 km^2 (Slough and Mowat 1996) to 783 km^2 (Bailey et al. 1986), and are larger in landscapes where snowshoe hare (*Lepus americanus*) are scarce (Kesterton 1988). Average home ranges of males are larger than for females (Koehler 1990, Slough and Mowat 1996). Home ranges of individual lynx appear to be relatively static through time unless the density of hares drops below one hare per km^2, below which home range area increases or lynx become nomadic (Ward and Krebs 1985, Poole 1994, Brand et al. 1976, Slough and Mowat 1996). The average reported home range area for studies conducted at the southern edge of the Canada lynx's geographic range was 151 km^2 for males and 103 km^2 for females (Aubry et al. 2000b).

Several factors might influence lynx habitat in eastern North America. McKelvey et al. (2000) illustrated an association with major vegetation types, and suggested that lynx are associated with forests that have a conifer component. Lynx are morphologically adapted to deep snow, and specialize their diet on snowshoe hare, another animal adapted to snow and often associated with conifer forests (Hodges 2000). However, vegetation types may not completely describe lynx distribution in eastern North America. Lynx may also be associated with high snowfall or low bobcat densities (Parker et al. 1983). Lynx that were introduced into the Adirondacks in New York experienced high vehicle collision mortality (Brocke et al. 1991): road mortality might have a

more significant affect in eastern North America, where road densities and traffic volumes are higher than the western United States and boreal Canada.

Lynx are associated with habitats where prey are abundant (Parker et al. 1983, Koehler 1990). Thus, knowledge of snowshoe hare habitat is critical to an understanding of lynx habitat ecology. Snowshoe hare habitat has been well documented in Maine at the stand scale; hares select for dense understories (Litvaitis et al. 1985, Long 1995) that often result from dense regeneration following clearcutting (Monthey 1986, Fuller 1999). Dense hare populations are not restricted to regenerating forest (Pietz and Tester 1983); however, in northern Maine, dense regeneration following human and natural disturbances provides the complex understory characteristics selected by hares (Litvaitis et al. 1985, Long 1995, Lachowski 1997, Fuller 1999).

Some biologists question the ability of immature forest to support populations of Canada lynx at the southern extent of their range (Buskirk et al. 2000). Immature forest might not provide adequete structure for hares in more xeric forests in some parts of the western USA. However, in the eastern part of the lynx's southern range, immature forest may support viable populations of lynx if other habitat requisites such as denning and resting habitat are available. Silvicultural practices likely affect forest structure in different ways throughout the historic range of the Canada lynx.

Lynx habitat associations in the western USA at limited scales should not form the basis of management in the eastern USA. Given that forestry and forest-based recreation are important aspects of Maine's economy, accurate knowledge of lynx habitat associations in this region are important. Geographic information systems (GIS) technology provides a relatively inexpensive and flexible tool for evaluating existing information on lynx occurrence and distribution relative to habitat characteristics across time and space. The purpose of this thesis was to couple existing information on lynx with GIS technology to evaluate changes in the historic distribution of lynx in

Maine, to determine snowshoe hare habitat associations in Maine at the sub-state scale, and to model and describe lynx habitat associations at both the international and sub-state scales.

CHAPTER 1

HISTORIC AND CURRENT DISTRIBUTIONS OF CANADA LYNX IN MAINE, 1833-1999

INTRODUCTION

On March 24, 2000, the US Fish and Wildlife Service (USFWS) published notice to list the contiguous USA population of Canada lynx (*Lynx canadensis*) as threatened under the federal Endangered Species Act (USFWS 2000). A recent synthesis of literature pertaining to Canada lynx in the contiguous USA noted that basic information on historic and current distribution of this species were needed before further study or conservation could proceed (Aubry et al. 2000).

Readily available data on Canada lynx distribution is scarce in the northeastern USA, especially Maine. Traditionally, lynx have been considered rare in northern Maine, and absent from the remainder of the state (Hunt 1964). However, the historic distributions of Canada lynx or bobcat (*L. rufus*) in Maine have not been rigorously studied, and some have questioned the evidence that lynx historically were resident in Maine. In 1998, the Maine Department of Inland Fisheries and Wildlife (MDIFW) stated that no direct evidence was available that lynx had ever been resident in Maine (MDIFW 1998). The agency's official position on the original proposal to list the lynx as a threatened species stated that historical occurrences in Maine could have been transients from Canada. Though the listing does not make the distinction between resident and transient animals (USFWS 2000), information on the historic and current breeding status of lynx in Maine is important for future management, research, and recovery efforts.

The objectives of this study were to determine if Canada lynx and bobcat were distinguished from each other historically in eastern North America; and if so, to document changes in occurrence, distribution, and relative abundance of Canada lynx in Maine over the past 200

years. Further I used historical records to assess evidence of reproduction by lynx in Maine during the period, 1833-1999.

METHODS

Historical records

Data on historical distribution of Canada lynx were compiled from museum collections, travel accounts, books, and journals. Additionally, biologists, game wardens, bobcat hunters, and trappers who could differentiate between Canada lynx and bobcats were interviewed by R. Joseph of the USFWS, Old Town, Maine, USA. Recent observations of lynx (1994–1999) were also provided by the MDIFW and USFWS.

I requested information regarding specimens of lynx from Maine in the collections of the Academy of Natural Sciences of Philadelphia; American Museum of Natural History; Bibliothèque Centrale du Muséum National d'Histoire Naturelle, Paris; Cornell University Museum of Vertebrates; Harvard Museum of Comparative Zoology; Museum of Zoology at the University of Michigan; National Museum of Natural History; Natural History Museum, London.

Data in publications, especially older periodicals, were difficult to locate. Even when located, many old publications were not indexed. I systematically searched the contents of *The American Naturalist,* 1867–1900, and the annual indexes to *Forest and Stream,* 1873-1911, a periodical used extensively by naturalists of the late 1800s (e.g., Seton 1929). The first two volumes (of five) of *Carleton's State of Maine Sportsman's Journal,* 1906-1907, were searched page by page. Only a few copies of *Hunting and Shooting* and the *Maine Sportsman* were available, and were searched. The Annual Reports of the Commissioners of Fisheries and Game, 1880-1931, were searched thoroughly. Weekly newspapers, such as *The Maine Farmer* and *The Maine Woods*, were only searched when citations were available from other sources.

Criteria to assess reliability

Written records of encounters with lynx, lynx tracks, and trapped lynx were evaluated for reliability with the following criteria: records had to be non-fictional; observations had to appear truthful and be consistent with what is now known of lynx behavior and ecology; and records had to correctly distinguish Canada lynx from bobcats. Each record was considered critically to determine if it met these criteria.

Fiction was usually easy to distinguish from non-fictional accounts. Stories of men surviving harrowing lynx attacks or sympathetic stories from the lynx's point of view were, in most cases, clearly fiction. However, some accounts were not as easy to distinguish from fiction. A heated controversy regarding the reliability of certain nature writers was fought in newspapers, magazines, and scientific journals (e.g. *Science*) from 1903 through 1907 by John Burroughs and then-President Theodore Roosevelt against the "Nature fakers" (Lutts 1990). Nature fakers tended to anthropomorphize their observations to appeal to the general public. The works of the Nature fakers were not relied upon for this study, with one exception. Ernest Thompson Seton published a four volume set on the Game Animals of North America (Seton 1929) decades after the controversy, in part to regain his scientific reputation. This later work received praise from Roosevelt (Seton 1928), and Seton's observations from this work are included in this analysis.

Several criteria were used to evaluate the truthfulness of observations. Authors who described lynx that were donated to museums were considered reliable because the museum specimen was tangible evidence. The details of published descriptions had to be consistent with lynx ecology. For example, lynx rarely prey upon deer, caribou, and moose (Parker et al. 1983, O'Donoghue et al. 1998), and a solitary lynx is unlikely to prevail in a fight with wolves. The reputation of the author was also an important criterion for evaluating reliability of observations. For example, the observations of J.J. Audubon were considered more reliable than observations by

anonymous writers. G.A. Boardman and A.E. Verrill also had national reputations as a reliable naturalist and biologist, respectively. Second hand observations were used only when the original observer was cited and the person reporting the information was known to be reliable (e.g. M. Hardy, J.G. Rich, C.H. Ames, or A.H. Norton). Finally, national publications with good reputations were considered to be more reliable than local newspapers. The sporting journal *Forest and Stream* was edited by G.B. Grinnell, the founder of the National Audubon Society and a well-known and respected author and naturalist of his day (Reiger 2001, Mitchell 1987).

Two observers, Manly Hardy and Joshua Rich, were responsible for nearly one-fifth of all observations, and both wrote articles that clearly distinguished Canada lynx and bobcat (Hardy 1907a, Rich 1862). Manly Hardy was the principal fur buyer for Maine east of the Penobscot River during the mid to late 1800s, and took part in the Maine State Scientific Survey in 1861 (Manly Hardy Collection, Fogler Library, University of Maine). Joshua Rich was a trapper and naturalist from western Maine. He corresponded with Louis Aggasiz, at Harvard, who once asked for live lynx to trade with a museum in Paris, France. Rich noted that one live lynx that he caught "…would stick her claws and teeth through the bag and my coat and into my back." (Rich 1892). An archivist at the Bibliothèque Centrale du Muséum National d'Histoire Naturelle in Paris, France confirmed that at least one live lynx was received from Louis Aggasiz in 1865 for their zoological gardens (M. Loiselet, National Museum of Natural History, Paris, France, personal communication).

Observations of individual lynx in the book *Lynx Hunting in Maine* by C.A. Stephens (1873) were not included in this analysis. Although Stephens' descriptions were consistent with lynx ecology, geographically detailed, and by a well-known and respected author, this author is considered a fiction writer (Whitney 1976). However, the appendix of *Lynx Hunting in Maine,* entitled "Field Notes," was assumed factual and was included in statewide harvest assessments.

Observations also were evaluated for their reliability in distinguishing Canada lynx from bobcats. Canada lynx and bobcat are morphologically similar, and some common names were sometimes used interchangeably (Table 1.1). By the late 1700s many biologists classified lynx and bobcat as separate species. Nine common names (Canada lynx, lynx, loup cervier, lucivee, Indian devil, wildcat, bob cat, catamount, and "wolverene"), and at least six different scientific names (*L. canadensis, L. lynx, Felis lynx, F. canadensis, L. borealis and F. borealis*), have been used to describe Canada lynx in Maine (Table 1.1). The scientific name *Lynx canadensis* was used for this publication in accordance with Wilson and Reeder (1993). Many observers provided illustrations (Seton 1929), photographs (Anonymous 1998), or detailed descriptions (Rich 1862, Anonymous 1892, Hardy 1907a) with commentary regarding the use and misuse of common (and scientific) names with regards to lynx and bobcats. The context of usage often provided clues regarding its meaning. For example, Williamson (1832) gave a reasonable description of a Canada lynx or bobcat (three times the size of a house cat, gray, short tail), but refers to the animal as a catamount or "evil devil," terms more commonly ascribed to mountain lions (*Puma concolor*). Similarly the caption to a photograph from the early 1900s of a man holding what is clearly a lynx (Anonymous 1998), referred to the animal as a bobcat. Alternatively, many authors went into precise detail distinguishing the lynx from the bobcat (Hardy 1907a, Anonymous 1892). The terms "loup cervier," "lucivee," and "*Lynx canadensis"* appeared to be used most accurately in the literature, and the term "Canada lynx" was used incorrectly in only a few newspaper accounts from the mid-1900s. Because the terms "*Lynx canadensis*," "Canada lynx," "lucivee" or "loup cervier" were used consistently, references that used these terms were considered reliable and included in the analysis. Records that used other common names were omitted, unless authors provided detailed descriptions that explicitly differentiated Canada lynx from other species.

Table 1.1 Common names used correctly or incorrectly to describe the Felidae in Maine from 1672 to present.

Common Name	Scientific name	Time period[1]	References
Canada lynx	usually *Lynx canadensis* [2]	1700s - recent	Emmons (1840)
	rarely *Lynx rufus*	1700's - recent	Penobscot (1879)
Loup cervier	*L. canadensis*	? - early 1900's	Richardson (1829)
Lucivee	*L. canadensis*	? - early 1900's	Hardy (1870, 1907a)
Lynx	usually *L. canadensis*	1700's - recent	Stephens (1873)
	sometimes *L. rufus*	unknown	Stephens (1873)
Wildcat or Wild Cat	usually *L. rufus*	1672 - recent	Hardy (1870, 1907a)
	often *L. canadensis*	1672 - recent	Boardman (1892)
Bay lynx	*L. rufus*	? - recent	Emmons (1840)
Bobcat or Bob cat	usually *L. rufus*	1879 - recent	Hardy (1870, 1907a)
	occasionally *L. canadensis*	early to mid 1900s	Hardy (1870, 1907a)
Catamount	usually *Puma concolor*	? - recent	Williamson (1832)
	rarely *L. canadensis*	? - 1832	Williamson (1832)

Table 1.1 continued

Indian devil	*P. concolor*	not recent	Warner (1981)
	occassionally *L. canadensis*	not recent	Warner (1981)
Lunxus or Lunkson	*P. concolor*	not recent	Ames (1893)
	G. gulo	not recent	Thoreau (1893)
	rarely *L. canadensis*	not recent	Williamson (1832)
"Wolverene" (sic)	usually *G. gulo*	1816 - recent	Penobscot (1879)
	rarely *L. canadensis*	? - 1879	Penobscot (1879)
Black cat[3]	*Martes pennanti*	unknown	Williamson (1832)

[1] Period of use is approximate.

[2] To add to the confusion regarding historic use of common names, the Canada lynx has at least four scientific names commonly in use. Canada lynx are either included as a subspecies of the Eurasian lynx, *Felis lynx* or *Lynx lynx* , or as a separate species, *Felis canadensis* or *Lynx canadensis.*

[3] *M. pennanti* or the fisher is not a member of the Felidae. However at least one historical reference (Williamson 1832) seemed to classify it as such.

Many of the recent records used in this study were from large carnivore track surveys (1995-1999) conducted by the MDIFW and records of lynx observed (1939-1999) during interviews conducted by R. Joseph, USFWS biologist. Joseph interviewed 63 biologists, game wardens, trappers, and bobcat hunters during 1998. Only observers who could discern Canada lynx from bobcat, as judged by Joseph during his interviews, were used in this analysis.

Spatial and temporal distribution

Based upon spatial resolution of the reported information, records were classified as statewide, multi-township, or township specific. Records that referred to presence or general distribution in the state were classified as statewide. Records that referred to an area encompassing more than one township were mapped as multi-township records. Records that were precise to at least the nearest township were mapped as township records. Township resolution records were mapped as accurately as possible. Some records merely mentioned the township, and the record was mapped in the middle of the township. Records that were specific to a certain bog, lake, dam, etc. were mapped as specifically as possible relative to hydrographic features of the 1:24,000 US Geological Survey (USGS) Digital Line Graphs.

The multi-township and township records were compared across three time periods (1833–1912, 1913-1972, and 1972-1999). These time periods correspond to groupings according to Jenk's optimization, the "Natural breaks" option in ArcView 3.1 (ESRI, Redlands, California, USA; use of trade names does not imply endorsement).

Evidence of reproduction

Lynx are usually solitary animals. Lynx that may travel together include a female and her offspring, males and females during the breeding season, and related adult females (Parker et al. 1983, Poole 1995, Mowat and Slough 1998). Records of multiple lynx tracks were not mapped as evidence of reproduction unless the observer noted a marked difference in track size.

RESULTS

John Josselyn (1672) was probably the first European to leave a written account of a Canada lynx. However, Josselyn did not give a detailed enough description to distinguish a lynx from bobcat. Indeed, lynx were not distinguished in the Maine literature from bobcat until the 1800s. Thus, the relative distributions of lynx and bobcat cannot be determined with certainty prior to 1800. Prior to 1800, lynx likely were distributed throughout Maine, and bobcat were likely absent from the state entirely or confined to coastal areas.

Searches resulted in 118 records of 509 lynx in Maine, 1833-1999. Because I sought to gather any information on the presence of lynx in Maine, observations were of many different types (Table 1.2). Three museums had specimens of Canada lynx from Maine in their collections (Appendix A). A total of 104 records of 181 individual lynx were specific at a resolution of a township or finer (Figure 1.1, Appendix A); 15 records of 187 individual lynx were resolved at a multi-township resolution (Figure 1.1, Appendix A); and 43 records referred to lynx at a statewide resolution (Appendix A). Prior to 1939, most sources were from published records. Records after 1938 were usually from interviews conducted by R. Joseph, USFWS, and from snow track surveys directed by MDIFW.

Spatial and temporal distribution

Canada lynx have been distributed throughout northern Maine from at least 1833 to 1999 (n = 368). Between 1833 and 1912, records of Canada lynx were distributed almost statewide (n = 217). The relative scarcity of observations in northern Maine during this period probably reflects few potential observers during a time when the region was sparsely settled and relatively inaccessible wilderness. During 1913-1972 records appeared across northwestern Maine (n = 62), with observations for 1973-1999, across central and eastern parts of the state (n = 89). Observations of lynx were absent from the southwestern part of Maine after 1912. Human

Table 1.2. The number of Canada lynx observed by different methods in each time period. Early records were from museum specimens and published harvest records. Most records from recent history were of tracks or from interviews.

Observation type	1833-1912	1912-1972	1972-1999	Total
Museum records	28	4	0	32
Snow tracks	5	17	59	81
Published harvest records and bounties	165	4	0	169
Published observations	12	0	0	12
Harvest records from interviews	0	33	6	39
Visual observations from interviews	0	4	13	17
Other	4	0	11	15
Total	214	62	89	365

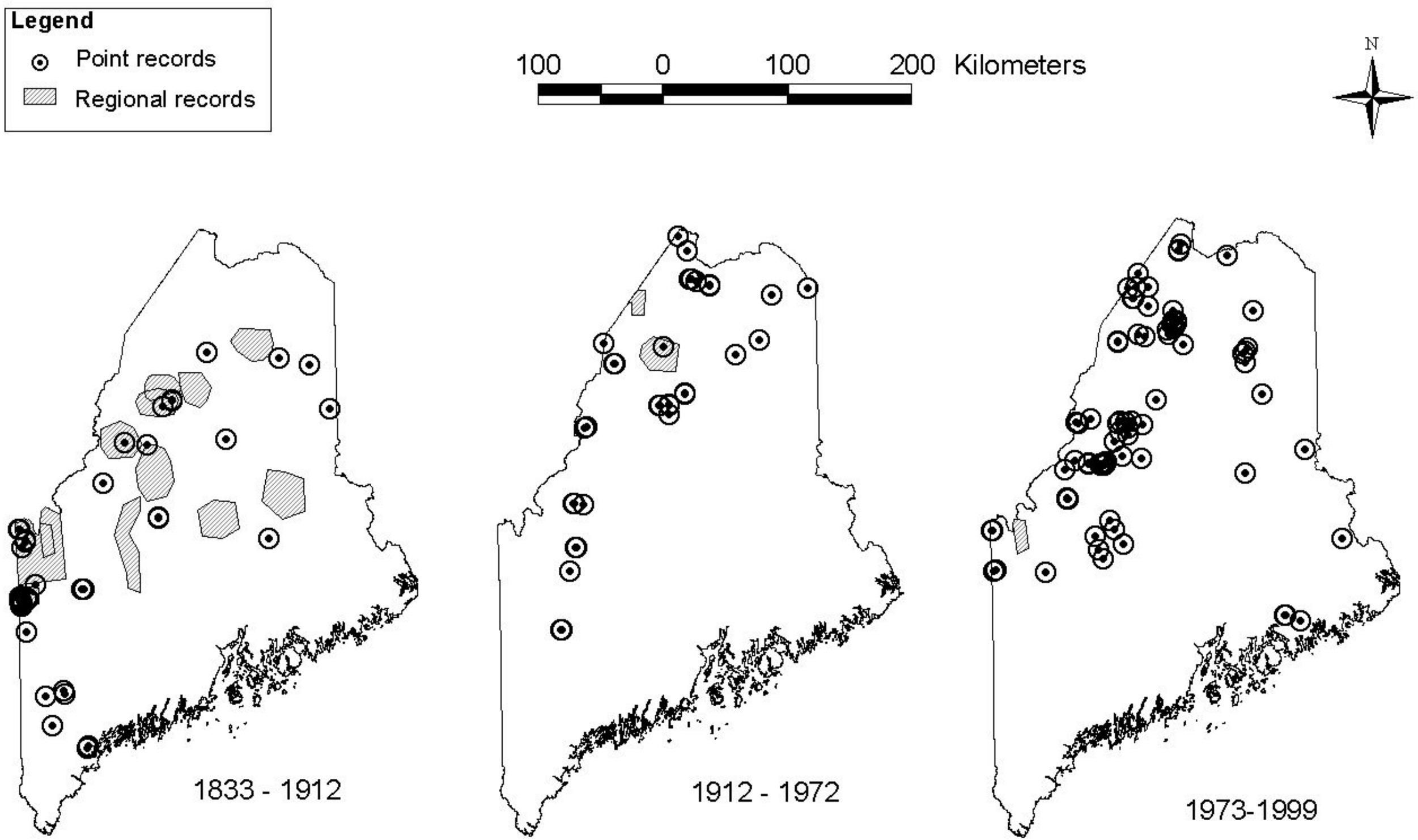

Figure 1.1. Township and multi-township observations of Canada lynx in Maine, 1833-1999. Data sources include trapping records, museum records, published accounts, interviews, and unpublished data from track survey and radio telemetry studies. See Appendices A and B for references to each observation.

population densities were higher in southern Maine than northern Maine; therefore the absence of lynx observations in southern Maine since 1912 likely indicates an absence of lynx, rather than a lack of potential observers.

The official bounty records for Canada lynx and bobcat could not be located at the Maine State Library or Archives. However, interviews and other historical records indicate that at least 30 lynx were bountied between 1833 and 1967, when the bounty on lynx ended. Furthermore, in the *Reports of the Commissioners of Inland Fisheries and Wildlife*, 141 lynx were reported as killed by licensed hunters and trappers (Appendix A). Between January 1, 1921 and June 30, 1922 (18 months), $12,340 was paid for the lynx and bobcat bounty. The bounty was $10 per lynx; therefore, approximately 1,234 lynx and bobcat were bountied. However, licensed hunters and trappers reported only 6 lynx and 155 bobcats during 1921-22. Many more lynx and bobcats were bountied than were reported by licensed hunters and trappers. As late as 1966, Schemnitz (1966) noted that "a few lynx" were bountied each year.

From 1833 to 1912 the annual number of observations of Canada lynx dropped steadily (Figure 1.2). Township and multi-township records were absent, 1913-1938. Observations of lynx were relatively steady, 1939-1972, and the number of observations of Canada lynx increased after 1973.

Evidence of reproduction

Records of 39 kittens, representing a minimum of 21 litters spanning 135 years, were discovered. Observations of kittens were distributed consistently in both time and space (Figure 1.3), suggesting that reproduction of lynx has occurred and continued to occur in Maine from 1864-1999.

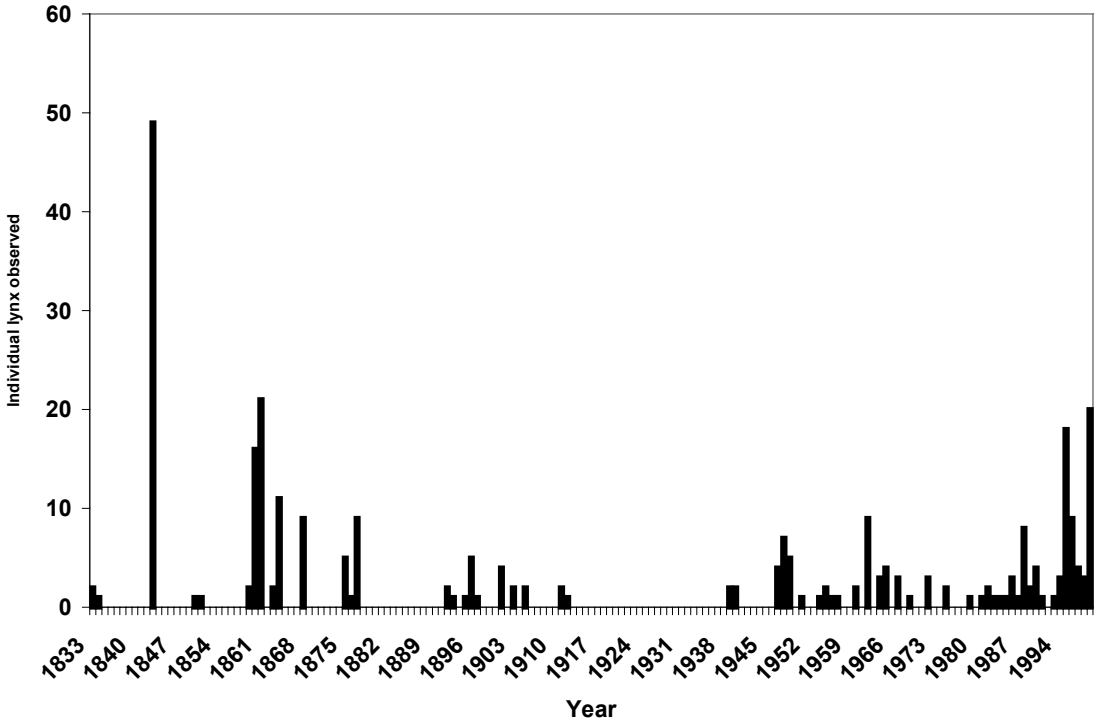

Figure 1.2. Canada lynx observed per year, 1933-1999. Records that were specific to township or region were used if they were specific to year.

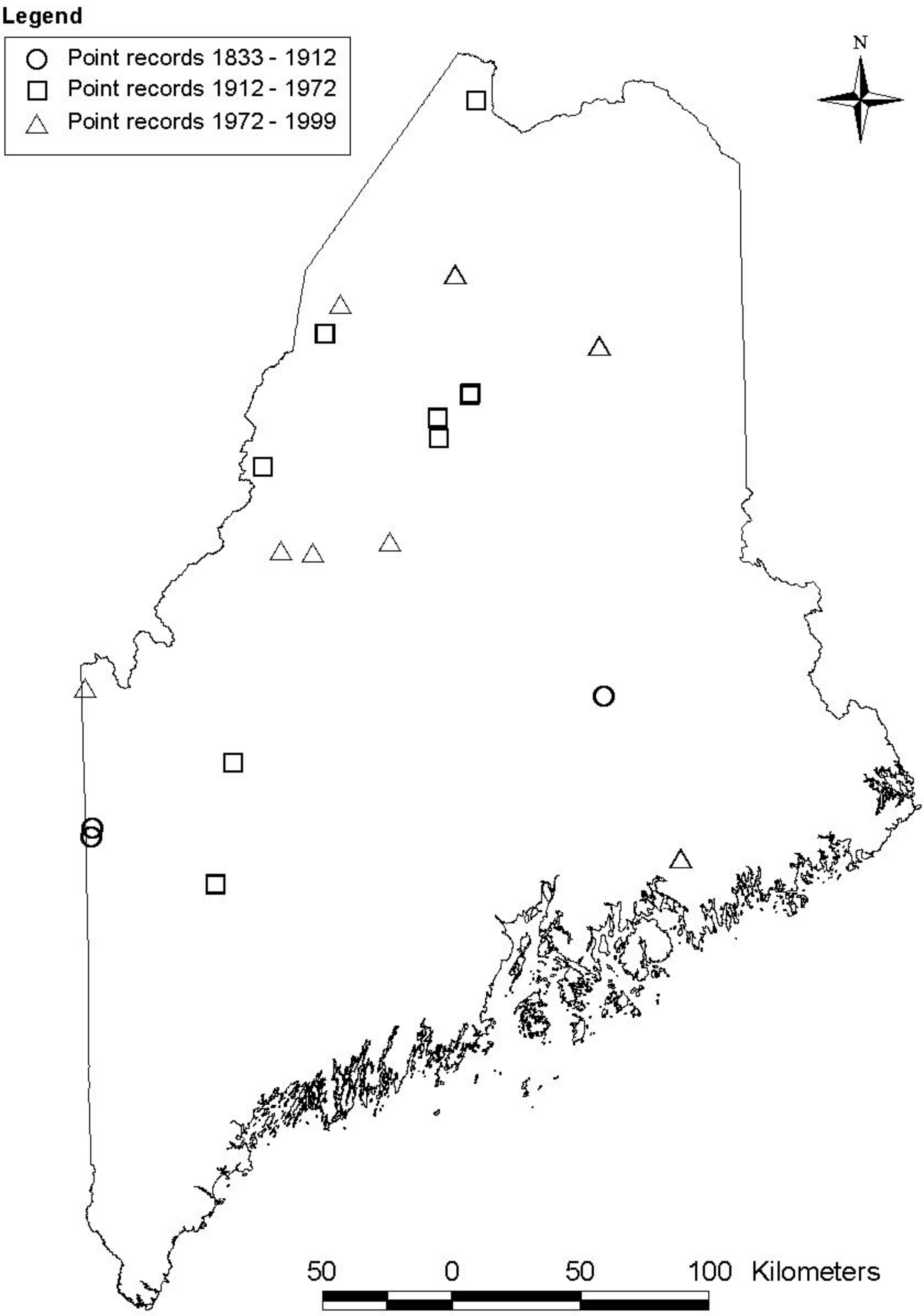

Figure 1.3. Locations of Canada lynx kittens observed in Maine during the period, 1840-1999.

Historical records beyond Maine

In the process of searching for lynx records within Maine, I came across many records of lynx occurrence outside of Maine (Table 1.3). These records suggest that further historic analysis on the distribution of Canada lynx may be fruitful as far south as Connecticut (Anonymous 1892) and Pennsylvania (Audubon and Bachman 1852, Rhodes 1903) in the eastern USA, and as far south as New Mexico (Hersey 1893) in the west. To the east of Maine, there are many references to lynx in the Canadian provinces of New Brunswick (Adams 1873, Jack 1905, Squires 1946, Palmer 1949, Cumberland et al. 1998) and Nova Scotia (Audubon and Bachman 1852).

The sample of citations in Table 1.3, while far from complete, suggests a contraction in the geographic range of lynx around 1900. In the 16 citations available, the last lynx observed in Pennsylvania was in 1899 (Rhodes 1903), in Connecticut in 1892 (Anonymous 1892), in Massachusetts in 1904 (Allen 1904), and New York in 1908 (Whipple 1908).

DISCUSSION

The criteria used to determine the reliability of the records were probably overly conservative. For example, some records of Canada lynx, which authors referred to as “wildcats” or “bobcats,” were probably left out of this analysis. Some published records were also missed given the difficulty in locating old books, journals, and newspapers. Older publications seldom were available as complete sets. Thus, the records presented herein should be considered a sample of Canada lynx observations, and not an inventory of every published record of Canada lynx in Maine.

Although the number of observations in 1999 was equal to the number of observations in 1861, this does not necessarily mean that the populations of Canada lynx were similar during these two years. The effort that went into observations is unknown and sources for the observations differed (Table 1.2). Historic records were derived from trapping, and recent records were derived

Table 1.3. A list of historical references (alphabetical by state or province) that refer to Canada lynx in states and provinces other than Maine. The following are citations discovered while searching for citations pertaining to Maine, and are not a comprehensive listing of all historical references of lynx at the southern edge of their geographic range.

Reference	State/province	Comments
Anonymous (1892)	Connecticut	occasionally killed
Moody (1912)	Idaho	carefully describes lynx dens in Idaho
Emmons (1840)	Massachusetts	once common, now rare
Allen (1904)	Massachusetts	"practically extirpated"
Audubon and Bachman (1852)	New Brunswick	common in regenerating "burnt districts"
Adams (1873)	New Brunswick	plentiful
Jack (1905)	New Brunswick	51 trapped in 2 years on Southwest Miramichi River
Chamberlain (1884)	New Brunswick	present
Palmer (1949)[1]	New Brunswick	several trapped in the Tobique region ~1860
Allen (1904)	New Hampshire	"rare"
Allen (1923)	New Hampshire	probably common formerly, now rare
Silver (1957)	New Hampshire	present in northern New Hampshire
Hersey (1893)	New Mexico	"quite numerous," distinct from bobcat
Audubon and Bachman (1852)	New York	present east of Albany, occasionally in north
Spears (1907)	New York	one caught south of Ithaca, NY
Whipple (1908)	New York	one caught in Ulster County
Audubon and Bachman (1852)	Nova Scotia	specimen from Halifax
Audubon and Bachman (1852)	Pennsylvania	one trapped ~ 1837
Rhodes (1903)	Pennsylvania	specific records for about 20 lynx

Table 1.3. Continued.

Reference	State/province	Comments
Fairchild (1874)	Quebec	lynx "swarmed through the settlements"
Allen (1876b)	Vermont	in Green Mountains, White Mountains, and Maine
Allen (1904)	Vermont	"rare"
Allen (1923)	Vermont	probably common formerly, now rare
Osgood (1938)	Vermont	lynx killed in 1928 in Windam

[1] R. Palmer was not the actual observer in this case. He published 21 letters from 1859-87 written by Rufus Philbrook to Manly Hardy. The original letters, contrary to a statement toward the bottom of page 454 of Palmer (1949), were not destroyed and are on file in the Manly Hardy Collection, Special Collections, University of Maine, Orono.

mainly from interviews. The actual populations of lynx among the three time periods are not directly comparable because of the absence of standardized surveys prior to 1994. These limitations notwithstanding, these records clearly show a continuous presence of lynx in Maine from at least 1833, and probably much earlier.

Harvest fluctuations

Manly Hardy was probably the first naturalist in this region to note that harvests of lynx fluctuated widely, though he attributed the fluctuations to migration rather than to changes in the resident population. He wrote:

> Lynx were so abundant that several hundred skins were sold in this market every year till about the last of the [Civil] war [i.e. 1864-1865], when in a short time all had left, so that not a single skin was offered for several years. Then they returned in such numbers that within a few years after they first came, I was buying some 200 yearly. (Hardy 1897: 2)

Although some of these skins might have originated in eastern Canada, Hardy's fur came mostly from Maine, excluding western Maine (Hardy 1897). Hardy noted that lynx were very abundant, very scarce, and very abundant, all in the course of several years. He was consistent in these observations, and wrote elsewhere of fluctuations in the harvest and of buying 200 skins per year (Hardy 1907a). Although Hardy may have been describing a population cycle of Canada lynx, he did not provide enough information on the timing of these fluctuations to document amplitude nor periodicity, data necessary to define a cycle.

Canada lynx and bobcats

Several naturalists of the nineteenth century noted that the range of bobcats expanded as the range of Canada lynx contracted. Hardy (1907a) noted that "With us the lynx is rarely found near settlements, or near the seashore, while the wildcat [bobcat] is rarely found twenty miles from salt water and often comes in to large towns." Available information suggests that the distributions of Canada lynx and bobcat were quite different historically (Figure 1.1, Appendix A), but that lynx

were not rare in the interior portions of Maine during the nineteenth century. Joshua Rich (1862: 137) noted:

> I have been informed of another kind of Lynx in this State, but have never seen one of that kind. It is said they live in the open cultivated regions, and have no fur on the bottoms of their feet, and are not so thickly furred, neither so handsome; but I cannot describe them from personal knowledge, and therefore will let them pass.

That Rich, who collected extensively for Louis Agassiz of the Harvard Museum (Rich 1862), had never seen a bobcat in western Maine is noteworthy. The first record of a bobcat trapped in western Maine was in 1903 (Heywood 1903). G.A. Boardman (1892), a respected naturalist in eastern Maine, stated that, "This wildcat [*Lynx canadensis*] a few years ago was very common in my woods, and *Lynx rufus* did hardly ever occur. Now it is much more abundant than *canadensis*." Lastly, the biologist, G.M. Allen (1923) remarked that, "It [*L. canadensis*] has been much depleted in numbers with us through persistent trapping and there is much reason to suppose that its place has been largely occupied by the more southern bay lynx [*L. rufus*]." Harvest records (MDIFW, unpublished data) from the 1980s and 1990s indicate that bobcats were relatively common in western and eastern Maine.

Potential causes of the decline, 1880-1920

The distribution of Canada lynx observations contracted northward about 1900 (Figure 1.1), and the number of observations declined through 1920. Without a measure of sampling effort, this cannot be taken as proof of a contraction in the distribution of lynx or a decline in their population. However, observers noted a decline in lynx abundance as bobcat moved north in Maine, 1880-1920 (Boardman 1892, Rich 1892, Ames 1893, Hardy 1907a, Allen 1923). The landscape of Maine was changing in many ways at the turn of the century. The extent of agriculture and forestland, the community of large mammals, and the climate were changing in ways that may have adversely influenced lynx during 1880-1920.

Changing forest composition

Canada lynx prey primarily on snowshoe hare (*Lepus americanus*); even at the southern extent of the range of lynx, snowshoe hare dominates in the diet of lynx (Aubry et al. 2000). Studies of snowshoe hare habitat at the scale of forest stands have indicated a strong positive relationship with areas of high stem densities (Litvaitis et al. 1985, Long 1995, Fuller 1999). This pattern is consistent with patterns that I observed at the statewide scale (Chapter 3). High stem densities usually result from regeneration after crown replacing fires or wind in natural systems, and following certain timber harvest practices, such as clearcut logging (Conroy et al. 1979, Monthey 1986). H.D. Thoreau (1893) noted that lynx were common in "the burnt lands," and Audubon and Bachman (1852) described lynx as occurring in regenerating forest following a large fire in Maine.

Timber harvest has been an important part of the Maine economy since at least the mid-1830s (Smith 1972). The methods of harvest and the volume harvested have changed dramatically over the past two centuries. Early timber harvest was concentrated on large diameter white pine (*Pinus strobus*). By the turn of the century, much of the harvest had shifted to relatively smaller diameter spruce (*Picea* spp.) for the paper industry. By the 1890s nearly a billion board feet were being harvested annually from the Maine woods (Smith 1972). By comparison in 1999, almost 2 billion board feet were harvested (Maine Forest Service 2000). Timber harvest has had a strong affect on Maine's forests throughout the nearly two centuries addressed in this study.

The amount of regenerating forest was likely affected by the economic depression of the 1873-1883 and subsequent changes in the lumber economy. The economic depression could have indirectly affected later lynx abundance in Maine. Much of the quality timber, especially white pine that was easily accessible from the rivers had been cut prior to 1873. During the depression of the 1870s, money was scarce and few logging operations were conducted in remote areas or on large

scales; overall cut diminished greatly during this time, and woods operations became smaller (Smith 1972). Reduced cutting during this depression may have resulted in a shortage of regenerating forest 15 to 25 years later (1890-1900). Correspondingly, the number of snowshoe hares in Maine may have declined, negatively influencing the population of Canada lynx.

Since 1982 the trend in forest age composition in Maine has been toward increasing regeneration (Griffith and Alerich 1996), an age class that provides good hare habitat (Fuller 1999, Chapter 3). An increase in hare habitat could partially explain the increase in Canada lynx observations, though the increase in lynx observations could also be explained by recent increases in surveying effort for lynx, restricted harvest lynx in Quebec to the north (Lafond 1995), and other factors such as climate change and competing carnivores.

Seton (1929) noted that, "…the Lynx is a thing of the primitive forests, and retreats as they fall, just as do the Marten, the Fisher, and the Wolf. The bobcat is a lover of the half open country… one of those creatures that expand their range with the onward march of the settler." Thus, the conversion of forest to farmland has also been hypothesized as an explanation of the shifts in range of Canada lynx and bobcat. When scrutinized, however, this hypothesis does not hold. The conversion of forest to farmland in Maine occurred largely between the late-1700s and the mid-1800s (Harper 1918). This conversion was concentrated in, but not limited to, the southern and south-central part of Maine. By the late 1800s and early 1900s, much farmland was reverting to forest, and the net area of forest relative to farmland was increasing (Harper 1918, Litvaitis 1993) during the same time that the range of lynx was decreasing (Boardman 1892, Heywood 1903, Allen 1923). The reversion of farmland to forestland likely created much regenerating forest favorable to snowshoe hare, and this may partially explain the increase in bobcats, but not lynx.

Climate change

Climate change may also have affected the distributions of Canada lynx. Parker et al. (1983) noted that bobcats invaded Cape Breton Island, Nova Scotia about 1955, after the island was connected to the mainland by a causeway. Shortly thereafter, the range of lynx contracted to the highlands in the northern part of the island. Parker et al. (1983) hypothesized that deeper snowfall in the highlands gave the lynx a competitive advantage over the bobcat. Morphologically, Canada lynx are better adapted to snow than bobcats. Lynx are lightweight and have large paws, which gives them lower foot-loading (weight per area of paw), providing greater efficiency in pursuing snowshoe hare in deep snow. Canada lynx also have proportionally longer legs than bobcat. When comparing the foot-loading and leg length of Canada lynx, bobcat, and several other forest carnivores, Canada lynx is distinct from the other carnivores that are adapted by either long legs (such as coyote) or low foot-loading (such as marten, *Martes americana*), but not both (Figure 1, Krohn et al. *In prep*).

Between about 1300 and the mid-1800s, the northern hemisphere experienced a period of unusually cold temperatures, often called the "Little Ice Age" (Lamb 1977). In the Northeast, the coldest temperatures occurred in 1776, with gradual warming through the 1800s (Baron 1992). During this time, snowfall occurred throughout a longer season; as late as 1917, snow in September and May was common in New England, even as far south as western Massachusetts (Brooks 1917).

If snowfall was a factor separating lynx and bobcat distributions on a geographic scale, lynx would have had an advantage over bobcat over a much larger area of New England during the Little Ice Age. As the climate warmed and the snowy season became shorter, lynx would have retreated north and to higher elevations as populations of bobcats expanded or snowshoe hare contracted. The timing of the contraction in lynx range matches the change in climate. The recent

distribution of lynx, 1987-1999, in eastern North America coincides spatially with mean annual snowfall in excess of 268 cm (Chapter 2), suggesting that deep snow is important to past, recent, and potential future distributions of lynx.

Climate change could affect habitat suitability of lynx across several time scales. Climate could affect lynx directly, via the relationship of foot-loading to snowfall. However, climate could also affect lynx at shorter time scales by affecting the susceptibility of snowshoe hares to predation in a given season. Over longer temporal scales, climate may affect lynx populations indirectly by affecting the species composition of forests. The extensive spruce-fir forest of Maine is a relatively recent phenomenon tied closely to the cool and moist climate of the Little Ice Age (Schauffler 1998, DeHayes et al. 2000). Prior to European settlement, the spruce-fir component of the Northeast was more pronounced, but since European settlement there has been an increase in the deciduous component of the forests (Russell et al. 1993). This change may reflect climate change, selective logging of conifers, or some combination of the two (Russel et al. 1993, Seymour 1992).

The superior morphological adaptations of lynx to deep snow might give lynx less competitive advantage over bobcats as climate warmed and snowfall decreased around the turn of the century. The regional climate of the past 20-30 years has been warmer with less snowfall (Chapter 2), which should have caused bobcat abundance to increase, and lynx to decrease. This explanation fails to account for recent increases in the number of lynx observations, but the increase in observations may result from increased awareness and search effort.

Changes in the carnivore community

The changes in the distributions of Canada lynx and bobcat appear to have been part of a broader change in the community of large mammals in Maine, 1890-1910. Wolves were relatively common in Maine during the mid-1800s and still present, though rare, in the 1880s (Hardy 1904). There are few reliable records of wolves after the 1880s, with the exception of isolated instances in

the twentieth century. Until the 1960s and 1970s, much of Maine was without a wild large canid; coyotes *(C. latrans*) invaded in the 1930s, but were initially rare (Richens and Hugie 1974). Caribou (*Rangifer tarandus*) were once found in northern and western Maine, and as far south as Bangor (Hardy 1899). By 1899 they were becoming scarce (Hardy 1899), and were extirpated shortly thereafter. White-tailed deer (*Odocoilius virginianus*), rare in northern and western Maine prior to the 1880s (Stanley 1906), were becoming abundant by the turn of the century (Churchward 1898, Stanley 1906).

Litvaitis and Harrison (1989) hypothesized that when coyotes invaded Maine in the early 1970s, bobcats switched from a diet dominated by deer to a diet dominated by snowshoe hare, which coincided with an overall decline in the bobcat population. Bobcats have high foot-loading relative to snowshoe hares (Krohn et al. *In prep*), and bobcats decline in areas of deep snow if forced to subsist entirely on snowshoe hares. Conversely, bobcats have low foot-loading relative to deer, and bobcats may prey (or scavenge on deer carcasses, especially in the late winter) and feed on deer when canids are absent (Litvaitis and Harrison 1989). The range expansion of bobcats coincided with the extirpation of wolves in Maine, and bobcat densities decreased after coyotes became established in Maine. The number of lynx observations declined after wolves were extirpated, and increased after coyotes invaded. Thus, lynx abundance in Maine might be positively associated with the presence of a large canid, whereas available data indicates that bobcat abundance (Litvaitis and Harrison 1989) in Maine may be negatively associated with the presence of a large canid. Further studies are needed to more clearly understand the interrelationships and dynamics of lynx, bobcats, coyotes, and wolves.

Historical records beyond Maine

There appears to be enough historical literature to justify additional study of historical lynx occurrences in New Brunswick, Nova Scotia, New York, Vermont, New Hampshire, and perhaps Massachusetts and Connecticut. For example, 216 Canada lynx were bountied in New Hampshire, 1931-1953 (Silver 1957). If the few citations in Table 1.3 are representative of the historical literature in those states and provinces, the range collapse of lynx observed in southern Maine around the turn of the century was part of a much larger, relatively rapid range collapse in eastern North America. Thus, it is likely that several of the explanations discussed previously acted in combination to effect the observed range contraction. Further historical study throughout eastern North America is needed to determine the regional patterns of past lynx distribution, and environmental factors affecting the regional range collapse.

CONCLUSIONS

Based on 118 records of 509 individuals, Canada lynx occurred throughout a substantial portion of Maine, 1833-1999. There was evidence of lynx reproducing throughout all but extreme southern Maine from at least 1863 through 1999. In the mid-1800s Canada lynx were not rare, and were widely distributed throughout much of Maine. The spatial distribution of Canada lynx observations contracted in the late-1800s through the early 1900s, coinciding with a range expansion by bobcats. The potential mechanisms for the decline in lynx are uncertain, and may related to changes in the composition of the forests, competition with bobcats, extirpation of wolves, or past changes in snowfall, or a combination of these factors. Prior to 1900, lynx were apparently widely distributed through much of eastern North America, but widespread extirpation occurred south of Maine about 1900. Additional studies are needed to evaluate the historical distributions of lynx in other jurisdictions of eastern North America.

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CHAPTER 2

BROAD-SCALE HABITAT RELATIONS OF CANADA LYNX IN NORTHEASTERN NORTH AMERICA

INTRODUCTION

In the eastern USA, the Canada lynx (*Lynx canadensis*) was once found as far south as Pennsylvania (Audubon and Bachman 1852, Rhodes 1903). Currently lynx in the eastern USA occur only in northern Maine (Chapter 1), and this population was recently listed as threatened under the federal Endangered Species Act (USFWS 2000). In a review of research needs for the conservation of lynx, Aubry et al. (2000a) highlighted the necessity for broad-scale studies of Canada lynx habitat relationships.

Canada lynx likely relate to their habitat at several spatial and temporal scales, including relatively broad spatial scales because of their tremendous dispersal potential. The maximum dispersal of a Canada lynx in the Northwest Territories was 930 km (Poole 1997), or roughly the distance from western Maine to Cleveland, Ohio. Similarly, lynx in the eastern United States have dispersed long distances. One lynx released in the Adirondacks of New York in the early 1990s was subsequently shot in Plaster Rock, New Brunswick, a straight line dispersal of about 780 km. Other lynx from northern Canada released in New York were later found in Ottawa, Ontario, New Jersey, and Pennsylvania (Kent Gustafson, New Hampshire Fish and Game Department, personal communication.) Thus, a lynx dispersing from northern Maine could be limited by the St. Lawrence Seaway to the north and the Atlantic Ocean to the east and south. To the southeast road densities, prey densities, and climatic factors probably affect the permeability of the landscape to dispersing lynx. This would roughly coincide with the southern border of New York.

When studying population level responses to habitat conditions, the spatial scale of the study should coincide with the scale of the regional population (Goodwin and Fahrig 1998), and the temporal scale of at least one generation time (McArdle et al. 1990). This study evaluates broad-scale habitat relation of lynx across a 512,000 km^2 region of eastern North America. Because recent analyses suggest that lynx in this region might be cyclic (McKelvey et al. 2000), a time period covering one full cycle (greater than 10 years) was considered more important than one generation time. Thus, this study considered lynx-habitat relations during the period 1987-1999. A contraction in the historic range of lynx in eastern North America appears to have occurred over a large region around 1900 (Chapter 1). Knowledge of the mechanisms driving broad-scale patterns of occupancy is needed to evaluate limiting factors that may influence future distribution and recovery efforts for lynx.

The objectives of this study were to determine which suite of environmental features best predict the current (1987-1999) presence of Canada lynx within the historic range of the species in eastern North America; and to develop and test a probability based model to predict and map the distribution of habitat for Canada lynx in eastern North America.

METHODS

Lynx presence and absence

A database of all spatially explicit observations of Canada lynx in the Northeast (eastern states from New York north and east to the eastern Canadian provinces of Quebec, New Brunswick, and Nova Scotia) was compiled for the period 1987-1999. For Canadian provinces, these data were compiled from unpublished reports (Cumberland et al. 1998, Forbes et al. 1999; New Brunswick) or other unpublished data on harvests and incidental kills archived by provincial wildlife biologists (Quebec and Nova Scotia). Records from Maine were predominantly track records from surveys conducted by the Maine Department of Inland Fisheries and Wildlife

(MDIFW) and interviews conducted by US Fish and Wildlife Service (USFWS) biologist R. Joseph, (Chapter 1). I also interviewed biologists in New York, New Hampshire, Vermont, and Massachusetts and recorded occurrences considered reliable. Records of the 83 lynx that were reintroduced to New York from the Yukon Territory in the early 1990s were not included in this analysis. Lynx observations were converted to a GIS point coverage (ArcInfo 7.2.1, Environmental Systems Research Institute (ESRI), Redlands, California, USA; use of trade names does not imply endorsement). Only observations that could be mapped to the nearest 1 km^2 were included in analyses.

Habitat features associated with occurrences were compared to random points using logistic regression (Hosmer and Lemeshow 1989). Ideally, data on verified absence of lynx are desirable because the logistic regression model assumes that presence and absence have been determined without error. Violating this assumption generally affects the power of the model. Because the region was not systematically surveyed, random points were used *in lieu* of verified absences. Random points were determined using the Movement extension in ArcView 3.1 (ESRI, Redlands, California, USA). Points were constrained to be 17 km from lynx occurrences and 5.6 km from each other to minimize spatial error and autocorrelation.

Snowfall

Snowfall has been hypothesized to be a factor in the broad-scale distribution of several forest carnivores including martens (*Martes americana*) and fishers (*M. pennanti,* Krohn et al. 1995, 1997) and some species of weasels (*Mustela* spp., Simms 1979). Patterns of regional snowfall may also affect the distribution of Canada lynx and bobcats (*L. rufus*) (Chapter 1, Parker et al. 1983) because of the morphological adaptations of lynx to deep snow and the higher foot-loading and shorter limb lengths of bobcats (Krohn et al. *In prep*).

Canadian Monthly Climate Data (CMCD) for the period 1849–1992 was purchased from Environment Canada, Atmospheric, Climate and Water Systems Branch. Daily climate data for the United States was extracted from the Cooperative Summary of the Day, published by the National Oceanic and Atmospheric Administration (NOAA) National Climatic Data Center (NCDC) for the years 1876-1997.

The total monthly snowfall was calculated from daily measurements in the USA. To match the daily data for the USA to monthly data for Canada, any month for the USA with snowfall data missing for more than 3 consecutive days or more than 5 days in a month were excluded. Monthly totals for snowfall in the USA and Canada were then summed by year from November through the following March. Years with one or more missing months of data were omitted.

Yearly snowfall (= cm snowfall for November of year x through March of year x +1) was averaged by decade for stations with at least 7 years of data per decade. Data were too sparse for decades prior to 1948 to model spatially. Weather stations were mapped using ArcInfo 7.2.1 using the latitude and longitude coordinates associated with each station. Stations north of the St. Lawrence Seaway in Quebec, those on Newfoundland and Prince Edward Island, or on smaller islands more than 20 kilometers from the mainland were excluded from analyses. Stations within 70 kilometers of Lake Erie or Lake Ontario were also excluded from analyses because of the difficulty in modeling lake-effect snowfall patterns (Petterssen and Calabrese 1959).

I downloaded 62 Digital Elevation Models (DEMs) at the 1:250,000 scale (resolution 1 km^2), from United States Geological Survey (USGS), Geospatial Data Clearinghouse, and joined them with 25 DEMs purchased from Geomatics Canada, Centre for Topographic Information, Sherbrooke. These DEMs were imported into ArcInfo Grid, and combined into one raster coverage using the MOSAIC command. All coverages in this analysis were conducted on maps in Albers Equal Area projection, which preserves area, but slightly distorts shape and direction. The raster

coverage of elevation provided elevation (in meters) for each weather station in Canada and the USA.

Using SYSTAT 8.0 (SPSS, Chicago, Illinois, USA), I performed multiple linear regressions with 10-year mean snow as the dependent variable and elevation, latitude, and longitude as independent variables for each decade from 1950-1990. The coefficients from the regression models and raster grids of elevation, latitude, and longitude were then used to map predicted snowfall in the Northeast for each decade at a 1 km^2 resolution.

Road density

Bobcats appear to be associated with areas of relatively fewer paved roads, and radio-collared individuals avoided crossing roads (Lovallo and Anderson 1996). A radio-telemetry study of lynx in the southern Rocky Mountains of Canada suggests that lynx did avoid crossing or including divided highways within their home range (Apps 2000). Road mortality was a factor in the failure of an attempted reintroduction of Canada lynx in to the Adirondack Mountains (Brocke et al. 1991). Because road avoidance behavior or mortality may affect habitat quality for lynx in the eastern USA, road density was included in this analysis.

Road densities were derived from US Geological Survey (USGS) Digital Line Graphs (DLG) and Geomatics Canada, National Topographic Data Base (NTDB) road layer. USGS 1:100,000 scale DLG files (N=654) were converted to coverages in ArcInfo and compiled into one database for all of Maine, New Hampshire, Vermont, Massachusetts, Connecticut, Rhode Island, and New York. Geomatics Canada NTDB road network files (N=680) at a 1:250,000 scale were converted into ArcInfo coverages and compiled into a database for all of Nova Scotia, New Brunswick, and the portion of Quebec south of the St. Lawrence Seaway. Because the cost of road data from Canada was calculated by kilometer of road, areas immediately around Montreal were omitted.

Roads classified in the USGS DLGs as arbitrary line extensions, closure lines, processing lines, trails, limited access roads, class 5 roads (those designated for 4-wheel drive vehicles), or those that were not classified, were deleted. The NTDB road data are available in two themes: "roads" and "road network." The "roads" theme contains only trails and roads designated for 4-wheel drive vehicles. The "road network" contains all roads passable by a 2-wheel drive vehicle. Only the "road network" was purchased and analyzed for the Canadian provinces. Although the two data sources have different map scales, edge-matching suggested that differences were more in positional accuracy, and less that smaller roads were omitted in the larger scale data set from the Canada.

The USGS DLG coverage was appended to the Geomatics Canada NTDB coverage to create one international map of all roads suitable for 2-wheel drive vehicles. The density of roads was then calculated from the international road coverage using the ARC-INFO Grid command LINEDENSITY. This procedure calculated the number of kilometers of road per square kilometer within a 100 km^2 circle (approximately the size of a lynx home range) around each 1 km^2 cell (to match the resolution of the land use and land cover data). The output was a raster map of road density at a 1 km^2 resolution.

Bobcat density

On a geographic scale, bobcat and lynx are largely allopatric, and at least two historic instances of bobcat replacing lynx in an area have been documented (Maine, Chapter 1; Nova Scotia, Parker et al. 1983). The mechanism for this allopatry has not been determined with certainty; although snowfall has been hypothesized as a mediator of exploitation competition between these two felines (Parker et al. 1983, Chapter 1). Because snowfall is only one of many possible explanations for spatial allopatry between lynx and bobcats (Chapter 1), bobcat harvest density as a rough index to bobcat density was also considered as a variable in this study.

The only data related to bobcat abundance available across for most of the study area was annual harvest, 1993-1998, by county, township, or management unit, with the exception of Quebec, New Hampshire, Connecticut and Rhode Island where bobcats are protected throughout the year (from harvesting). Bobcat were harvested in Massachusetts, but the trapping methodology was different from other states where leg-hold traps were permitted. This difference probably would have resulted in biased estimates of harvest density relative to harvests in areas where hounds and leg-hold traps are legal. Harvest was considered to be zero for Massachusetts, where only box traps were allowed.

Each state or provincial agency in the study area for which harvest data on bobcats was available provided harvest information. County boundaries in Nova Scotia were derived from digital census data purchased from Geomatics Canada, Centre for Topographic Information Sherbrooke. The New Brunswick Department of Natural Resources and Energy, Fish and Wildlife Branch provided digital coverages of their wildlife management units. Vermont Department of Fish and Game provided a paper map with harvests by management units, based on highways. The Vermont map was digitized using USGS DLGs at a scale of 1:100,000. Harvests of bobcats in Maine were summarized by township, and the Maine Office of GIS provided the township coverage (i.e. digital map). County boundaries for New York were downloaded from the Cornell University Geospatial Information Repository. Harvest was considered zero in New Hampshire and Quebec. I calculated the mean harvest, 1993-1998, and divided the mean harvest by the area of the township, county, or management unit. Data were combined into one map and converted to a raster grid at a resolution of 1 km^2.

Land use and land cover

Canada lynx have often been described as a boreal forest species (McCord and Cordoza 1982, Quinn and Parker 1987, Aubry et al. 2000b), and thus lynx would presumably be more likely

to be found in areas with a high conifer component, and rarely in areas dominated by deciduous forest. To investigate this association, I downloaded from the USGS Earth Resources Observation Systems (EROS) a copy of the North America Land Cover Characteristics Data Base, a raster image of Advanced Very High Resolution Radar (AVHRR) imagery classified according to the USGS Land Use/Land Cover System (Anderson et al. 1976). The satellite imagery was taken from April 1992 through March 1993. The image was converted to an ArcInfo grid with a cell size of 1 km^2. The classification of the imagery was fairly coarse. Deciduous, coniferous, and mixed forest were differentiated, but at this scale there was no data on successional stage or type of forest management.

Two measurements were derived from the classified AVHRR imagery. A moving window function (FOCALMEAN function in ArcInfo) was used to calculate the percentages of deciduous forest and of coniferous forest within a 100 km^2 circular window, which was established to approximate the area of a lynx home range in the southern portion of the species' geographic range (Aubry et al. 2000a).

Logistic regression models

The predicted snowfall (1980-1990), bobcat harvest density, road density, and the proportions of deciduous and coniferous forest within 100 km^2 were calculated for each lynx observation and random point. Based on published literature for Canada lynx, we could not justify the inclusion of a long list of other variables (such as human density or various landscape metrics). Consideration of too many variables could result in spurious correlations and model over-fitting (Burnham and Anderson 1998).

All five variables were included in a multiple logistic regression model. I then used 18 subsets of this model that I thought were potentially meaningful and biologically relevant. I used SYSTAT 9.0 for the regression analyses. All models were assessed for goodness-of-fit using the

Hosmer-Lemeshow P statistic (Hosmer and Lemeshow 1989) and McFadden's ρ^2 (McFadden 1974). The predictive power of the final models was verified by testing a reserved set (N = 278) of 126 points where lynx were known to be present and 152 random points, and evaluating the ability of the model to correctly classify the reserved observations.

Models were ranked using Akaike's Information Criterion (AIC; Akaike 1973), a method that ranks biologically sound models in terms of the fit of the model to the data and the simplicity (or "parsimony") of the model (Burnham and Anderson 1998, Anderson et al. 2000). Because AIC values are relative, the Δ AIC's were also calculated ($\Delta AIC_i = AIC_i$ – minimum AIC). As a "rough rule of thumb," those models with Δ AIC values > 10 are considered inferior and should be omitted from further analysis (Burnham and Anderson 1998). Maps of the probability of occurrence and maps of residuals were created for the models with the lowest overall AIC score, and for 2 comparable models with a Δ AIC < 10. Models were verified by selecting, at random, 278 points (presence and absence). The models were then recalculated without those points, and the resulting models were used to predict the reserved data.

RESULTS

Lynx presence and absence

There was a strong north-south gradient in the density of Canada lynx locations (Figure 2.1), with most locations concentrated on the Gaspé peninsula of Quebec and Cape Breton Island, Nova Scotia. Seventy-nine percent of all location records (n = 1,150) were from Quebec (n = 909), and represented lynx that were harvested by trappers (n = 840, Table 2.1).

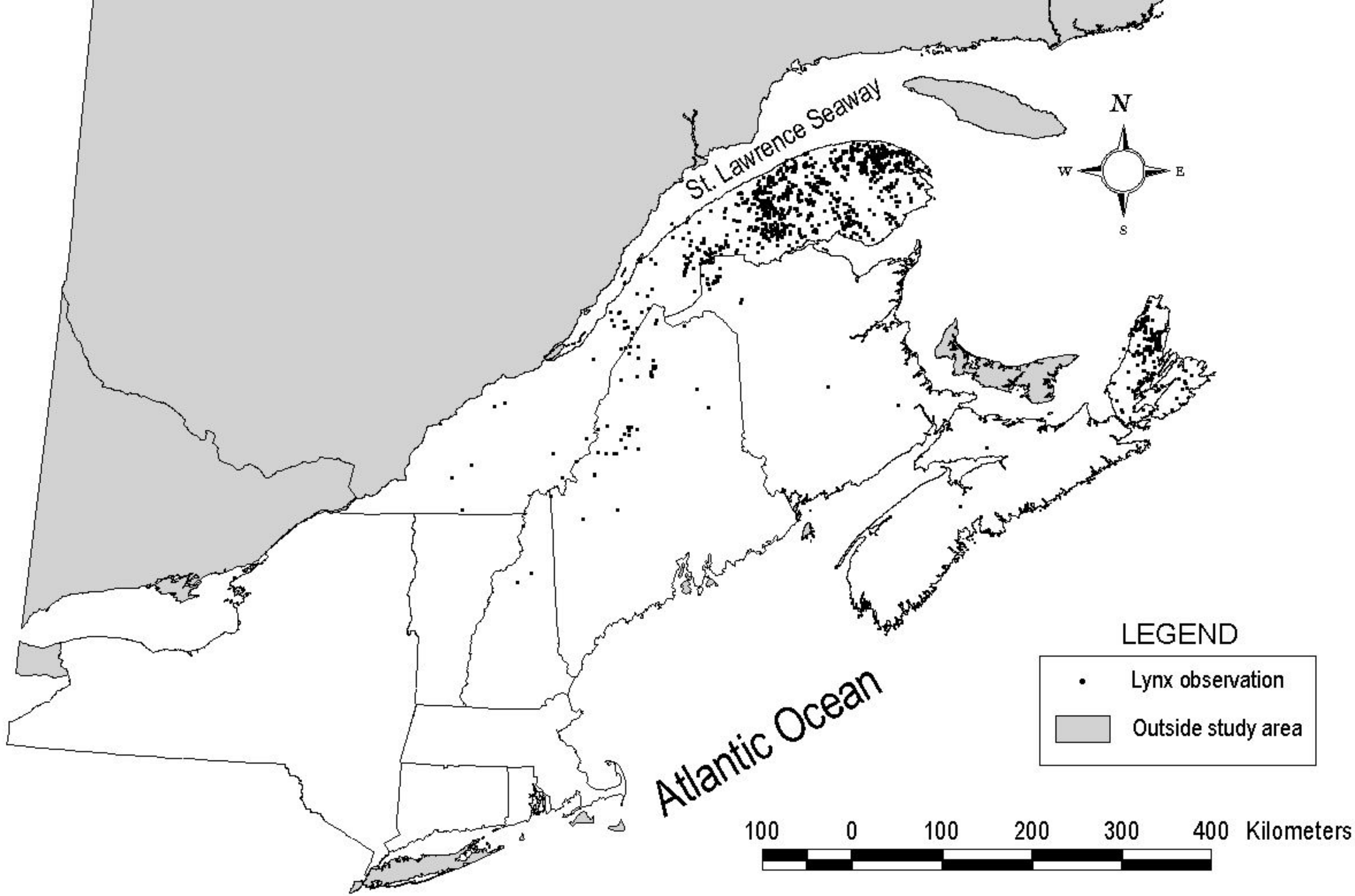

Figure 2.1. Visual observations, tracks, or harvest locations of Canada lynx in eastern North America, south of the St. Lawrence Seaway, 1987-1999.

Table 2.1. Data sources, years, and number of Canada lynx observations in the northeastern United States and eastern Canada, 1987 - 1999.

State or Province	N	Years	Sources				
			Trapping	Tracks	Visual	Roadkill	Other
Quebec	909	1988-1999	823	-	-	8	78
Nova Scotia	167	1994-1999	-	45	45	(~ 30)[1]	77
Maine	50	1987-1999	2	30	8	-	10
New Brunswick	21	1992-1999	15	6	-	-	-
New Hampshire	3	1987-1995	-	-	3	-	-
Total[2]	1150	1987-1999	840	81	56	8	165

[1] About 30 of the 77 lynx in "Other" are roadkills from Cape Breton Island. (J. Nocera, University of New Brunswick, personal communication.)

[2] Lynx reintroduced to New York were not included in these totals

Snowfall

Snowfall models were produced for four different decades, but only the most recent decade, 1980-1990, was included in the logistic regression models. The adjusted r^2 for the 1950-60 model (n = 433) was 0.70; for 1960-70, r^2 = 0.63 (n = 500); for 1970-80, r^2 = 0.65 (n = 607); and for 1980-90, r^2 = 0.67 (n = 590). For each of the four time periods, the coefficients for elevation and latitude were significant ($P < 0.0001$). The coefficients for longitude were significant for 1960-70 and 1980-90 ($P < 0.0001$), but not for 1950-60 and 1970-80 ($P = 0.131$ and $P = 0.160$, respectively). Areas of heavy snowfall (greater than 240 cm) were steady 1950-1970, then shifted southward in the 1970s and northward in the 1980s (Figure 2.2).

Weather stations (n = 1,321) were not uniformly distributed, but occurred most densely in a 200 km band running north-south through the middle of the study area. Mapping the residuals of spatial models can highlight geographic areas where model fit was poor. For 1980-90, the distribution of residuals (Figure 2.3) indicated that the model seriously under-predicted (residuals > 150 cm) snowfall at 5 stations, moderately under-predicted 92 stations (25 - 150 cm), predicted 286 stations well (within 25 cm), moderately over-predicted for 124 stations, and seriously over-predicted 2 stations. Most of the residuals did not show strong spatial patterning; although the models did under-predict snowfall in the western Adirondacks, and slightly under-predicted snowfall surrounding the Bay of Fundy. The maps of residuals were similar among the models for the four decades, and large residuals were generally associated with local effects of large bodies of water on snowfall.

Road density

Road densities were highest in the southern extremes of the study area (Figure 2.4). Northern Maine, northern New Brunswick, the interior of the Gaspé region in Quebec, the Cape

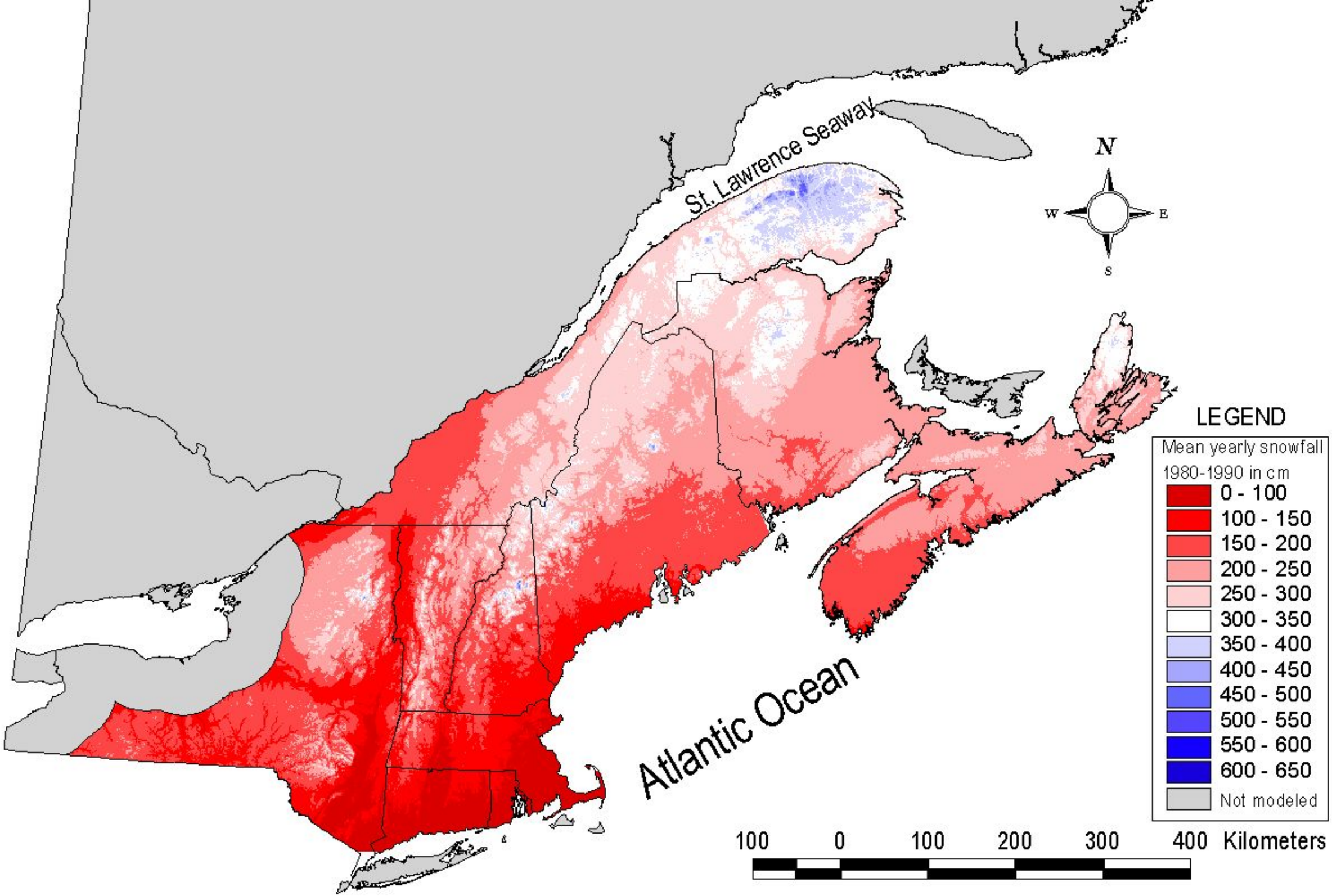

Figure 2.2. Predicted mean annual snowfall for northeastern North America, south of the St. Lawrence Seaway, 1980-1990, based on 590 weather stations in the USA and Canada. Significant variables in the model used to predict snowfall included elevation, latitude, and longitude.

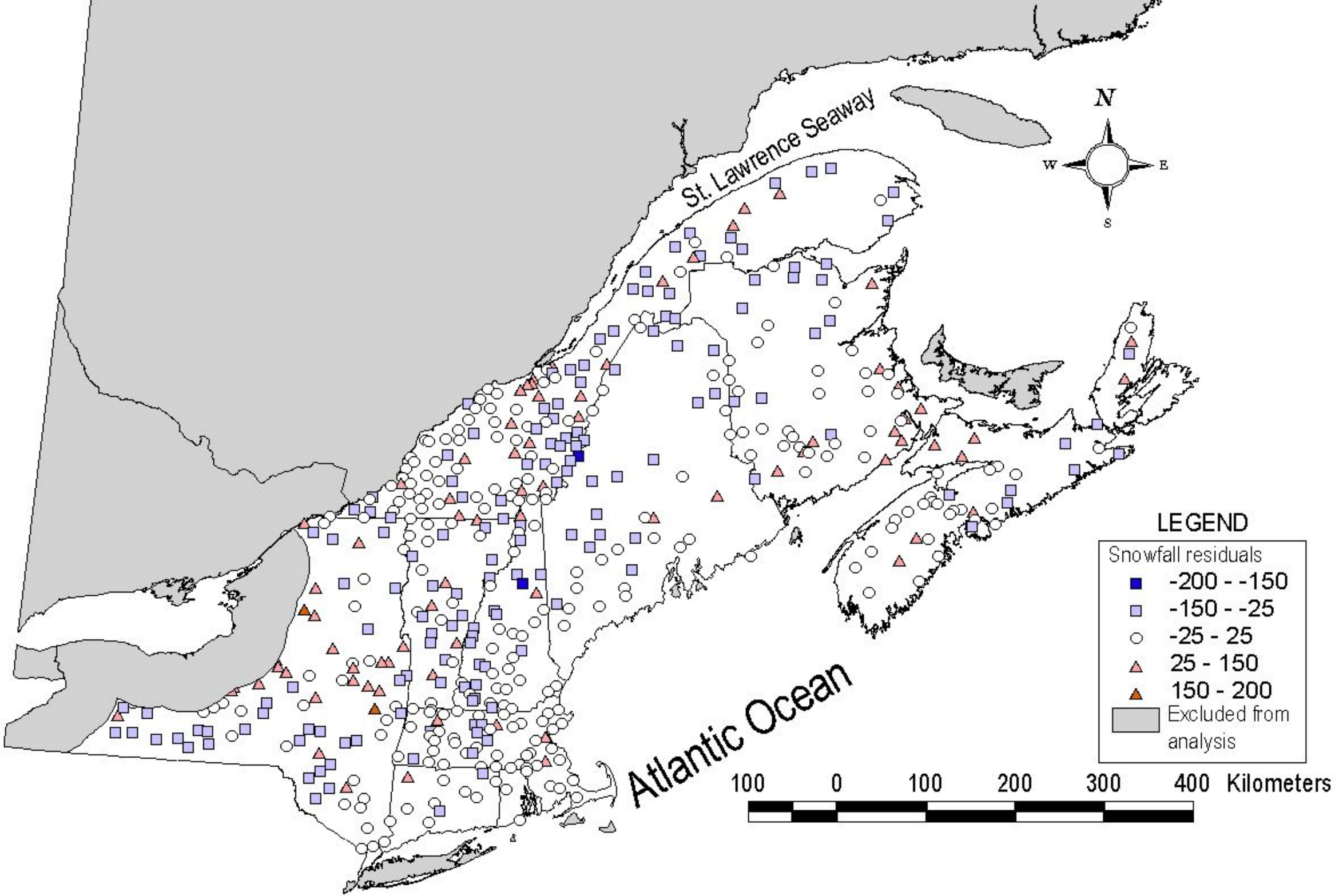

Figure 2.3. Spatial distribution of residuals in centimeters from a snowfall model developed for northeastern North America, 1980-1990.

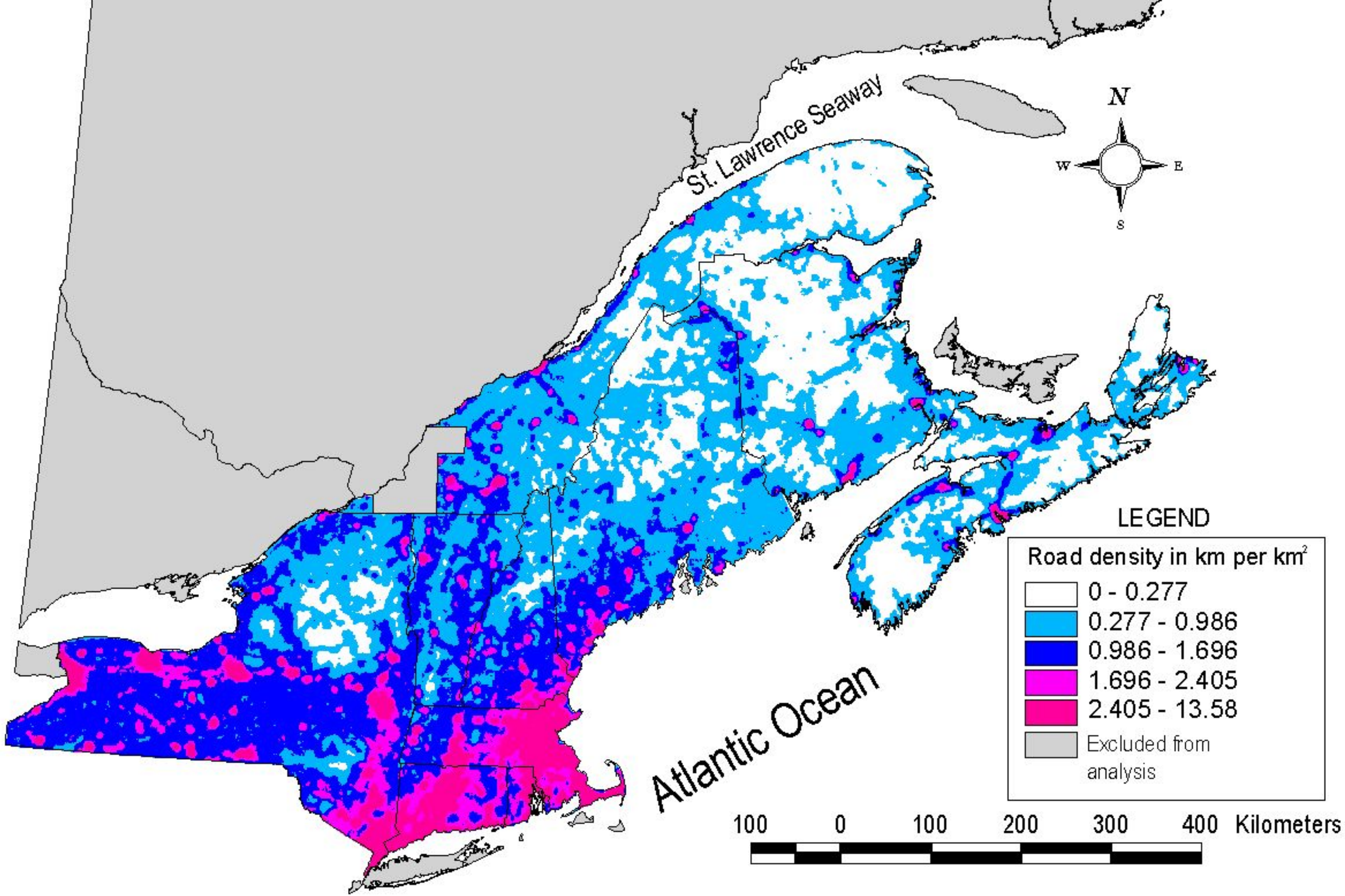

Figure 2.4. Density of paved and major dirt roads (km/km^2 within a 100 km^2 circular moving window) in northeastern North America, based on U.S. Geological Survey Digital Line Graphs and Geomatics Canada, National Topographic Data Base.

Breton highlands, and the Adirondacks of New York all had relatively low road densities (< 0.6 km/km^2), as did smaller areas in mountainous regions of New Hampshire, Vermont, and western and southern New York.

Bobcat density

Harvest densities of bobcats were highly variable across the region (Figure 2.5). Harvests were highest in a band extending from Nova Scotia, extreme southern New Brunswick, mid-Maine, Vermont, to an area east of the Adirondacks in New York. However, bobcat densities were likely underestimated in southern Quebec, New Hampshire, Massachusetts, and Connecticut where bobcats occur, but are seldom reported because of harvest restrictions.

Land use and land cover

At a 1 km^2 resolution, the northeast region is dominated by forestlands of three major types (Figure 2.6). Extensive areas of deciduous forest are confined largely to southern and inland areas. Extensive areas with 1 km^2 pixels dominated by coniferous forests are confined primarily to the coastal areas of Maine, New Brunswick, and Nova Scotia where growing seasons are cool and wet.

Logistic regression models

Canada lynx were positively associated with 10 year mean annual snowfall in each of the 11 models where it was included as an independent variable (Table 2.2). Lynx were negatively associated with the proportion of a 100 km^2 landscape in deciduous forest cover in each of the 9 models in which it was included. The proportion of conifer forest, road density, and bobcat harvest density were inconsistent; these variables were positively associated or negatively associated with lynx occurrences in different models.

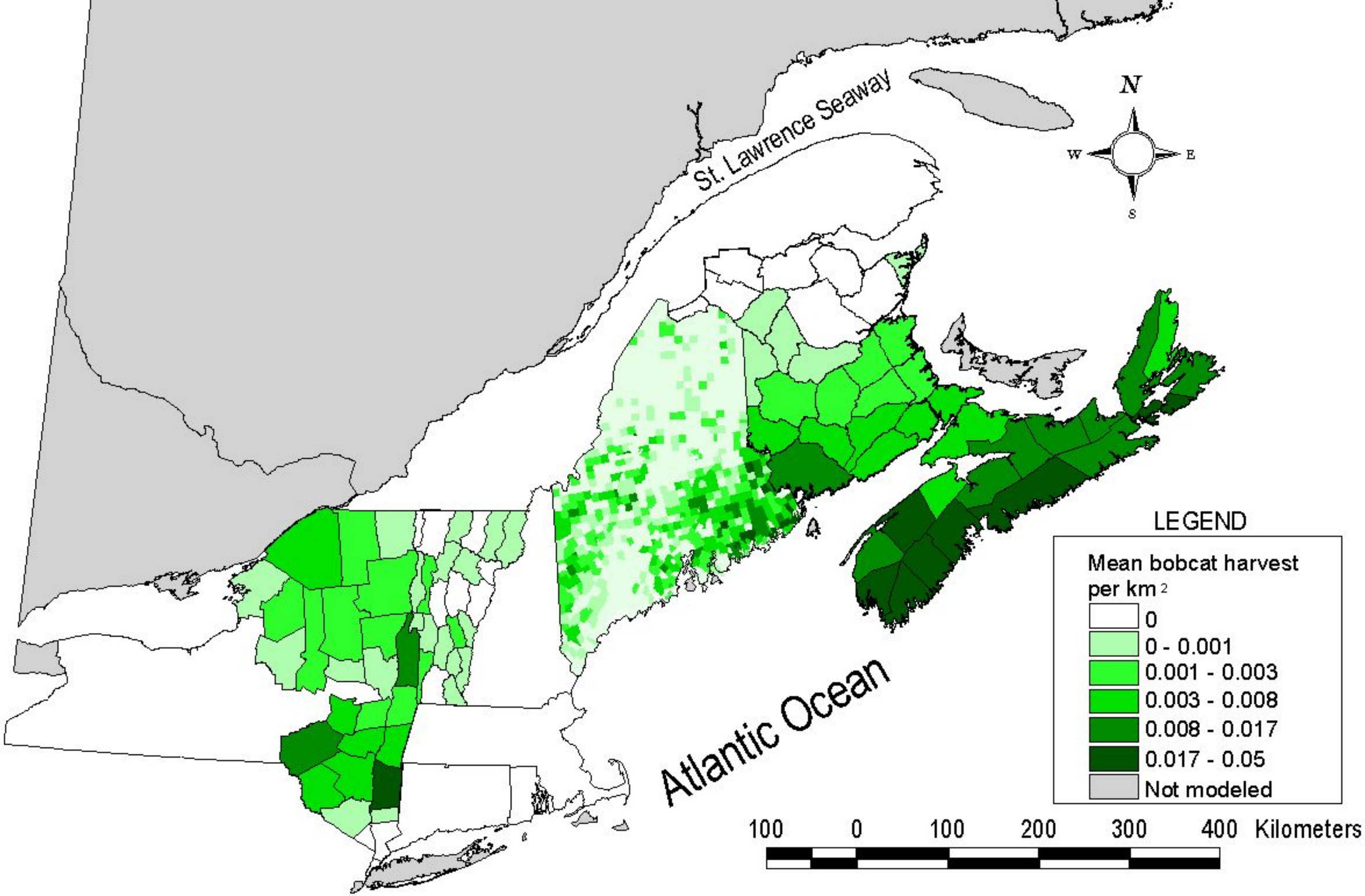

Figure 2.5. Mean density (no/km^2) of bobcat harvested in northeastern North America, 1993-1998. Bobcat harvest seasons are closed in Quebec, New Hampshire, western New York, Connecticut, and Rhode Island. Bobcat harvest in Massachusetts is limited to box traps, and is not comparable to harvest densities in other areas.

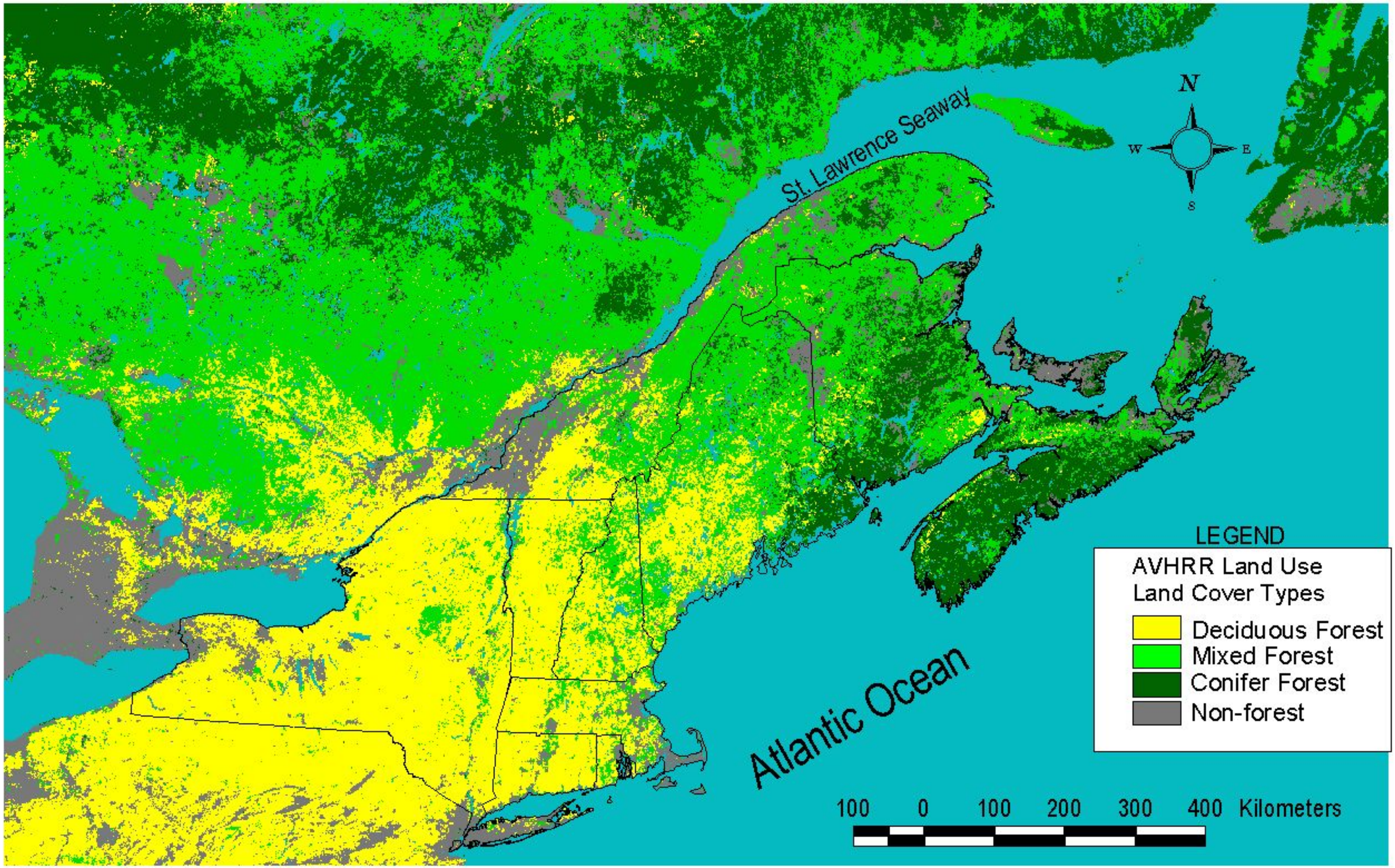

Figure 2.6. Forest cover at a 1 km^2 resolution from Advanced Very High Resolution Radar (AVHRR) satellite imagery classified by United States Geological Survey Land Use Land Cover system. Only codes 411 (Deciduous Broadleaf forest), 422 (Evergreen Needleleaf Forest), and 430 (Mixed Forest) are depicted.

Table 2.2. Four estimates of model performance for 19 broad-scale models comparing 1,150 presences and 1,288 random points in eastern North America where Canada lynx were not reported. Models are ranked by AIC. Note that models can be broken into 4 groups by AIC or McFadden's ρ^2: models 1-6 are good, models 7-11 are moderate, models 12-17 are poor, and models 18 and 19 are very poor.

Rank	Model	McFadden's ρ^2	Hosmer-Lemeshow P	AIC	ΔAIC
1	Deciduous (-), Snowfall (+), Conifer (-)[1]	0.723	0.610	955.314	0
2	Deciduous (-), Snowfall (+), Bobcat (+), Roads (+), Conifer (-)	0.724	0.611	958.302	3
3	Deciduous (-), Snowfall (+)	0.720	0.537	963.218	8
4	Deciduous (-), Snowfall (+), Roads (+)	0.720	0.694	964.820	10
5	Deciduous (-), Snowfall (+), Bobcat (+)	0.720	0.511	965.068	10
6	Deciduous (-), Snowfall (+), Bobcat (+), Roads (+)	0.720	0.776	966.616	11
7	Snowfall (+)	0.688	0.705	1072.528	117
8	Snowfall (+), Roads (-)	0.688	0.782	1072.684	117
9	Snowfall (+), Roads (-), Bobcat (+)	0.689	0.712	1073.082	118
10	Conifer (+), Snowfall (+)	0.688	0.645	1074.376	119
11	Conifer (0), Snowfall (+), Roads (-)	0.688	0.752	1074.684	119
12	Deciduous (-), Bobcat (-), Roads (-)	0.530	0.011	1681.620	726
13	Deciduous (-), Roads (-)	0.464	0.123	1914.466	959
14	Conifer (+), Bobcat (-), Roads (-)	0.416	0.120	2087.194	1132
15	Deciduous (-)	0.391	0.000	2173.708	1218
16	Conifer (-), Roads (-)	0.373	0.000	2241.558	1286
17	Roads (-)	0.361	0.000	2277.490	1322

Table 2.2. continued

18	Bobcat (-)	0.035	0.000	3437.472	2482
19	Conifer (+)	0.012	0.000	3521.374	2566

[1] Signs indicate direction of effect: (+) lynx are more likely to occur with higher values of that variable, (0) no effect, and (-) lynx are less likely to occur with higher values of that variable.

The 19 models were grouped into 3 sets according to ΔAIC (Table 2.2). Models that included snowfall and deciduous cover were best (models 1 - 6 in Table 2.2), those models that included snowfall and lacked deciduous forest as a predictor variable were intermediate in AIC and model performance (models 7 - 11 in Table 2.2), and the remaining models (12 - 19 in Table 2.2) performed poorly. Models that lacked either snowfall or deciduous cover had very low Hosmer-Lemeshow P values and poor predictability. Three models had ΔAIC values below 10. In order of increasing ΔAIC these were: 1) snowfall, deciduous cover, and coniferous cover; 2) the global model with all variables - snowfall, deciduous cover, coniferous cover, bobcat density, and road density, and 3) a model with only snowfall and deciduous cover. These 3 models also had high Hosmer Lemeshow P values (Table 2.2) indicating good fit to the logistic curve, and high predictability (Table 2.3).

The top three models each correctly classified 94% of 278 reserved data points (Table 2.3). Of the points predicted to have lynx present, 7% were absent, and of the points predicted to have lynx absent, 4%-6% had lynx present. Kappa (the proportion of specific agreement) is a statistic that incorporates all of the information in the correct classification rate (CCR), false positive rate, and false negative rate (Fielding and Bell 1997). All 3 models had Kappa greater than 0.75, which denotes “excellent” agreement (Fielding and Bell 1997).

The probabilistic maps of regional scale lynx habitat derived from the top three models were similar (Figures 2.7 - 2.9). The habitats with the highest probabilities of occurrence by Canada lynx were on the Gaspé peninsula in Quebec, in northern Maine, in northern New Brunswick, and on Cape Breton Island in Nova Scotia. At the time of this study (1987-1999) the Adirondack Mountains in New York, the Green Mountains in Vermont, and the White Mountains in New Hampshire appeared to include little potential lynx habitat. Although snowfall could be high in those areas, they apparently had too large a deciduous component to support lynx.

Table 2.3. Verifications of a model to predict occurrences of Canada lynx in eastern North America derived from a building set of 2,160 (n = 1,024 presences, n = 1,136 absences) and a training set of 278 (n = 126 presences, n = 152 absences). Models are ranked based on AIC scores (Table 2.2).

Rank	Model	CCR	false positive	false negative	Kappa
1	Deciduous (-), Snowfall (+), Conifer (-)[1]	0.94	0.07	0.06	0.877
2	Deciduous (-), Snowfall (+), Bobcat (+), Roads (+), Conifer (-)	0.94	0.07	0.05	0.884
3	Deciduous (-), Snowfall (+)	0.94	0.07	0.04	0.884
4	Deciduous (-), Snowfall (+), Roads (+)	0.93	0.07	0.06	0.862
5	Deciduous (-), Snowfall (+), Bobcat (+)	0.94	0.07	0.06	0.870
6	Deciduous (-), Snowfall (+), Bobcat (+), Roads (+)	0.94	0.07	0.05	0.877
7	Snowfall (+)	0.92	0.07	0.09	0.840
8	Snowfall (+), Roads (-)	0.92	0.07	0.08	0.848
9	Snowfall (+), Roads (-), Bobcat (+)	0.92	0.08	0.07	0.848
10	Conifer (+), Snowfall (+)	0.92	0.06	0.10	0.847
11	Conifer (0), Snowfall (+), Roads (-)	0.92	0.06	0.10	0.847
12	Deciduous (-), Bobcat (-), Roads (-)	0.85	0.16	0.14	0.697
13	Deciduous (-), Roads (-)	0.81	0.31	0.06	0.618
14	Conifer (+), Bobcat (-), Roads (-)	0.76	0.36	0.10	0.527
15	Deciduous (-)	0.77	0.38	0.05	0.558
16	Conifer (-), Roads (-)	0.77	0.30	0.15	0.544
17	Roads (-)	0.75	0.31	0.18	0.500

Table 2.3. continued

18	Bobcat (-)	0.64	0.55	0.13	0.306
19	Conifer (+)	0.51	0.25	0.77	-0.021

[1] Signs indicate direction of effect: (+) lynx are more likely to occur with higher values of that variable, (0) no effect, and (-) lynx are less likely to occur with higher values of that variable.

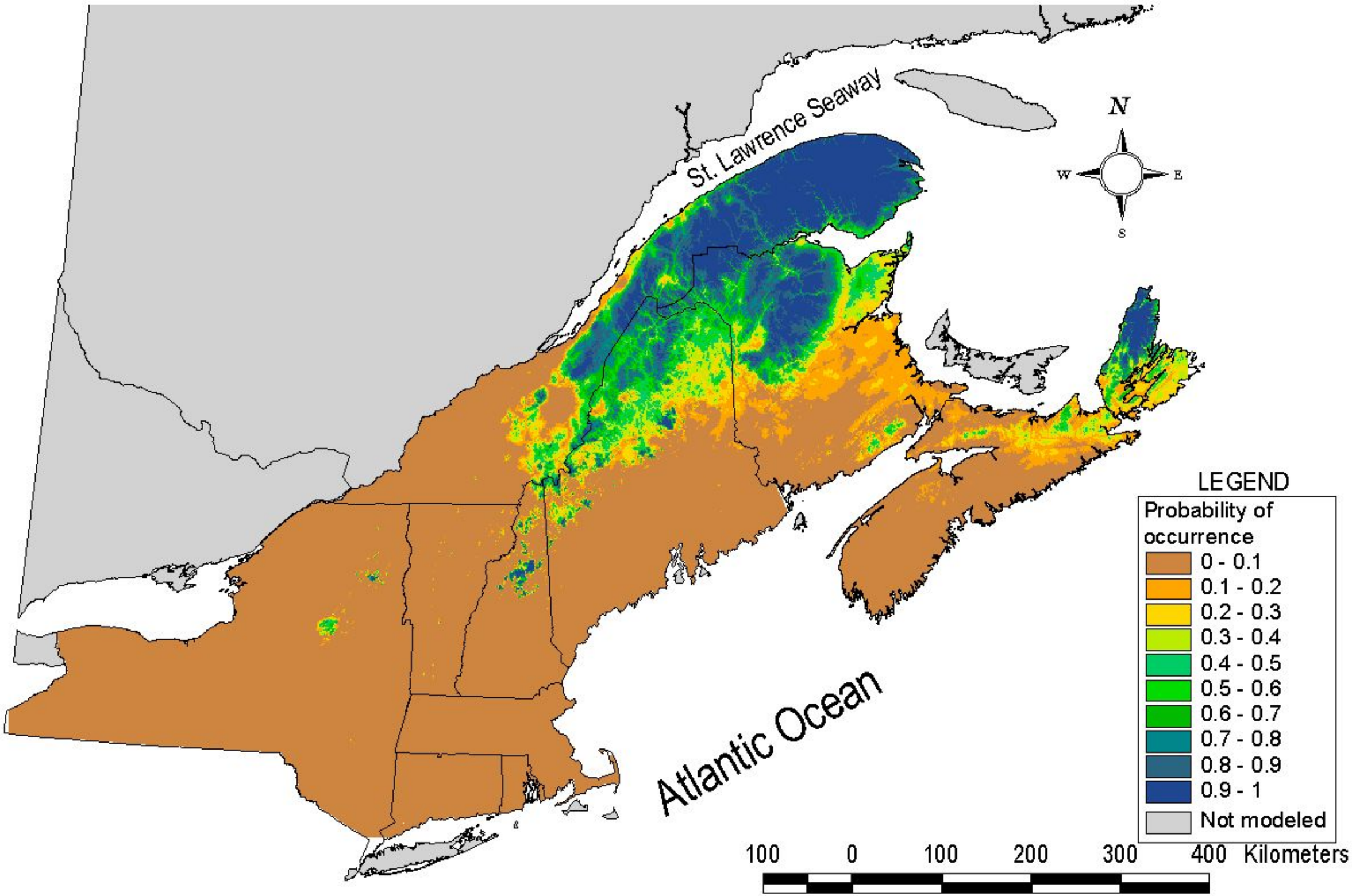

Figure 2.7. Probability of the presence of Canada lynx habitat in northeastern North America, south of the St. Lawrence Seaway, based upon a logistic regression model of mean snowfall, deciduous forest density, and coniferous forest density.

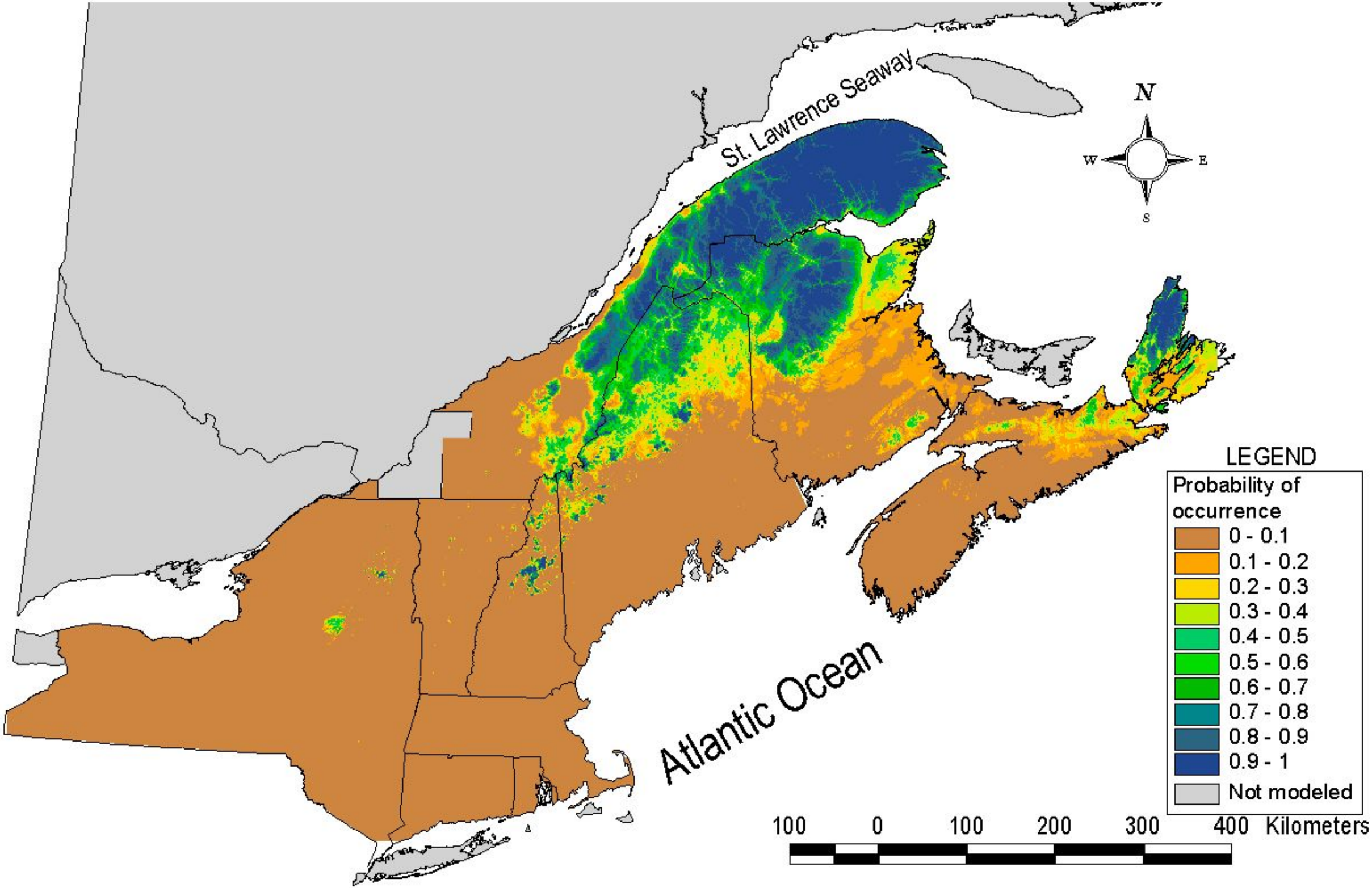

Figure 2.8. Probability of the presence of Canada lynx habitat in northeastern North America, south of the St. Lawrence Seaway, based upon a logistic regression model of mean snowfall, deciduous forest density, coniferous forest density, bobcat harvest density, and road density.

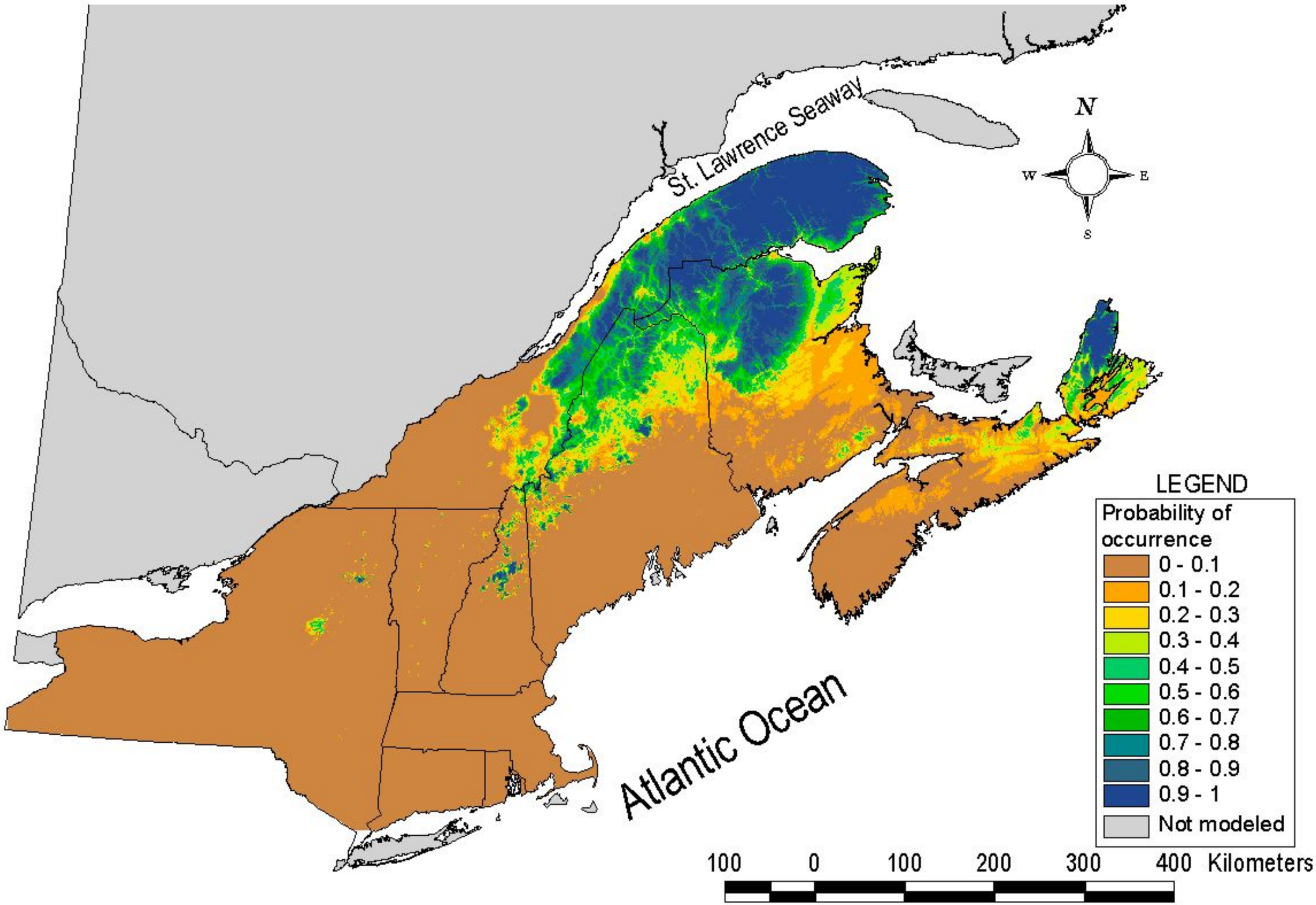

Figure 2.9. Probability of the presence of Canada lynx habitat in northeastern North America, south of the St. Lawrence Seaway, based upon a logistic regression model of mean snowfall and deciduous forest density.

The residuals (Figures 2.10 - 2.12) did not show systematic spatial patterning over the entire study area. Instead, large negative residuals (corresponding to potential habitat without lynx occurrences) were clustered on the Northumberland plateau in north-central New Brunswick, and a few large positive residuals (corresponding to lynx observed in areas with low habitat potential) occurred in southern Quebec.

DISCUSSION

Canada lynx appear to be isolated into two separate populations (Figure 2.1), although historically they probably were one. The larger population occurs along the northernmost spine of the Appalachian Mountains from the Gaspé peninsula through northwestern New Brunswick to northern and western Maine. The other population is isolated on Cape Breton Island in Nova Scotia. The broad-scale distribution of lynx in eastern North America can be predicted primarily based on snowfall and the proportion of deciduous cover.

Several biologically meaningful models could be constructed with different combinations of five variables: snowfall, deciduous cover, coniferous cover, bobcat harvest density, and road density. Models that had high McFadden's ρ^2, high predictive power, and relatively few variables also had relatively low AIC values.

When predictability was considered by state or province (Table 2.4), predictability was poorest in New Brunswick. The low CCR was driven entirely by a high proportion of false positives. The maps of residuals (Figures 2.10 - 2.12) confirmed that model fit is poor in northern New Brunswick, where the model predicted that lynx should have been present. Reasons for the apparent absence of lynx in northern New Brunswick are unknown. Canada lynx may have been present, but not observed. This part of New Brunswick has low human population densities, and has not been searched systematically for Canada lynx (G. Forbes, University of New Brunswick,

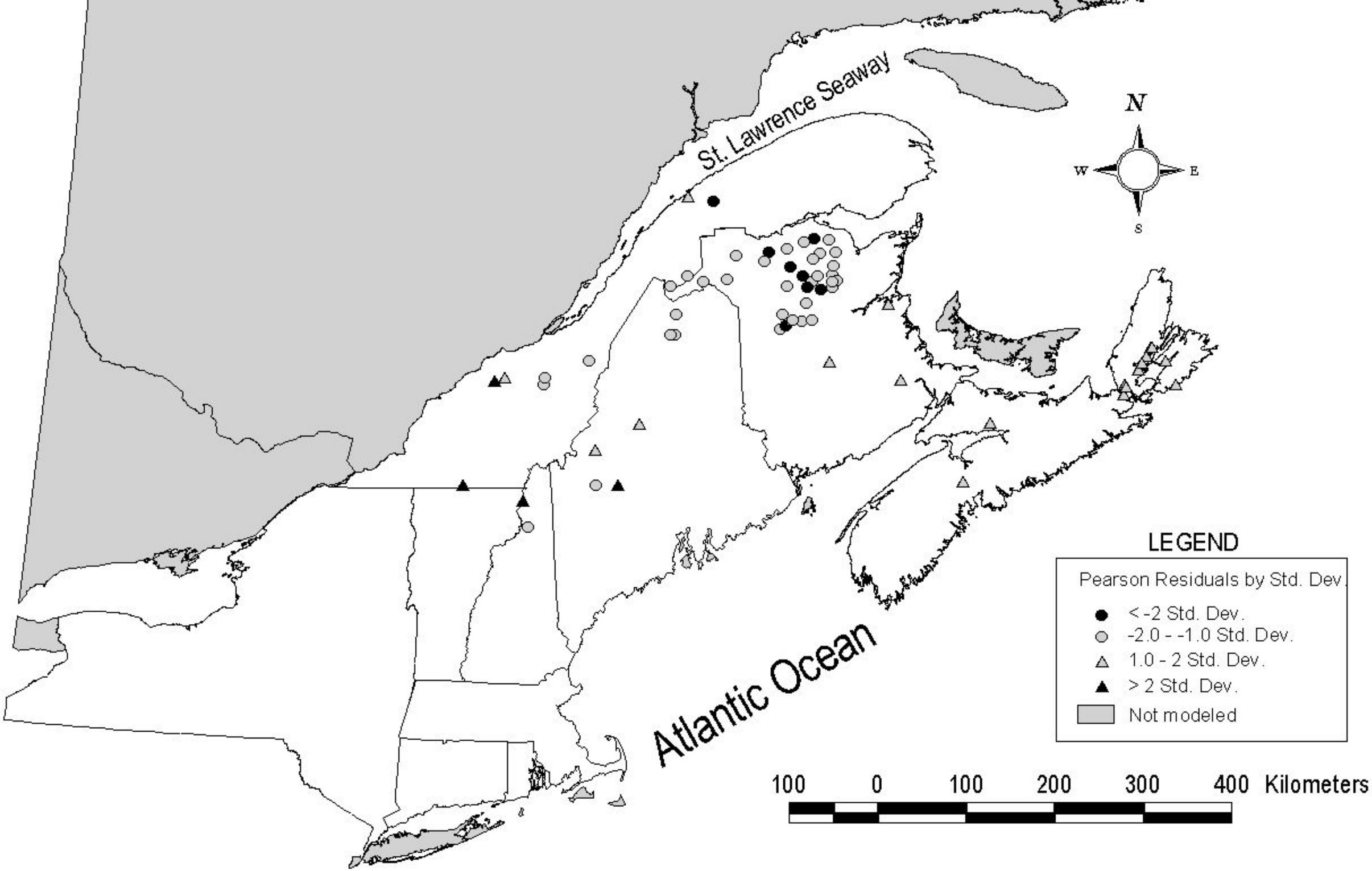

Figure 2.10. Spatial distribution of Pearson residuals of the logistic regression model of mean snowfall, deciduous forest density, and coniferous forest density. Triangles correspond to observations of Canada lynx in areas predicted to be poor habitat based on probability contours, whereas circles represent a lack of observations in areas predicted to be good habitat based on probability contours.

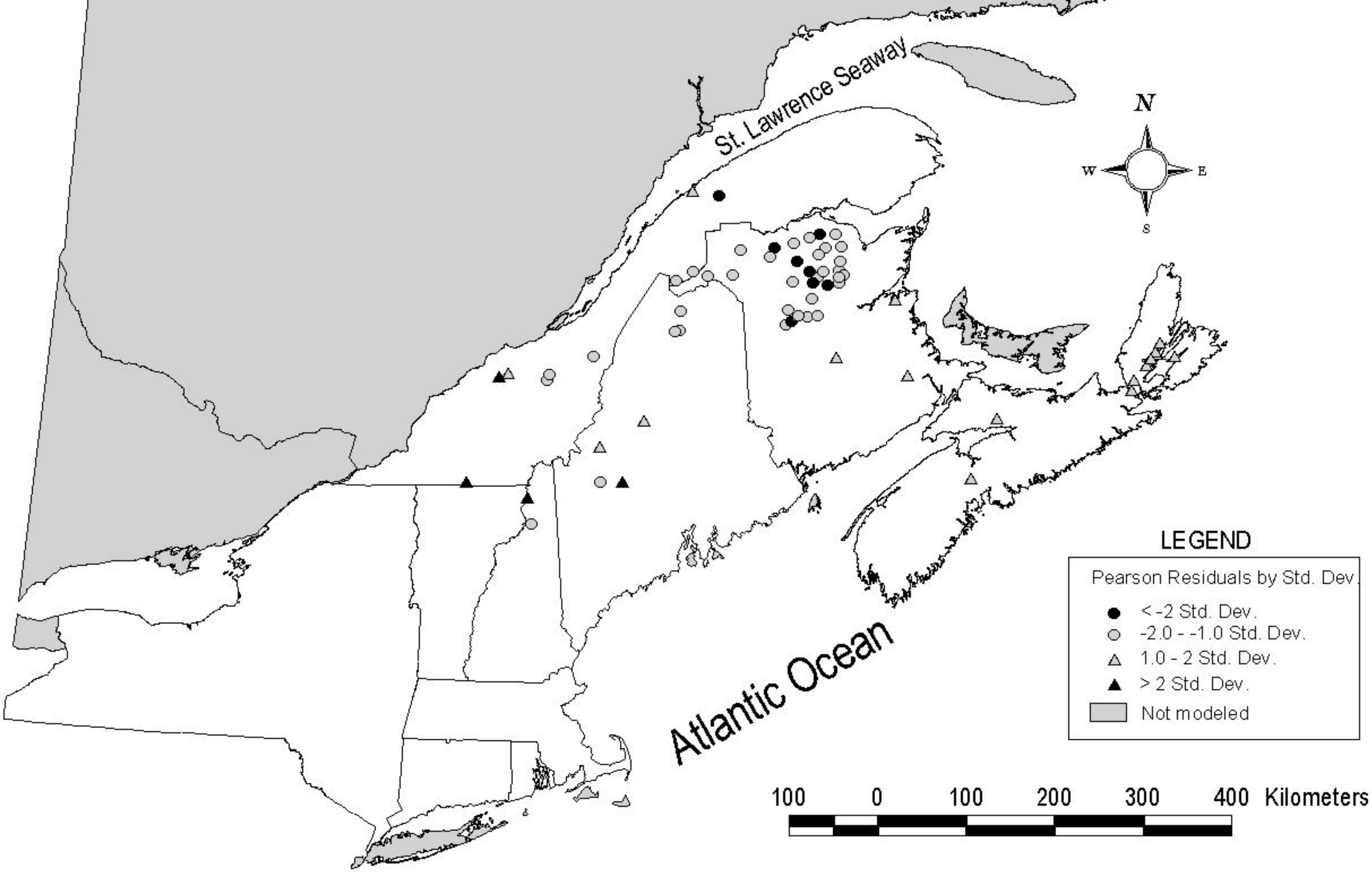

Figure 2.11. Spatial distribution of Pearson residuals of the logistic regression model of mean snowfall, deciduous forest density, coniferous forest density, bobcat harvest density, and road density. Triangles correspond to observations of Canada lynx in areas predicted to be poor habitat based on probability contours, whereas circles represent a lack of observations in areas predicted to be good habitat, based on probability contours.

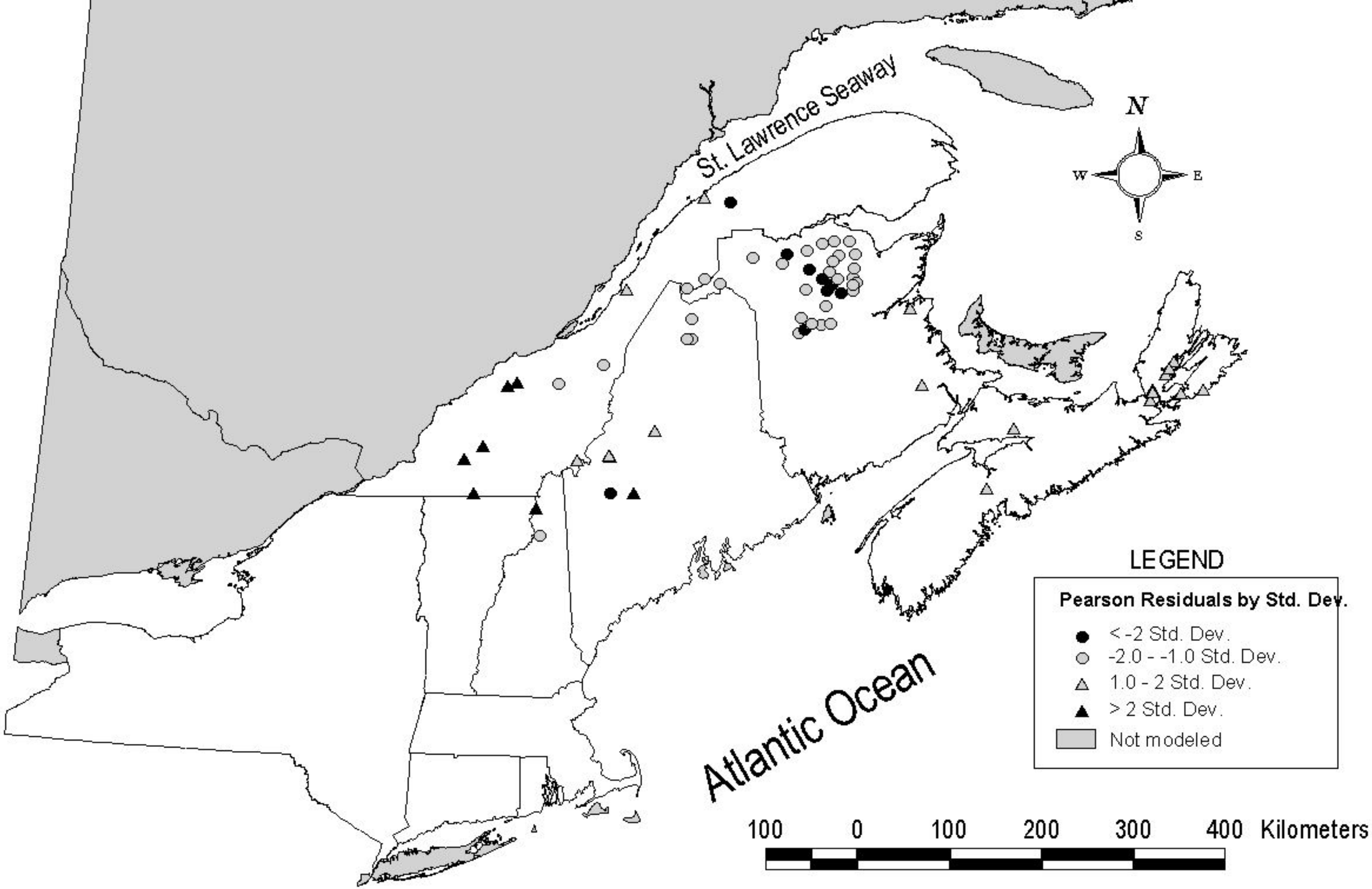

Figure 2.12. Spatial distribution of Pearson residuals of the logistic regression model of mean snowfall and deciduous forest density. Triangles correspond to observations of Canada lynx in areas predicted to be poor habitat, based on probability contours, whereas circles represent a lack of observations in areas predicted to be good habitat, based on probability contours.

Table 2.4. Model verification by state and province for the three highest ranking models (i.e. the lowest AIC scores) of Canada lynx habitat in eastern North America. Verifications were based on a building set of 2,160 (n = 1,024 presences, n = 1,136 absences) and a training set of 278 (n = 126 presences, n = 152 absences).

Model	State or Province	CCR	false positive	false negative
Deciduous, Snowfall, Conifer				
	Maine	0.86	0.07	0.43
	New Brunswick	0.82	0.19	0.00
	Nova Scotia	0.91	0.00	0.20
	Quebec	0.97	0.20	0.00
	Other states[1]	1.00	NA	0.00
Deciduous, Snowfall, Bobcat, Roads, Conifer				
	Maine	0.88	0.07	0.29
	New Brunswick	0.82	0.19	0.00
	Nova Scotia	0.91	0.00	0.20
	Quebec	0.97	0.20	0.00
	Other states[1]	1.00	NA	0.00
Deciduous, Snowfall				
	Maine	0.89	0.07	0.29
	New Brunswick	0.79	0.23	0.00
	Nova Scotia	0.94	0.00	0.13
	Quebec	0.97	0.20	0.00
	Other states[1]	1.00	NA	0.00

[1] Connecticut, Massachusetts, New Hampshire, New York, Rhode Island, and Vermont had no actual or predicted locations.

personal communication) Alternatively, lynx could have been absent because habitat was poor at finer spatial scales. The forest in this area has been extensively harvested, and regenerating forest may be too young to support adequate densities of the lynx's preferred prey, the snowshoe hare (*Lepus americanus*). A systematic survey for lynx within the high elevation areas of New Brunswick's Northumberland plateau is needed to evaluate the preceding hypotheses.

The reserved dataset included no Canada lynx presences in the states south of Maine; the CCR for this area was 100%. Some might argue that these results are trivial, and because viable lynx populations do not occur, these states should not be considered in the predictive habitat model. However, 83 lynx were reintroduced to the Adirondack region of New York, 1989-1991 (Kent Gustafson, New Hampshire Fish and Game, personal communication), where this model predicts barely enough habitat to support the hypothetical 100 km^2 home range requirements of a single lynx. Further, this area is within the historic geographic range of the lynx (Chapter 1).

Spatial dependence

Recently, there has been interest in applying spatial statistics to ecological data (Legendre and Fortin 1989, Legendre 1993), and especially to habitat models (Augustin et al. 1996). Spatial data often exhibit spatial autocorrelation or spatial dependency. Data points exhibiting spatial dependency should not be considered independent in the classical statistical sense. However, most ecological processes have a spatial component, and are to some degree spatially dependent. Removing the spatial dependence within the data would often remove the very patterns of interest to ecologists. Two types of spatial effects, often called "first-order" and "second-order" effects (Bailey and Gatrell 1995), should be considered when considering ecological processes spatially. First-order effects are the immediate processes of interest to the ecologist. Second-order effects are the spatial patterning that remains after the first-order effects have been taken into account. For example, the probability that a tree will be attacked by mountain pine-beetles (*Dendroctonus*

ponderosae) is a function of both a tree's diameter, a first order effect, and the distance to another colonized tree, a second order effect (Preisler 1993).

In the present study, the effects of deciduous cover, coniferous cover, road density, bobcat harvest density, and snowfall would be considered first-order effects. Nearly all of the spatial pattern in Canada lynx distribution can be modeled with only snowfall and deciduous cover. The residuals of the models show relatively little spatial patterning (Figures 2.10-2.12), suggesting that second-order effects were weak or non-existent. Thus, the clumped nature of lynx observations could be explained primarily from first order effects (ecological processes), and in this case it was unnecessary to model second order effects (spatial dependence) explicitly.

Bobcats and roads

Bobcat harvest density and road density were relatively poor predictors of presence and absence of lynx in northeastern North America. The predictive power of models that included these variables could be improved by leaving them out. However, because both variables did contribute to the second best model according to the AIC rankings, the effects of bobcat density and road density could not be discounted entirely.

Lynx were absent in areas where bobcat harvest was assumed zero, such as southern Quebec and western New York (n=294). However, Canada lynx were present in large numbers (n =173) on Cape Breton Island, which had some of the highest harvests of bobcats densities in the region. Harvest data for bobcats were corrected for the area of administrative units, but accessibility, harvest effort, or season length were highly variable across the region and likely biased these results. Areas with closed or severely restrict harvests were assumed to have few or no bobcats, but this was not always true. Areas such as northern New Hampshire and western Massachusetts and Connecticut are adjacent to areas of relatively high bobcat harvest in Maine and New York. As a result, the relative densities of bobcats in western Connecticut and

Massachusetts were treated as 0 in the models, which likely reduced the power of the models in detecting spatial relationships between bobcats and lynx. Thus, the variability in effort, harvest regulations, and the coarse scale of the harvest data may have masked patterns of allopatry, such as those observed by Parker et al. (1983).

Road density (Figure 2.3) was low in several areas, such as the Adirondacks and southern Nova Scotia where lynx were absent. For this reason, it was not a particularly effective predictor of lynx presence or absence. However, at least 8 Canada lynx were killed by vehicle collisions, 1987-1999 in southern Quebec, and as many as 30 were killed during the same time period on Cape Breton Island (Table 2.1). The median road density of absence points (median=0.8 km/km^2) was similar to the median road density where vehicle mortalities occurred (median=0.67 km/km^2), and much higher than the overall median road density where lynx occurred (median=0.16 km/km^2). Only 6 lynx (two of which were road-kills) occurred in areas with road densities greater than 1 km/km^2. The number of confirmed road-kills (n = 8) is too low to draw definite conclusions regarding the effect of road mortality on the population; however, these data suggest that lynx may suffer significant mortality from vehicles in areas with densities of roads > 0.67 km/km^2.

Lynx and climate change

Canada lynx are strongly affected by climate, both directly via snowfall, and indirectly on longer time scales via the effects of climate on the distribution of deciduous forests (Appendix B). Climatologists predict that we are entering a period of warming climate (Kattenberg et al. 1995), and a change in climate could result in a loss of habitat for Canada lynx in the study region via increases in deciduous forest and reduced snowfall.

Between about 1300 and the mid-1800s, the climate of the northern hemisphere cooled considerably (Lamb 1977). Forest reconstructions from pollen analyses show that pine (*Pinus* spp.) and spruce (*Picea* spp.) increased during this time (Russell et al. 1993). At the end of this period,

Canada lynx were found as far south as Pennsylvania (Audubon and Bachman 1852, Rhodes 1903, Chapter 1). A combination of changing climate and forest management caused much of the forest in this region to revert back to a largely deciduous component (Russell et al. 1993). Average snowfall over the region appears to have decreased over the same time period (Brooks 1917). The range contraction of Canada lynx in eastern North America during the late 1800s through early 1900s coincides roughly with past changes in snowfall and the character of the forest in this region (Chapter 1).

Lynx appear to be sensitive to the direct and indirect effects of climate and climate change. This could have serious implications for the future of Canada lynx in the eastern USA if the climate continues to warm. The effect of changing climate on the future distributions of tree species has been modeled for the eastern USA, given several predictions of future climate (Prasad and Iverson 1999). Under several predicted future climate regimes, Maine would likely be comprised of more deciduous forest than currently exists.

Models to predict future climate in the face of increasing CO_2 are equivocal regarding changes in precipitation (Kattenberg et al. 1995); however, increasing temperatures would probably cause a larger proportion of precipitation to fall as rain and less as snow. When snowfall is considered independent of deciduous forest, lynx were unlikely to occur in areas with a 10-year mean annual snowfall of less than 268 cm. The sensitivity of the logistic regression model that incorporated snowfall and deciduous forest to realistic changes in snowfall was explored. I projected future habitat based on the snowfall from 1970-1980 (Figure 2.13). In the context of the past four decades, the 1970s were unusually snowy, and the 1980s had relatively little snow (snowfall for 2000 had not yet been compiled for the USA and Canada at the time this thesis was written). The difference in snowfall between these decades represents a large, but possible,

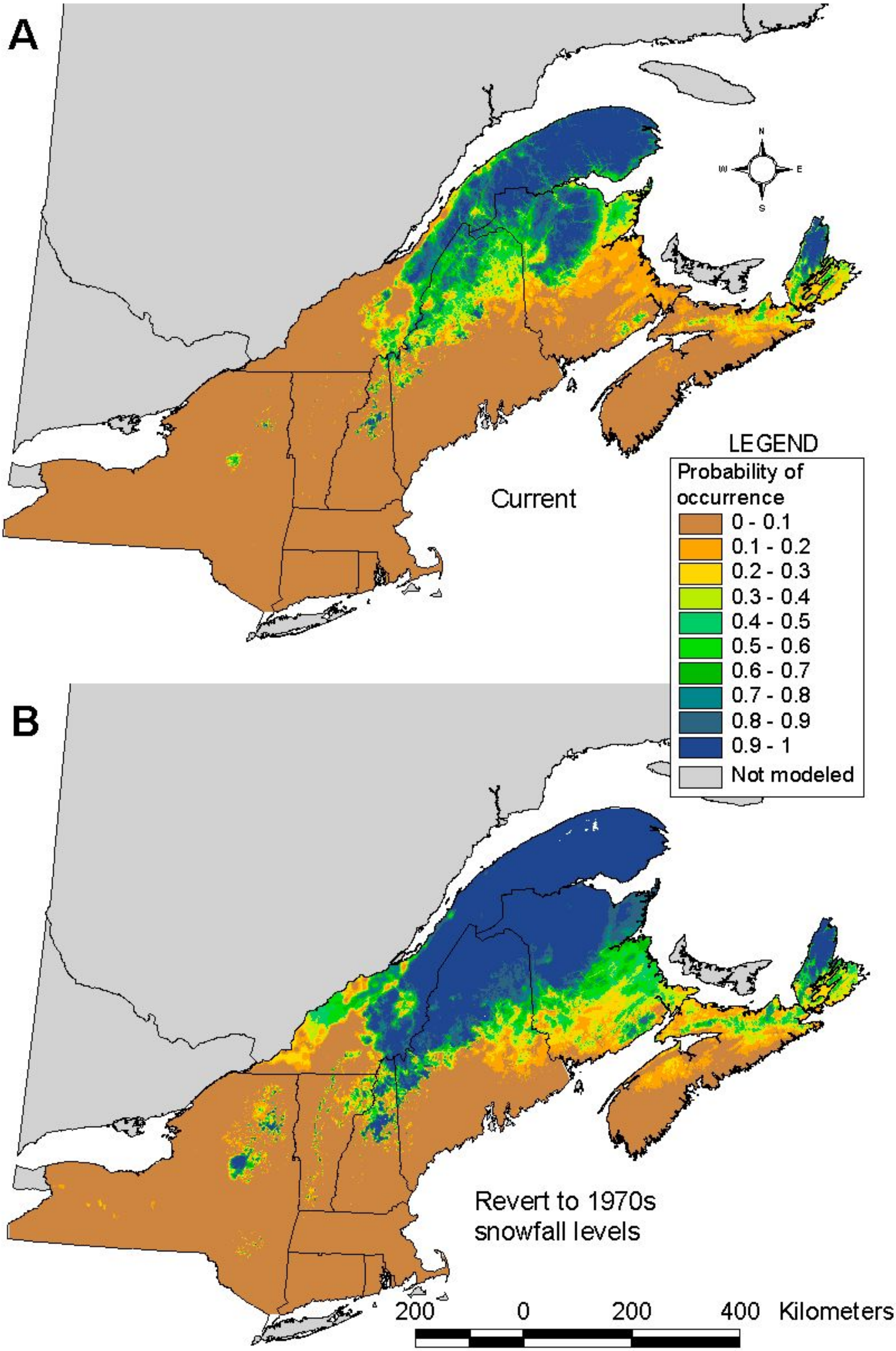

Figure 2.13. Projection of Canada lynx habitat assuming (A) future snowfall levels do not change but remain at the 1980-1990 level, and (B) future snowfall levels increase back to 1970-1980 levels.

change in snowfall over a 10-year period. This difference in observed snowfall between the 1970s and 1980s (along with half the difference and twice the difference) was used to project the effect of possible warming into the future (Figure 2.14). If snowfall decreased from 1980s levels by the same amount as the decrease from the 1970s to the 1980s (scenario B in Figure 2.14), essentially no Canada lynx habitat would remain in the eastern USA. A larger change in snowfall could restrict Canada lynx habitat largely to Cape Breton Island (scenario C in Figure 2.14). Populations of Canada lynx in the northeastern North America are relatively isolated. The Atlantic Ocean is an absolute barrier to dispersal to the north on the Gaspé peninsula and Cape Breton Island. Based on these projections, climate change could have serious effects on future distributions of lynx in this region. However, it should be stressed that these are not predictions based on models of future climate. They are projections of future habitat given changes in snowfall observed during the recent past. Nevertheless, the sensitivity of the models in response to climate change was striking.

CONCLUSIONS

The habitat of lynx at the regional scale can be modeled with good predictive power using only two variables: snowfall (a positive association) and proportion of an area in deciduous cover (a negative association). Lynx were most likely to occur in areas with greater than 268 cm of mean annual snowfall. Given recent snowfall and forest patterns, the model accurately predicts a concentration of suitable habitat on Cape Breton Island and the Gaspé Peninsula, extending into northern New Brunswick and Maine. Little potential habitat currently occurs in the eastern United States outside of Maine. This model is sensitive to potential changes in climate. The geographic range of the Canada lynx likely shifted in the past with changes in climate, and could contract significantly if the climate warms in the future. Climatic changes could result in the elimination of suitable habitat south of the USA-Canada border and the demographic isolation of populations on the Gaspé peninsula and Cape Breton highlands.

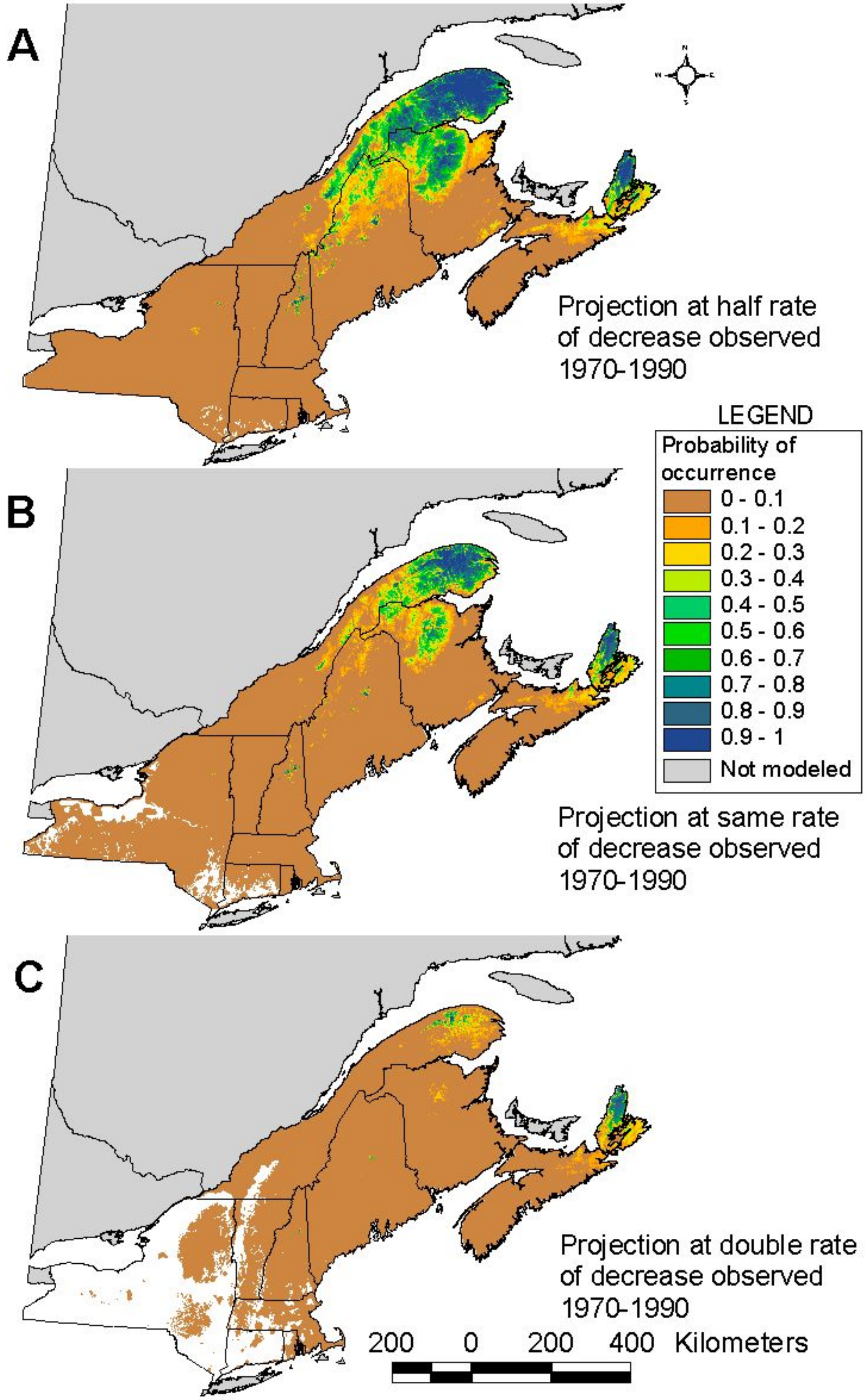

Figure 2.14. Projection of Canada lynx habitat assuming (A) future snowfall levels decrease at ½ the rate of change between the 1970s and 1980s, (B) future snowfall levels decrease at a rate equal to the rate of change between the 1970s and 1980s, and (C) future snowfall levels decrease at twice the rate of change between the 1970s and 1980s.

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CHAPTER 3

HABITAT RELATIONSHIP MODELS FOR SNOWSHOE HARES IN NORTHWESTERN MAINE

INTRODUCTION

Habitat relationships of snowshoe hare (*Lepus americanus*) in Maine have been well documented at the stand scale. Hares are most abundant in areas of high stem densities and low overhead canopy closure (Litvaitis et al. 1985, Monthey 1986, Long 1995, Lachowski 1997, Fuller 1999), and the highest stem densities in Maine usually occur in areas of regenerating forest (Monthey 1986, Fuller 1999). Based on pellet surveys conducted in north-central Maine, snowshoe hare densities were highest in regenerating forest (1.61 hare/ha, SE = 1.00), lower in mature conifer forest (0.09 hare/ha, SE = 0.04), and lowest in mature deciduous and partial harvest stands (0.01 hare/ha, SE = 0.01 and SE = 0.0, respectively) (Fuller 1999).

Modeling is a useful and increasingly common way to describe a species' relationships to habitat (Turner et al. 1995, Morrison 1998). Most models describe occurrence as a function of several descriptive habitat variables that vary spatially. Spatial models often assume that habitat and species' relationships to habitat do not change through time. This assumption is realistic when changes in the habitat and species populations are small relative to the duration of the study, but is not tenable for species whose densities are known to fluctuate dramatically, such as snowshoe hare (Krebs et al. 2001).

The population cycles of snowshoe hare and Canada lynx (*Lynx canadensis*) have been well documented in the boreal forests of Canada and Alaska (Elton and Nicholson 1942, Keith 1966, Brand et al. 1976, Mowat et al. 1996). The cycle is exceptional both for its synchrony over a large geographic area and its relatively regular periodicity of 8 to 11 years (Keith 1963, Blasius et

al. 1999, King and Schaffer 2001). The cycle results from both predator-prey and prey-vegetation interactions (Krebs 1996, Keith 1990, King and Schaffer 2001), and the synchrony of the cycle seems related to climatic fluctuations, such as the North Atlantic Oscillation (Stenseth et al. 1999). Traditionally, snowshoe hare populations were thought not to cycle at the southern extent of their range (Wolff 1981). A recent meta-analysis, however, suggests that hare populations near the southern limit of their range, such as those in Maine, may cycle synchronously with those in northern latitudes, but with dampened amplitude relative to northern cycles (Hodges 2000). Though suggestive, without a standardized survey that spans several decades, the presence of a cycle in Maine cannot be determined with certainty.

Changes in population density, including population cycles, can affect species habitat models in many ways (Table 2 in Krohn 1996). Models constructed at low population densities may have poorer long-term predictive power than those developed on populations at higher densities (Johnson and Krohn, *In press*). The direction of model coefficients can even reverse as population densities change through time (O'Connor 1986). The effects of population density on habitat models have often been seen as confounding effects to be avoided (Van Horne 1983), but insofar as dynamic changes in habitat associations are real, they can provide biological insights.

Understanding habitat relationships of snowshoe hare is a prerequisite to understanding habitat relationships of lynx (Chapter 4). Canada lynx prey primarily on snowshoe hare (van Zyll de Jong 1966, Parker et al. 1983, Koehler 1990). Secondary prey, such as red squirrels (*Tamiasciurus hudsonicus*), are somewhat important at lows in the hare population cycle and at the southern edge of their range, but hare dominate the diet of lynx even when or where hares are scarce (Table 13.1 in Aubry et al. 2000).

Patterns of habitat selection by hare at the stand scale cannot be assumed to apply at the statewide scale. The primary objective of this study was to model relative densities of hare in

response to coarse-grained habitat associations at a resolution of 19 ha within Maine to facilitate understanding of the spatial distribution of Canada lynx in northwestern Maine (Chapter 4). Because temporal effects were strong in the model, a secondary objective was developed to explore the affects of increasing population densities of snowshoe hare on the results derived from habitat models.

METHODS

Track surveys

Beginning in December 1994, the Maine Department of Inland Fisheries and Wildlife (MDIFW) conducted an annual statewide survey of medium-size mammals based on snow-tracks. Private contractors and biologists used snowmobiles to survey for the presence or absence of tracks of bobcat (*L. rufus*), marten (*Martes americana*), and fisher (*M. pennanti*) on each 1 km segment of transect. Further, the relative number of snowshoe hare tracks per 1 km transect were also recorded as absent (zero tracks), rare (1-5 tracks), common (6-19 tracks), or abundant (<20 tracks). Data sheets had entries for observer, date, township, number of nights of tracking conditions, and animal traveling and detectability criteria (e.g., temperature, crusting conditions.) Most observers recorded the geographic location of each transect on copies of maps (usually from the *Maine Atlas and Gazatteer*, Anonymous 1993) at a scale of 1:125,000. For this analysis, November or December of year x-1 were combined with year x of January through April to reflect one complete winter season. For example, data from the winter of 1994-1995 was reported as "1995."

Additionally, surveys were conducted specifically for Canada lynx and wolf (*Canis lupus*) tracks in northern and western Maine. The methodology for these transects was only slightly different; they were not always conducted in the same place each year, and those conducting the surveys were trained to distinguish likely lynx and wolf tracks from other felids and canids known to

occur in northern Maine. The data on relative abundance of snowshoe hare from these transects were combined with data from the standard furbearer track surveys.

Data sheets that included maps were incorporated into a Geographic Information System (GIS) (ArcInfo, ESRI, Redlands, California, USA; use of trade names does not imply endorsement) using heads-up digitizing. “Heads-up” digitizing is a method to digitize on the computer screen, in this case with satellite imagery, and base coverages of roads, hydrographic features and townships in the background. Because most transects were conducted on roads, I used a statewide mosaic of the United States Geological Survey (USGS) Digital Line Graphs (DLG) at 1:24,000 scale for a base coverage. The hydrographic DLG layers and township outlines from the Maine Office of GIS were used to increase precision when locating transects. Landsat Thematic Mapper (TM) imagery was used to trace the few roads that could not be located in the USGS DLGs. Transects that did not follow any discernable route on the DLG or TM imagery were omitted from analyses.

Because snowmobile odometers were seldom accurate (e.g., tracks often slip in soft snow), transects were divided into the correct number of segments rather than the correct number of kilometers. For example, a transect of 8 km with 10 segments would have been divided into 10 segments of 0.8 km in length. Segments greater than 1.5 km or less than 0.5 km were omitted from analysis. For each segment of transect, the proportion of each vegetation type within 190 m of the transect segment was calculated.

The Maine Vegetation and Land Cover map (Hepinstall et al. 1999) was used to determine vegetation characteristics surrounding each segment. This map, at a 1:100,000 scale, was based on a classification of TM satellite imagery from 1991 and 1993, and the map was resolute to a grid of 30 m^2 cells. The map contained 37 vegetation types. A relatively small subset of types were considered likely to describe snowshoe hare habitat, and many vegetation types (e.g., coastal, agricultural, and urban types) were not present in parts of Maine that were surveyed. The

vegetation types considered likely to describe hare habitat were recent clearcut, early regeneration, late regeneration, heavy partial harvest, mature deciduous forest, mature conifer forest, and forested wetland. Recent clearcut areas were generally harvested between 1991 and 1993, and contained little vegetation biomass. Early regeneration was generally clearcut prior to 1991, and had less than 50% canopy closure in 1993. Similarly, late regeneration was generally clearcut prior to 1991, but had greater than 50% canopy closure in 1993. Heavy partial harvest corresponded to a variety of silvicultural practices including improvement thinning, shelterwood, and selection harvest. Deciduous species contributed to greater than 75% of the dominant cover in the mature deciduous forest type, and conifer species contributed to greater than 75% of the dominant cover in the mature conifer forest type.

The vegetation types were not developed from maps of known stand histories. Thus, with the exception of clearcuts, the harvest classes did not represent stands of known age. The differences between early and late regeneration, for example, are structural and represent differences in biomass and reflectance patterns. Although the harvest classes correspond to interpreted aerial videography (see Hepinstall et al. 1999 for details on accuracy), the exact age and specific method of harvest were not available.

Wetlands were incorporated into the Maine Vegetation and Land Cover map directly from the U.S. Fish and Wildlife Service National Wetlands Inventory (Hepinstall et al. 1999). Four forested wetland categories (deciduous forested, coniferous forested, deciduous scrub-shrub, and coniferous scrub-shrub) from the Maine Vegetation and Land Cover map were combined into one forested wetland vegetation type.

Habitat models

I used logistic regression (Hosmer and Lemeshow 1989, Agresti 1996) and an information-theoretic approach (Burnham and Anderson 1998, Anderson et al. 2000) to model snowshoe hare

habitat in Maine. The information-theoretic approach is an alternative to null hypothesis testing that ranks several models, based on their approximation of reality, rather than test the null hypothesis that snowshoe hares do not respond to the habitat characteristics measured. Previous studies (Litvaitis et al. 1985, Monthey 1986, Long 1995, Lachowski 1997, Fuller 1999) have established that clearcuts, regenerating forest, partial harvests, forested wetlands, mature deciduous forest, and mature coniferous forest are likely to affect densities of snowshoe hare. Therefore, null hypothesis tests would not be likely to provide new information. A more interesting question is which combination of the above variables (e.g., which model) best describes snowshoe hare associations. Using the information-theoretic approach, models can be ranked using Akaike's Information Criterion (AIC) (Akaike 1973, Burnham and Anderson 1998), which balances goodness-of-fit and simplicity. The AIC of different models (i.e. different combinations of variables) constructed on the same data were compared. Models with low AIC provide the best trade-off of good fit with the fewest variables. A common way to rank models is to compare all models to the model with the lowest AIC by the equation: $\Delta AIC_i = AIC_i$ – minimum AIC. As "a general rule of thumb" models with the lowest overall AIC and ΔAIC values less than 2 can be considered "best" and equivalent (Burnham and Anderson 1998).

The vegetation classes from the Maine Vegetation and Land Cover map did not correspond exactly with vegetation classes considered in previous studies. Regeneration in Fuller's (1999) study might correspond with late regeneration, early regeneration, or both when classified from remotely sensed satellite imagery. Therefore, three combinations were considered in addition to types on the Maine Vegetation and Land Cover map: early and late regeneration were also considered combined as a regeneration class; light and heavy partial cut were combined into partial harvest; and four categories of wetland (deciduous forested, coniferous forest, deciduous scrub-shrub and coniferous scrub-shrub) were combined into one forested wetland type.

In the information-theoretic approach the combinations of variables that constitute the set of models considered are selected relying on inferred knowledge of the system from other scientific studies (Burnham and Anderson 1998). Extensive exploratory analysis to select variables (often called “data-dredging”) can invalidate the information-theoretic approach by picking up spurious relationships. In this analysis variables were screened with a univariate test, not to select variables, but to remove from consideration those variables that were unlikely to contribute to the multivariate models. Most variables were proportions, and deviated greatly from the normal distribution, even after arc-sine transformations. Therefore, a nonparametric Kruskal-Wallis was used to detect differences among the four abundance categories. A generous P value of 0.2 was used to screen variables.

Hare abundance was recorded on an ordinal scale. Methods exist to incorporate ordinal scale dependent variables (such as absent, rare, common, and abundant) into a multinomial or ordinal logistic regression (Agresti 1996), but these models were unable to correctly classify the two middle classes of hare abundance. Thus, segments with abundant hares were compared to segments with no hare tracks using a traditional logistic regression model (Hosmer and Lemeshow 1989) in SYSTAT 9.0 (SPSS Inc. Chicago, Illinois, USA). Because year effects were strong, the data were subset by year, and models were developed for each year. AIC rankings are only valid for models using identical data (Burnham and Anderson 1998). Therefore, models were ranked within year, but not among years.

RESULTS

Track surveys

Between 1995 and 1999, MDIFW surveyed roughly 7,335 segments of transects throughout northern and central Maine (Figure 3.1). For several reasons (missing map, transect start unrecorded, roads could not be located) only 4,079 km of transect representing 4,336

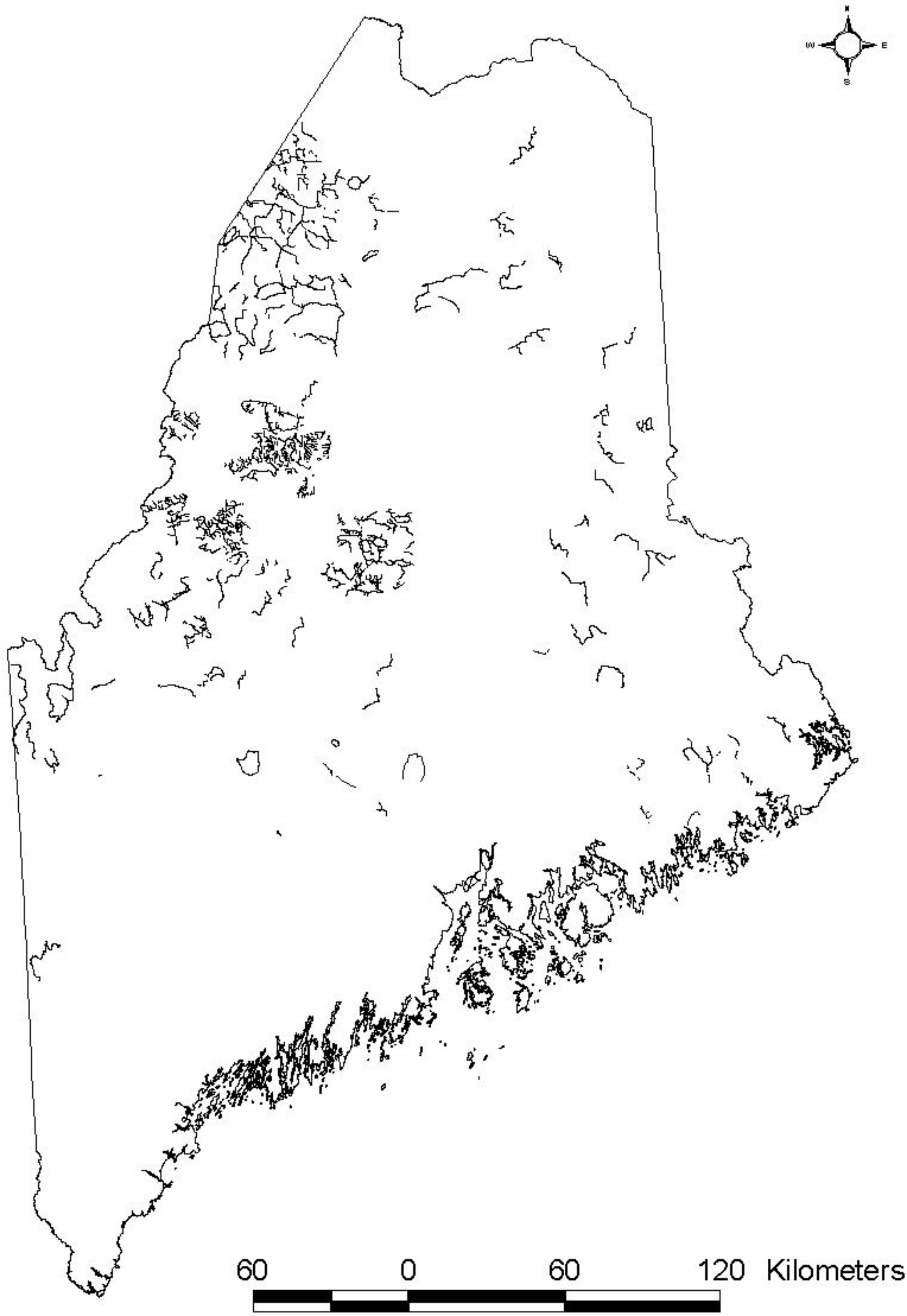

Figure 3.1. Locations of snow-track transect routes used to index relative abundance of snowshoe hares in Maine, 1995-1999 (excluding routes surveyed in 1997).

segments (59% of the total) were digitized. Actual segment lengths varied from 0.5 km to 1.5 km, likely because odometers on snowmobiles were inconsistent in different snow conditions. Most transects that were surveyed repeatedly had differing numbers of segments each year so that individual segments could not be compared through time. Only 600 km (14.7% of survey routes) of transects representing 637 segments were surveyed repeatedly across years, which precluded meaningful analysis of individual segments through time.

Habitat models

The population of snowshoe hare appears to have increased from 1996 to 1999 (Figure 3.2). The proportion of transects on which hares were absent decreased by 66%, while the proportion on which hares were abundant increased by 404%. Because of the change in abundance though years, separate models were developed for each year with the exception of 1997, which was omitted because sampling effort was too low (less than half the number of transects digitized compared with previous and subsequent years). In 1997, the number of transects classified as “abundant” hare was only 14, which was an insufficient sample for modeling purposes.

Based on *a priori* knowledge of snowshoe hare habitat associations in Maine, 14 vegetation types or combinations of vegetation types from the Maine Vegetation and Land Cover map were chosen as likely to contribute to a statewide snowshoe hare model. The year of the survey and 3 other variables relating to detectability (snow depth on transect, temperature during survey, and the number of nights since last snowfall) were also considered. Univariate screening resulted in 14 variables with P-values < 0.2 (Table 3.1). Despite the apparent relationship of temperature (P = 0.089) and nights since last snowfall (P < 0.0001) with the recorded abundance of hares, these 2 variables were recorded on too few transects to include in subsequent modeling. The combination of the two regeneration categories was not used, because early regeneration had

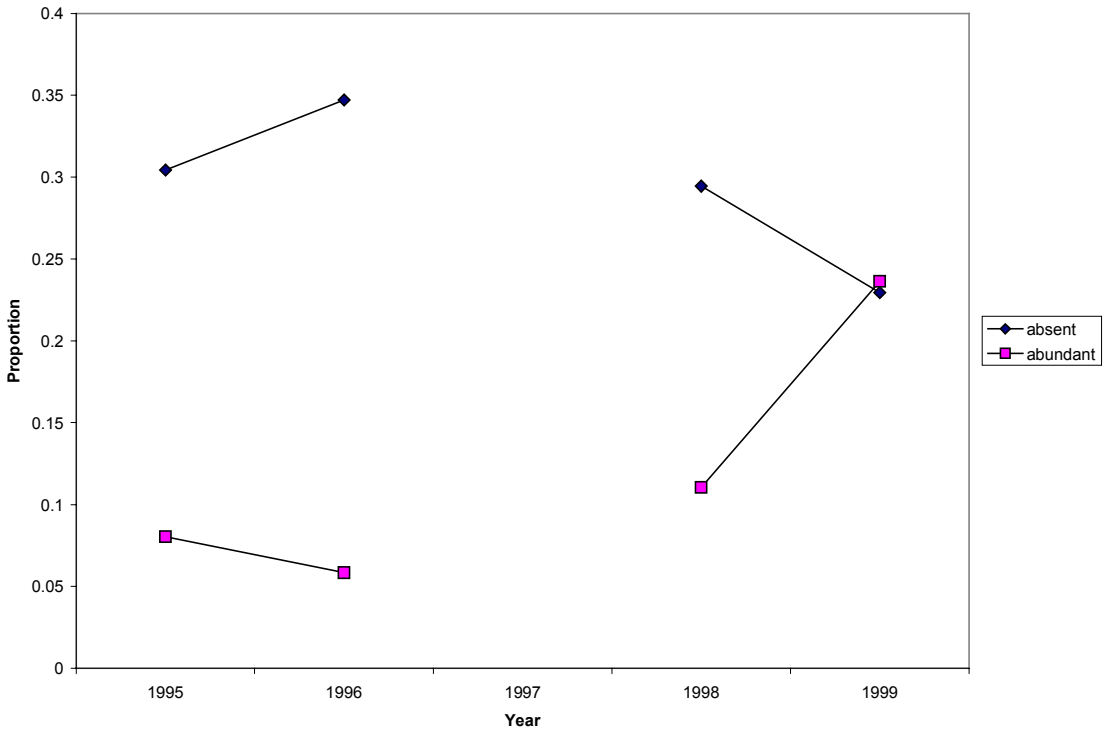

Figure 3.2. Proportions of transect segments on which snowshoe hare tracks were categorized as abundant and as absent during winters 1995-1999. Because of low sampling effort (less than 1000 km of transect surveyed) and difficulty digitizing 1997, only 346 segments were available, and only 14 were classified as abundant; therefore, data for 1997 were excluded.

Table 3.1. Mann Whitney U Test statistics for potential explanatory variables to include in a logistic regression model describing relative abundance of snowshoe hares in Maine. Variables with P < 0.2 that were recorded on a majority of transects were subsequently modeled using logistic regression.

Variable	N	Mann Whitney U	P	Association
Year	1,477	146206	0.000	+
Nights of tracking conditions	649	33715	0.000	+
Late Regeneration	1,477	175572	0.000	+
Late and early regeneration combined	1,477	172771	0.000	+
Forested Wetland	1,477	169809	0.000	+
Mature Deciduous	1,477	235817	0.000	-
Coniferous forested wetland	1,477	176473	0.000	+
Deciduous scrub-shrub wetland	1,477	181274	0.000	+
Heavy Partial Cut	1,477	228027	0.002	-
Early Regeneration	1,477	186150	0.003	+
Deciduous forested wetland	1,477	196190	0.007	+
Temperature on transect	826	71594	0.089	-
Clearcut	1,477	226135	0.010	-
Light and heavy partial cut combined	1,477	216933	0.122	-
Snow depth above crust	853	63719	0.219	n/a
Light Partial Cut	1,477	201984	0.444	n/a
Mature Conifer	1,477	200698	0.537	n/a
Coniferous scrub-shrub wetland	1,477	204928	0.623	n/a

the opposite effect of late regeneration. The combined (light and heavy) partial harvest variable was not included because light partial harvest did not appear to affect hare abundance (P = 0.444); however, heavy partial harvest (P = 0.002) was retained for multivariate modeling. The forested wetland types were combined because they are scarce on the landscape and the combination of the 3 sub-types had the lowest Mann-Whitney U test statistic (Table 3.1). The remaining 6 variables were not correlated (Pearson r < 0.4) and were considered for inclusion in multivariate models (Table 3.1).

After *a priori* consideration of the combinations of variables that would be the most likely to explain snowshoe hare habitat, five alternative models were chosen for statistical evaluation. The first model was the global model incorporating all six variables: late regeneration, early regeneration, clearcut, heavy partial harvest, mature deciduous forest, and forested wetland. Another model was similar to the global model, but did not incorporate clearcut, because some clearcuts may have matured into early regeneration during the duration of the snow-tracking study. Another model eliminated both clearcut and early regeneration because of potential effects of these types maturing during the study. A third model incorporated only late regeneration and partial harvest, which were the habitats with the highest and lowest hare densities from Fuller (1999). Another model considered only the effects of mature deciduous cover and late regeneration, the two habitats with the extremes in stem densities as reported by Monthey (1986). The final model consisted of only mature deciduous cover and forested wetlands; this model was considered as an alternative to the model that incorporated deciduous cover and late regeneration. These 6 models were analyzed for each year, and for a combined across-years analysis (30 models total).

In the majority of the models, snowshoe hare abundance was positively associated with late regeneration and forested wetlands, and negatively associated with mature deciduous forest and heavy partial harvest. Recent clearcut and early regeneration had a weaker, and usually

negative affect on the models (Appendix C). The magnitude and precision of the effects of each variable were different among years, and thus relative AIC ranks changed through time (Table 3.2).

Variables were consistent in the direction of the effect that they had in different years. Even when variables were not significant at a P value of 0.05, most coefficients retained the same sign (Table 3.3). Transects with high proportions of recent clearcut, early regeneration, heavy partial cut, and mature deciduous forest were consistently more likely to have no snowshoe hares; whereas transects with high proportions of late regeneration or forested wetland were more likely to have abundant hares.

Patterns of habitat association changed through time as hare density increased (Table 3.3). In 1995, when hares were absent from many transects, only positive associations were significant ($P < 0.05$) and negative associations were not significant ($P > 0.05$). Both positive and negative associations were significant ($P < 0.05$) in 1996 and 1998. When hare densities were relatively high in 1999, negative habitat associations were significant ($P < 0.05$) and positive associations were not significant ($P > 0.05$) (Table 3.3).

Most models were significantly different than a null model, but had relatively low to moderate goodness of fit and predictive power (Table 3.2). However, the McFadden's ρ^2, roughly comparable to the r^2 of linear regression models (McFadden 1974), was low for all models in all years. A McFadden's ρ^2 of 0.2 is generally considered satisfactory, and only in 1998 did models even approach that level ($\rho^2 = 0.18$). Another measure of goodness-of-fit is the Hosmer-Lemeshow P statistic, which evaluates how well models fit the logistic (Hosmer and Lemeshow 1989). Most models (except some in 1998) had moderate to poor fit ($P = 0.007 – 0.485$).

The goodness of fit of models changed through time with density. McFadden's ρ^2 was low in 1995 and 1996 when hare were absent on a large proportion of transects, but McFadden's ρ^2 increased in 1998 when hare were moderately abundant, and then decreased in 1999 when hare

Table 3.2. Performance of logistic regression models describing snowshoe hare habitat in Maine, based on McFadden's ρ^2, Hosmer-Lemeshow P, sensitivity, specificity, AIC and ΔAIC statistics. Vegetation types[1] were derived from the Maine Vegetation and Land Cover map (Hepinstall et al. 1999).

Year	Model	McFadden's ρ^2	Hosmer-Lemeshow P	Sensitivity	Specificity	AIC	ΔAIC
1995	DEC, LREG, EREG, HPART, FWET	0.11	0.007	0.301	0.861	385.07	0.0
1995	DEC, LREG, HPART, FWET	0.105	0.091	0.297	0.814	385.39	0.3
1995	CLEAR, DEC, LREG, EREG, HPART, FWET	0.113	0.031	0.305	0.816	385.99	0.9
1995	DEC, LREG, HPART	0.066	0.022	0.263	0.806	399.38	14.3
1995	DEC, LREG	0.058	0.025	0.26	0.805	400.93	15.8
1995	DEC, FWET	0.03	0.357	0.237	0.799	412.52	27.4
1996	DEC, LREG, HPART, FWET	0.127	0.265	0.236	0.871	266.95	0.0
1996	DEC, LREG, EREG, HPART, FWET	0.127	0.228	0.237	0.872	268.80	1.8
1996	CLEAR, DEC, LREG, EREG, HPART, FWET	0.128	0.232	0.237	0.872	270.65	3.7

Table 3.2 *continued*

Year	Model	McFadden's ρ^2	Hosmer-Lemeshow P	Sensitivity	Specificity	AIC	ΔAIC
1996	DEC, LREG, HPART	0.08	0.45	0.189	0.863	278.04	11.1
1996	DEC, LREG	0.036	0.261	0.162	0.859	289.45	22.5
1996	DEC, FWET	0.088	0.192	0.212	0.867	299.89	32.9
1998	DEC, LREG	0.163	0.958	0.401	0.775	202.15	0.0
1998	DEC, LREG, HPART	0.167	0.983	0.403	0.776	203.24	1.1
1998	DEC, LREG, EREG, HPART, FWET	0.18	0.462	0.411	0.779	204.36	2.2
1998	DEC, LREG, HPART, FWET	0.168	0.85	0.403	0.776	205.08	2.9
1998	CLEAR, DEC, LREG, EREG, HPART, FWET	0.18	0.324	0.412	0.779	206.35	4.2
1998	DEC, FWET	0.113	0.372	0.354	0.758	213.75	11.6
1999	DEC, LREG	0.092	0.562	0.565	0.554	433.55	0.0

Table 3.2 *continued*

Year	Model	McFadden's ρ^2	Hosmer-Lemeshow P	Sensitivity	Specificity	AIC	ΔAIC
1999	DEC, LREG, HPART	0.095	0.477	0.567	0.556	434.22	0.7
1999	CLEAR, DEC, LREG, EREG, HPART, FWET	0.105	0.073	0.575	0.562	436.39	2.8
1999	DEC, FWET	0.086	0.126	0.563	0.55	437.69	4.1
1999	DEC, LREG, EREG, HPART, FWET	0.095	0.019	0.569	0.556	439.37	5.8
1999	DEC, LREG, HPART, FWET	0.089	0.485	0.565	0.552	439.96	6.4
ALL[2]	DEC, LREG, HPART, FWET	0.049	0.142	0.319	0.738	1443.4	0.0
ALL	CLEAR, DEC, LREG, EREG, HPART, FWET	0.052	0.062	0.321	0.739	1443.7	0.3
ALL	DEC, LREG, EREG, HPART, FWET	0.05	0.052	0.32	0.738	1444.1	0.6
ALL	DEC, LREG, HPART	0.04	0.127	0.31	0.735	1455.7	12.3
ALL	DEC, LREG	0.029	0.402	0.302	0.731	1469.4	26.0
ALL	DEC, FWET	0.025	0.776	0.298	0.73	1476.6	33.2

Table 3.2 *continued*

[1] DEC = Mature deciduous forest.

LREG = Late regeneration forest harvested before 1991, sapling to poletimber with greater than 50% canopy closure.

EREG = Early regeneration forest harvested before 1991, seedling to sapling size trees .

HPART = Heavy partial cut, greater than 50% of canopy removed.

CLEAR = Clearcut between 1991 and 1993, greater than 90% canopy removed.

FWET = Deciduous or coniferous scrub-shrub or forested wetlands.

[2] ALL depicts models with data from 1995, 1996, 1998, 1999 pooled.

Table 3.3. Direction of coefficients within the logistic regression models describing abundance versus absence of hares along 1 km snow-track segments in Maine. A single "-" or "+" denotes a negative or positive association that is not significant at the 0.05 level. A "--" or "++" denotes a negative or a positive association that is significant at the 0.05 level.

	1995	1996	1998	1999	Pooled
Late regeneration	**++**	+	**++**	+	**++**
Forested Wetlands	**++**	**++**	+	-	**++**
Mature Deciduous	+	-	**--**	**--**	**--**
Heavy Partial Cut	-	**--**	-	-	**--**
Clearcut	-	-	+	**--**	-
Early regeneration	-	-	-	+	+

were abundant on a large proportion of transects (Figure 3.3). The Hosmer-Lemeshow P statistic showed a similar pattern (Figure 3.4). Model fit was best at intermediate densities of snowshoe hares, and most consistent across models at medium densities of hares.

DISCUSSION

State scale habitat relationships

The state-scale habitat affinities that emerged from my modeling using remotely sensed satellite imagery were consistent with the stand-scale habitat relationships of snowshoe hare previously reported (Litvaitis et al. 1985, Monthey 1986, Long 1995, Lachowski 1997, Fuller 1999), which used stand characteristics quantified on the ground. Snowshoe hare appeared to have been more common in forest wetlands or extensive areas of regenerating clearcut (the late regeneration

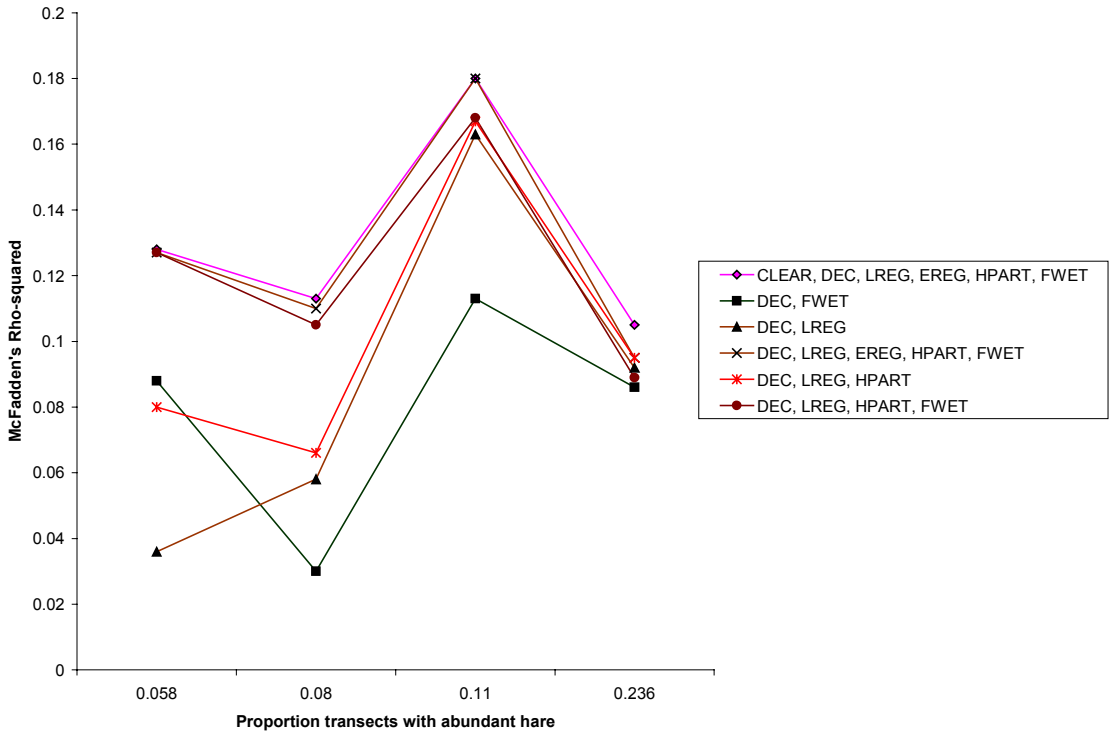

Figure 3.3. Changes in McFadden's ρ^2 of logistic regression models of snowshoe hare abundance relative to the density of hares as indexed by the proportion of transects on which hares were classified as abundant.

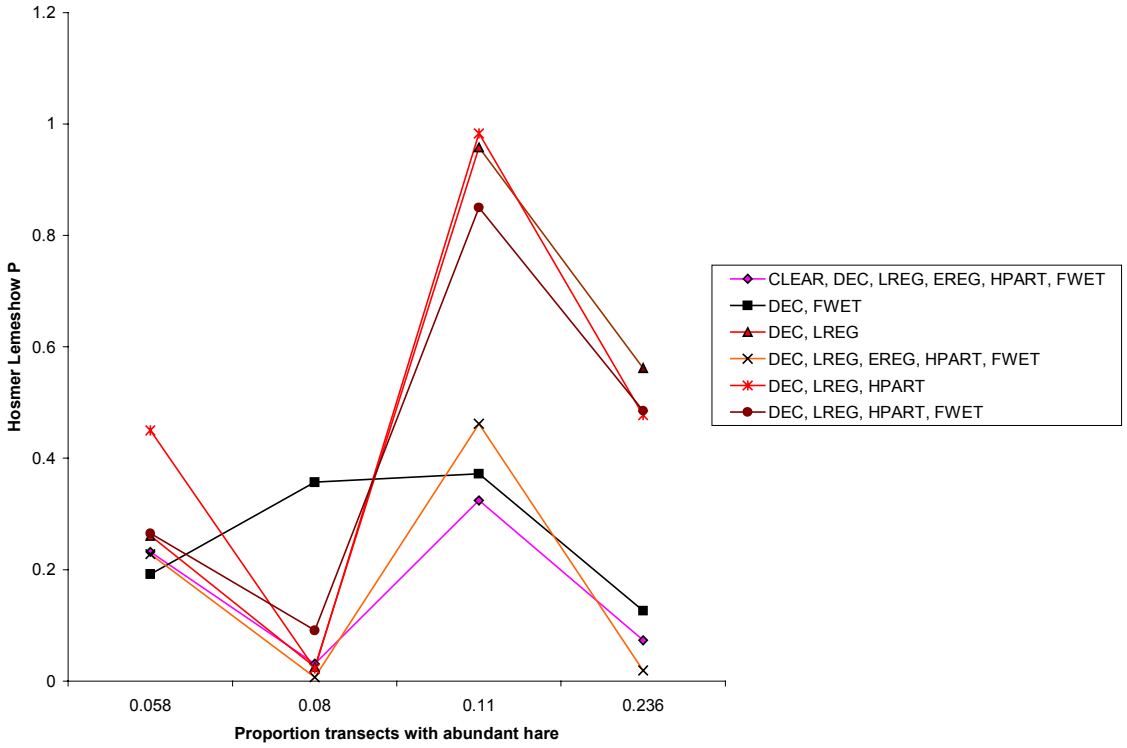

Figure 3.4. Changes in Hosmer Lemeshow P of logistic regression models of snowshoe hare abundance relative to the density of hares as indexed by the proportion of transects on which hares were classified as abundant.

variable). Both stand types tended to have dense understories. Similar to the findings of Fuller (1999), heavy partial harvest (corresponding to greater than 50% crown removal) and mature deciduous forest were negatively associated with densities of hares.

Classification accuracy of the logistic regression models was weak (sensitivity = 0.162 – 0.575) for abundant segments, but substantially stronger for absences (specificity = 0.55 – 0.872). Weak models likely resulted from several factors: first, 1 km segments were probably too long to give an accurate picture of hare habitat. Home ranges of hare generally average between 2.78-9 ha (Dolbeer and Clark 1976, Wolff 1980). A 9 ha circular home range would be only 0.34 km in diameter, and 1 km transect segments included 38 ha (0.38 km^2), an area much larger than an individual hare's hypothetical home range. Second, snow track transects should take into account the number of days since the last significant snowfall (Halfpenny et al. 1995). A survey in poor habitat that accumulates tracks over several days may appear to have more hares than a survey in good habitat with only 24 hours to accumulate tracks. Periods of extreme cold likewise can affect the movement patterns of mammals with high surface to volume ratios such as snowshoe hare. Though track nights and temperature were noted for many transects, these variables were recorded too inconsistently to be incorporated into models that were already subset by year. Additionally, segments should be sampled repeatedly to determine abundance with precision. Finally, logistic regression models work best on presence and absence data. Other models (e.g., poisson regression) are better for count data. Ordinal data are more difficult to model and assume a similar response curve for each level. These methodological constraints likely increased the variability within the data, and decreased the predictive power of the models.

An alternative explanation for poor model fit is that the data simply did not fit a logistic curve. To explore this possibility I modeled the same data using Classification and Regression Tree (CART) analysis (Appendix F). CART uses a simple rule to determine hierarchical

relationships in the data (Clark and Pregibon 1992, De'ath and Fabricius 2000). The CART analysis results were similar to those from logistic regression. Areas with much late regeneration or forested wetlands were likely to have abundant hares, and areas with much mature deciduous forest were likely to have no hares. However, these three variables only explained 6% of the variance, strongly suggesting that poor model fit was caused by variability inherent in the system or introduced by methodological constraints, and not a result of the data not fitting the logistic curve.

Temporal change in habitat selection

Implicit in most models of habitat association is the assumption that population density reflects habitat quality (Krohn 1996). This assumption is often not tenable, especially for species in strongly seasonal environments or with high reproductive capacities (Van Horne 1983), such as snowshoe hare. Habitat selection in birds can change relative to density and carrying capacity (O'Connor 1985, Johnson and Krohn *In press*). Several authors have noted that habitat selection by snowshoe hares changes with density, and that at low densities hare populations are concentrated in "refugia" of dense cover (Keith 1966, Wolff 1980, Fuller and Heisey 1986). In these studies, hares were associated with dense cover during population lows, but were found in other more open forested habitats as population densities increased. Predation risk likely contributed to this pattern.

Several alternative explanations exist that might explain the observed changes in model fit and apparent shifts in habitat association over time. One alternative explanation is that poor model fit reflected changes in habitat succession. All models were based on vegetation types derived from satellite imagery taken in June/July 1991 and September/October 1993. Some of the vegetation types on the map were becoming less reliable as time passed. For example, modeling of track survey data from 1999 was likely confounded by clearcuts that were classified by satellite in 1993 but had matured to early regeneration by 1999; similarly, some late regeneration had

probably grown into mature forest. If succession were driving model fit, however, the fit of the models would have decreased steadily from 1995 to 1999. Instead, model fit increased to 1998, and then dropped sharply (Figures 3.3, 3.4).

Another possible explanation for poor model fit was changing sample size. The number of segments sampled varied from 198 in 1998 to 408 in 1995. Contrary to expectations, however, the McFadden's ρ^2 and Hosmer-Lemeshow P both increased with decreasing sample size. Perhaps the best explanation for the change in model fit through time is that snowshoe hares selected habitats differently depending on population density. Shifts with density corresponded with trends in the strength of habitat associations through time (Table 3.3).

The proportion of transects on which hares were abundant quadrupled over the course of the study (0.06 in 1996 to 0.24 in 1999). The snowshoe hare model fit poorly at both low and high densities, but had better fit at intermediate densities (Figures 3.3, 3.4). At low densities hares were abundant in late regeneration or forested wetlands, but were equally absent in areas with much and with little mature deciduous forest, heavy partial harvest, or clearcut (Table 3.3). At high densities snowshoe hares were abundant in areas with much or little late regeneration or forested wetlands, but absent only in areas with much mature deciduous forest or clearcut (Table 3.3). The differential filling of certain habitats before others suggests that habitat use may be density dependent (Fretwell and Lucas 1970).

Based on a hierarchical pattern of habitat occupancy (Brown 1969, Fretwell and Lucas 1970, O'Connor 1985) hare abundance should increase initially on transects near relatively good habitat (a high proportion of late regeneration or forested wetlands). Abundance should increase subsequently on transects near relatively poor vegetation types (mature deciduous forest, heavy partial harvest, or clearcut). This pattern was most clear for transects with much (in the upper quartile) forested wetland and late regeneration (Figure 3.5). The proportion of transects with

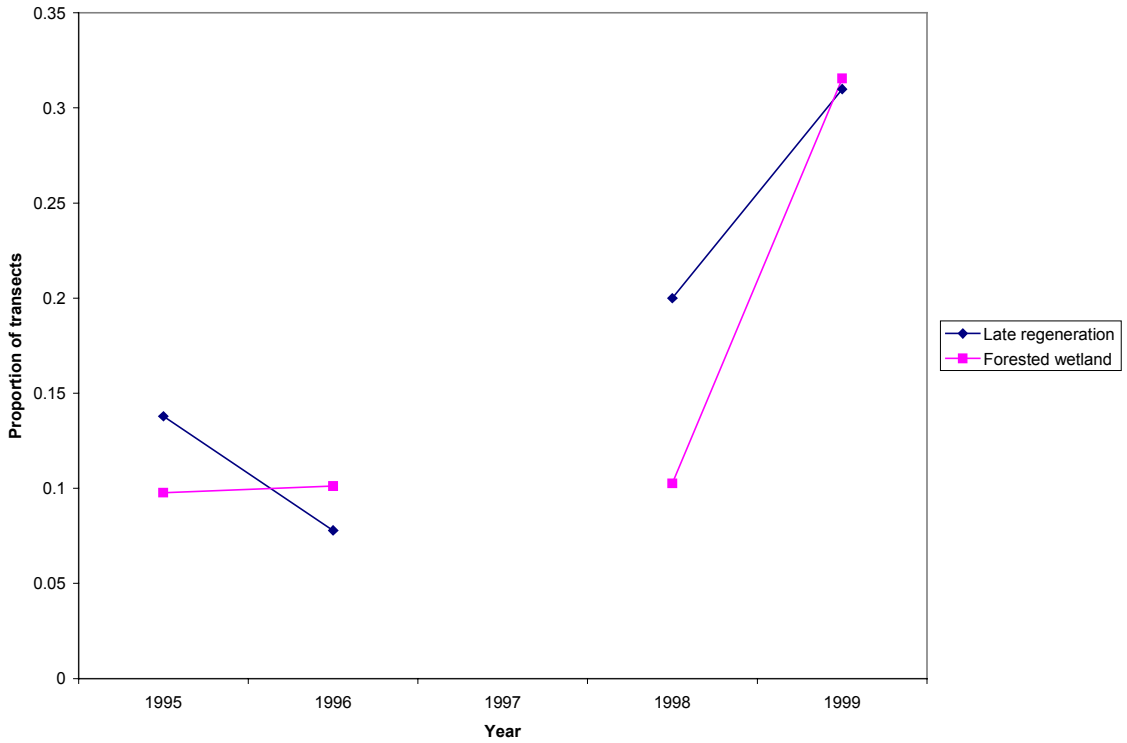

Figure 3.5. The proportion of transects that reported hares as abundant among transects in the top quartile of late regeneration and in the top quartile of forested wetland, based on statewide track surveys for snowshoe hare in Maine, 1995-1999.

abundant hare rose dramatically starting in 1996 on transects with much late regeneration, but did not rise on transects with much forested wetland until 1998. Hare abundance apparently increased first near late regeneration, and then later near forested wetlands.

Patterns were not so clear among mature deciduous, heavy partial harvest, and clearcut. Clearcut was likely maturing into early regeneration, a different vegetation type, and when classifying the satellite imagery some heavy partial harvest was misclassified as late regeneration (Hepinstall et al. 1999). Therefore, a comparison of density-dependent selection of these vegetation types could not be reliably evaluated.

Models of r-selected species such as snowshoe hares, which have populations that fluctuate or cycle, may need to incorporate temporal changes into spatial habitat models. The model for 1998 appeared to have satisfactory fit (somewhat low McFadden's $\rho^2 = 0.163$ and high Hosmer-Lemeshow P = 0.958), only late regeneration and mature deciduous forest were significant at the 0.05 level, and a model with these two variables had the lowest AIC. Thus, forested wetland, heavy partial cut, clearcut, or early regeneration could mistakenly be interpreted to have no significant association with snowshoe hares. However, all but one of these variables (early regeneration) was significantly associated with relative hare abundance at some other population density. The habitat associations were clearer when all four years were combined, but model fit was very poor (McFadden's $\rho^2 = 0.049$ and high Hosmer-Lemeshow P = 0.142) (Table 3.2). Habitat models for fluctuating or cycling populations must explicitly consider temporal, as well as spatial, changes in habitat association.

The snowshoe hare cycle in Maine

Changes in local distribution or habitat association with changing population density have been documented for snowshoe hare in Alberta (Keith 1966), Minnesota (Fuller and Heisey 1986) and Alaska (Wolff 1980). In all three studies, changes in population density were associated with

population cyclicity. The temporal extent of this study was too short to determine if snowshoe hare (and by extension Canada lynx) exhibit regular population cycles in Maine. Over the 5 years of transect data available, the track index of snowshoe hare densities increased substantially, but because some areas were surveyed more intensively during certain years, I could not determine with certainty if the observed changes in density were entirely temporal or partly spatial. Although this does not seriously affect the patterns of model fit with density, it does limit the inferences that can be made regarding the presence of a synchronized change in population density across all of northwestern Maine.

The existence of a regular population cycle in snowshoe hares in Maine would have important implications for future research and management of Canada lynx in eastern North America. A recent meta-analysis by Hodges (2000) suggested that hare populations cycle at low amplitude in the southern parts of the hare's geographic range, including Maine. However, her conclusions were based on only two sets of data, one of 11 years (Keith 1963) and one of 29 years (Hodges 2000).

Hare populations appeared to cycle in Quebec, west of Maine, but on the Gaspé peninsula, north of Maine, populations have fluctuated without a regular cyclicity (Godbout 1999). The Québec Ministre de l'Environnement et de la Faune recently enacted a special management plan for Canada lynx with regard to population fluctuations (Lafond 1995). The agency monitors snowshoe hare populations via snaring harvests, and when hare numbers decline for several consecutive years, the lynx harvest is closed until hares become abundant (Lafond 1995). The lynx harvest was closed in 1995, indicating that hare populations were entering a low period in Quebec. Snow surveys indicate that hare populations were also relatively low in Maine at this time. The lynx harvest in Quebec was opened in 1998, which coincided with a recovery of hare populations in Maine. Populations fluctuations of lynx in this region are suggested by historical evidence that

mention large changes in lynx populations (Hardy 1907, Chapter 1) and by evidence from elsewhere within the southern portion of the lynx's range (Smith 1983, Hodges 2000). However, another meta-analysis of the geographic extent of the snowshoe hare cycle found little evidence for a cycle in this region (Murray 2000). Snowshoe hare populations might fluctuate synchronously in northern Maine and southern Quebec, but further study is needed to verify this pattern.

CONCLUSIONS

Though model fit was generally poor, habitat associations at the statewide scale were similar to associations reported at the stand-scale (Litvaitis et al. 1985, Monthey 1986, Long 1995, Lachowski 1997, Fuller 1999). Snowshoe hare abundance was positively associated with late regeneration and forested wetlands, and negatively associated with mature deciduous forests, heavy partial cuts, and recent clearcuts as classified on the Maine Vegetation and Land Use map (Hepinstall et al. 1999). A relative index of snowshoe hare abundance from track surveys increased, 1995-1999. Model fit changed through time with changes in density, as habitats appear to have filled differentially. Evidence for a population cycle of snowshoe hare in Maine is weak but suggestive. Further long-term study is needed to determine if snowshoe hare populations cycle or merely fluctuate in Maine.

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CHAPTER 4

A LOGISTIC REGRESSION MODEL FOR CANADA LYNX IN NORTHWESTERN MAINE

INTRODUCTION

At the turn of the century, it was commonly perceived was that lynx (*Lynx canadensis*) inhabited remote, "primeval" forests largely unoccupied by people (e.g., Seton 1929, Hardy 1907). This perception has changed little over the last hundred years. Popular literature (e.g., Kobalenko 1997) and a ruling by a federal judge have inferred that lynx require mature forest, and that industrial forest management degrades lynx habitat (US Department of the Interior 1997). A recent scientific report by the US Forest Service contended that "old gap-phase forest" provided temporally stable lynx habitat at the southern edge of the geographic range of the Canada lynx (Buskirk et al. 2000). Although this hypothesis could be consistent with patterns of habitat occupancy by lynx in xeric areas of the western United States, lynx might be less restricted to over-mature forest in the more mesic forests of eastern North America where species diversity and structural complexity of forests are generally more diverse.

The Canada lynx is a specialist predator on snowshoe hare (*Lepus americanus*) (Saunders 1963, van Zyll de Jong 1966, Nellis et al. 1972, Parker et al. 1983). The percentage of snowshoe hare occurring in lynx scats can be as high as 97% (Parker et al. 1983), and populations of lynx cycle with a two to three year time lag behind the snowshoe hare cycle (Brand and Keith 1979, O'Donoghue et al. 1998). In the northern boreal forests of Canada and Alaska, lynx are associated with habitats where hare are abundant (Parker et al. 1983, Koehler 1990, Staples 1995), although lynx appear to select for slightly more open habitats than hare (O'Donoghue et al. 1998).

Snowshoe hare reach their highest densities in dense shrublands or dense immature forest (Tompkins and Woeher 1979, Pietz and Tester 1983, Orr and Dodds 1982), and select more for high understory density rather than cover type or plant species (Litvaitis et al. 1985, Long 1995). In Maine, high densities of snowshoe hare are associated with dense regeneration that usually follows clearcutting at both the stand (Monthey 1986, Lachowski 1997, Fuller 1999) and statewide scales (Chapter 3). At the statewide scale, hare were positively associated with late regeneration and forested wetlands, and were negatively associated with mature deciduous forest, heavy partial harvests, and recent clearcuts (Chapter 3).

Spatially explicit habitat models have become increasing popular tools in the conservation of wide-ranging animals (Turner et al. 1995). Mladenoff et al. (1995) used wolf (*Canis lupus*) pack territories and unoccupied areas to build a predictive model of habitat occupancy in Wisconsin, and then applied the model to predict areas in Minnesota, Wisconsin and Michigan where wolves were likely to colonize as their populations expanded. They found that their model correctly classified 18 of 23 new pack territories (Mladenoff et al. 1999). Logistic regression modeling was also used to predict grizzly bear (*Ursus arctos*) activity in Yellowstone relative to human activity, trails, and roads (Mace et al. 1999). Krohn et al. (1995, 1997) used broad-scale models to explore the habitat relationships of fisher (*Martes pennanti*) and interspecific relationships between fishers and marten (*M. americana*), and Carroll et al. (1999) used logistic regression to model and map fisher habitat in northwestern USA.

Logistic regression models are particularly well suited to situations where the response variable is binary. In the case of habitat models, the binary response variable is usually species presence and absence. Many studies have relied on presence and absence data from radio-telemetered animals (Mladenoff et al 1995, Mace et al. 1999). Telemetry studies, though accurate at fine scales, are difficult and expensive to conduct over large landscapes. Carroll et al. (1999)

used remote camera and sooted track plate surveys to determine presence and absence of fishers over a 67,000 km^2 area. Several studies have evaluated the usefulness of snow track surveys to determine presence, absence, and relative abundance of lynx in Alaska (Stephenson 1986, Schwartz and Becker 1988, Stephenson and Karczmarczyk 1989, Golden 1994). When surveys were consistent through time, among observers, and among areas, snow track surveys were generally considered reliable for detecting presence and absence of lynx. Halfpenny et al. (1995) outlined methods to reduce variability when detecting lynx from snow track surveys.

The objective of this study was to develop and evaluate an exploratory habitat model for lynx in northwestern Maine, giving special attention to positive or negative associations with the amount of mature and regenerating forest on the landscape. I used logistic regression modeling of lynx occurrence and absence on standardized surveys to evaluate whether lynx in Maine are more strongly associated with landscapes that have a high proportion of mature forest, or with landscapes containing a high proportion of regenerating forest. Additionally, I used statistical relationships of lynx with vegetation types to predict and map where lynx are likely to occur in Maine and to prioritize areas for future population surveys.

METHODS

In December 1994, the Maine Department of Inland Fisheries and Wildlife (MDIFW) initiated an annual track survey in northern and western Maine specifically to detect the presence or absence of wolves and lynx. Surveys were conducted by private contractors from snowmobiles during the winter. Observers who surveyed northern and western Maine were trained to distinguish Canada lynx and bobcat (*L. rufus*) tracks. Tracks of lynx, bobcats, and the relative density of snowshoe hare (Chapter 3) were recorded along each 1 km segment of transect surveyed. The locations of transects were recorded on copies of a DeLorme atlas (Anonymous 1993) at a scale of 1:125,000.

Survey routes and the presence or absence of the aforementioned mammals were digitized into Arc-Info (ESRI, Redlands, California, USA; use of trade names does not imply endorsement) using heads-up digitizing. US Geological Survey (USGS) Digital Line Graphs (DLG) were used as background coverages (i.e. digital maps) when digitizing transects. The transportation layer (roads and trails) of the DLG was displayed at a 1:24,000 scale. The hydrography layers (lakes, ponds, rivers, and streams) of the DLG were displayed at the 1:100,000 scale. A coverage of township lines at the 1:250,000 scale, available from the Maine Office of GIS, was also used to increase accuracy and to aid spatial interpretations. Each transect was divided into segments, approximately 1 km in length, to match the datasheets and maps.

Lynx are highly mobile and have large home ranges, which average about 100 km^2 in the southern boreal forest (Aubry et al. 2000). Therefore, lynx tracks occurring on adjacent segments likely resulted from double sampling of a single individual. However, tracks separated by more than 5.6 km (the radius of a hypothetical, circular 100 km^2 home range) were unlikely to represent the same individual because most transects were conducted 24 to 48 hours after the previous snowfall. To maximize independence of occurrence data and to increase the likelihood that lynx were indeed absent from transects where they were not detected, I selected a subset of transect segments at random such that the subset segments were separated by at least 5.6 km.

The percentages of each vegetation type within 5.6 km of each selected segment with lynx presence or absence were calculated from the Maine Vegetation and Land Cover map (Hepinstall et al. 1999). The map was based on a classification of Thematic Mapper (TM) satellite imagery to represent 1993 conditions (1991 and 1993 TM data used) and was resolute to a 30 m^2 grid. This map was generalized to 90 m^2 cell size using RESAMPLE in ARC-INFO Grid because of limits on processing time.

I developed logistic regression models for the Canada lynx in northwestern Maine based on presence or absence on the snow track surveys. I evaluated 9 *a priori* models that included variables deemed important to lynx or hare based on a thorough literature search, rather than using an *a priori* statistical model to define the relation. Statistical null hypothesis testing is prevalent in ecological literature, but may be uninformative in some modeling situations, especially when selecting descriptor variables or models (Anderson et al. 2000). Testing a lynx logistic regression model against a null model would not result in much new biological insight. The question was not whether the variables have an effect significantly greater than zero, but which combination of variables best approximate the real biological system. The information-theoretic approach is an alternative to model selection via null hypothesis testing (Burnham and Anderson 1998, Anderson et al. 2000). In the information-theoretic approach, a model is constructed using all variables that are considered likely to describe the system based on scientific knowledge. For example, the proportion of late regeneration was included in a lynx model because it had been previously identified as important in describing the abundance of the lynx's primary prey, the snowshoe hare (Chapter 3). Longitude or the density of meadow voles (*Microtus pennsylvanicus*), for example, have little biological justification based on the literature and scale of our study; therefore, extraneous variables such as these were excluded from my list of potential descriptor variables.

The Maine Vegetation and Land Cover map delineated 37 vegetation types (Hepinstall et al. 1999). A relatively small subset of types were considered likely to describe lynx habitat, and many types (e.g., coastal, agricultural, and urban types) were not present in northwestern Maine. The vegetation types considered likely to describe lynx habitat were recent clearcut, late regeneration, partial harvest, mature deciduous forest, mature conifer forest, and forested wetland. Late regeneration forest was generally clearcut prior to 1991, and had greater than 50% canopy

closure. Recent clearcut areas were generally harvested between 1991 and 1993, and contained little vegetation biomass. Partial harvest was a combination of two vegetation types, light partial cut and heavy partial cut, and corresponded to a variety of silvicultural practices including improvement thinning, shelterwood, and selection harvest. Deciduous species contributed to greater than 75% of the dominant cover in the mature deciduous forest type, and conifer species contributed to greater than 75% of the dominant cover in the mature conifer forest type.

The vegetation types were not developed from maps of known stand histories, but were based on reflectance patterns as captured in TM data. Thus, with the exception of clearcuts, the harvest classes did not represent stands of known age. The differences between early and late regeneration, for example, are structural and represent differences in biomass and reflectance patterns. Although the harvest classes correspond to interpreted aerial videography (see Hepinstall et al. 1999 for details on accuracy), the exact age and specific method of harvest were unavailable.

Wetlands were incorporated into the Maine Vegetation and Land Cover map directly from the US Fish and Wildlife Service National Wetlands Inventory (Hepinstall et al. 1999). Four forested wetland categories (deciduous forested, coniferous forested, deciduous scrub-shrub, and coniferous scrub-shrub) were combined into one forested wetland vegetation type. Mean snowfall on each transect segment was also calculated based on the snowfall model described in Chapter 2.

Nine combinations of the above variables were considered to be potentially biologically meaningful (Table 4.1). One model incorporated the variables that were important in at least one year of the snowshoe hare models: late regeneration, partial harvest, forested wetlands, clearcut, and mature deciduous forest. A model similar to the regional model was also considered: mature deciduous forest and 10-year mean annual snowfall. A global model that included all variables (late

Table 4.1. Means of model performance in terms of McFadden's ρ^2, Hosmer-Lemeshow P, sensitivity, specificity, AIC_c and ΔAIC_c for 20 different replications, based on random selections of snow transect segments where Canada lynx were present and absent in northwestern Maine. Vegetation types[1] were derived from the Maine Vegetation and Land Cover map (Hepinstall et al. 1999).

Model	Chi-square	McFadden's ρ^2	Hosmer-Lemeshow P	sensitivity	specificity	AIC_c	ΔAIC_c
CLEAR, PART, LREG, FWET, DEC	0.000	0.310	0.590	0.380	0.911	73.98	0.00
CLEAR, PART, LREG, FWET	0.000	0.267	0.560	0.329	0.904	75.38	1.40
CLEAR, PART, LREG, FWET, DEC, CON	0.000	0.311	0.622	0.381	0.911	76.20	2.22
CLEAR, PART, LREG	0.000	0.228	0.421	0.309	0.901	76.73	2.75
PART, LREG, FWET, DEC	0.001	0.237	0.510	0.296	0.899	77.92	3.94
CLEAR, PART, LREG, FWET, DEC, CON, SNOW	0.001	0.301	0.556	0.383	0.912	78.42	4.44
CLEAR, LREG, FWET	0.007	0.148	0.362	0.219	0.888	82.72	8.74
LREG	0.018	0.074	0.491	0.179	0.882	84.80	10.82
DEC, SNOW	0.256	0.034	0.428	0.146	0.878	90.87	16.89

Table 4.1. continued

[1] CLEAR = Clear-cut between 1991 and 1993, greater than 90% canopy removed.

PART = Heavy and light partial cut, includes selection harvest, shelterwood, and improvement thinning.

LREG = Late regeneration forest harvested before 1991, sapling to poletimber with greater than 50% canopy closure.

FWET = Deciduous or coniferous scrub-shrub or forested wetlands.

DEC = Mature deciduous forest.

CON = Mature coniferous forest.

SNOW = predicted 10 year mean annual snowfall from weather station data, 1980-1990, from Chapter 2.

regeneration, partial harvest, forested wetlands, clearcut, mature deciduous forest, mature conifer forest, and snowfall) in any model was created. A series of progressively simpler models was also created by removing what were the least likely to be important variables, based on a review of the literature.

Track surveys pose challenges to habitat modeling because tracks that are clumped in space represent an unknown number of individuals. When sample sizes are large, a random selection of tracks with spacing criteria is probably adequate. When sample sizes are small, any one random selection may poorly represent actual species-habitat associations. Thus, I chose to evaluate 20 random combinations of tracks where lynx were present and absent to more accurately determine model parameters for my small sample size. Models were not averaged using the technique advocated by Burnham and Anderson (1998) to account for model selection uncertainty, nor was any measure of variance reported, because at issue was the accuracy, not the precision, of the model. Burnham and Anderson's (1998) technique accounts for uncertainty that arises from selecting among different models constructed from the same data set. In the case of the lynx models, the same model was constructed from 20 slightly different data sets. Means of each model parameter were reported; variance was not reported because each random selection resulted in several of the same lynx occurrences being selected. For this reason each random selection was not independent of the others, and any variance reported would have been misleading because of pseudo-replication among the data sets. Most parameters were similar across the 20 replicates, with the exception of the Hosmer Lemeshow P statistic, which seemed highly variable because of small sample size (Appendix E).

Using logistic regression (Hosmer and Lemeshow 1989, Agresti 1996) 180 models were computed: 20 replicates of 9 different combinations of variables. For each model, the second order Akiake's Information Criterion (AIC_c) (Burnham and Anderson 1998) was calculated. The second

order AIC (AIC_c) is an AIC corrected for small sample size. McFadden's ρ^2 (McFadden 1974), X^2, Hosmer Lemeshow P (Hosmer and Lemeshow 1989), sensitivity, and specificity were calculated in SYSTAT 9.0 (SPSS, Chicago, Illinois, USA), and were averaged across the 20 replicates for each of the 9 combinations of variables. The 9 combinations were then ranked by mean AIC_c. AIC values provide a relative rank of models built upon the same set of data. A useful statistic when comparing models is the ΔAIC_c, which is the difference between each model and the model with the lowest AIC_c: $\Delta AIC_{ci} = AIC_{ci}$ – minimum AIC_c. "As a rough rule of thumb," models with ΔAIC_c values that are within 2 can be considered equivalent (Burnham and Anderson 1998: 48). The models with the lowest (best) mean ΔAIC_c were used to predict habitat on a cell by cell basis for northwestern Maine. Lynx were unlikely to occur in southern and eastern Maine because of broad-scale climatic and vegetation influences (Chapter 2). Therefore, portions of southern and eastern Maine with a less than 10% probability of lynx occurrence at the broad-scale (Chapter 2) were excluded from consideration in the models.

Because sample sizes were too low to reserve data for testing, and because additional systematic trapping or surveys were not feasible, these models were not formally tested. To evaluate the models, capture locations for 25 radio-collared lynx (captured 1999-2000), part of an ongoing telemetry study in northern Maine (Maine Department of Inland Fisheries and Wildlife, unpublished data), were compared to the probabilities of occurrence on the landscape.

RESULTS

Two thousand two hundred and forty one kilometers of snow track transect were surveyed for the presence or absence of tracks, 1995-1999. Because of inconsistent snowmobile odometers, the 2,241 kilometers of survey were divided into 2,664 transect segments. Lynx tracks were present on 66 (2.9%) segments, but after omitting segments within 5.6 km of randomly chosen positive segments, lynx were considered present on only 13-15 segments for this analysis.

Although lynx were not detected on 2,598 segments, only 107-119 segments were randomly selected in any one replicate based on my spacing criteria.

Two models had mean ΔAIC_c below 2, and were thus considered equivalent as the best approximating models in balancing goodness of fit with parsimony. The logistic regression model with the lowest ΔAIC_c (Table 4.1) incorporated clearcut, partial harvest, late regeneration, forested wetlands, and mature deciduous forest (hereafter referred to as CPLFD). An equivalent model (ΔAIC_c = 1.4) was similar, but did not include mature deciduous forest (hereafter referred to as CPLF). The models fit the data well (mean McFadden's ρ^2_{CPLFD} = 0.31, mean McFadden's ρ^2_{CPLFD} = 0.27). Both models indicated a strong positive association of lynx presence with late regeneration ($\beta_{LREG, CPLFD}$ = 34.42, SE = 12.06; $\beta_{LREG, CPLF}$ = 40.77, SE = 11.63), strong negative associations of lynx presence with partial cuts ($\beta_{PART, CPLFD}$ = -45.59, SE=20.34; $\beta_{PART, CPLF}$ = -44.07, SE = 17.07) and recent clearcuts ($\beta_{CLEAR, CPLFD}$ = -56.33, SE = 26.57; $\beta_{CLEAR, CPLF}$ = -50.26, SE = 26.06), and a moderate negative association with forested wetlands ($\beta_{FWET, CPLFD}$ = -23.78, SE = 12.17). Mature deciduous forest had a weak negative association with lynx presence ($\beta_{DEC, CPLFD}$ = -8.34, SE = 4.86). Other models that included mature conifer forest and snowfall had ΔAIC_c greater than 2 (Table 4.1). Mature conifer and snowfall had no significant affect in any model (β_{SNOW} and β_{CON} < 1.0, Appendix D).

The direction of effects was consistent across models (e.g., late regeneration had a positive affect in all models (Appendix D) in which it was considered). McFadden's ρ^2, comparable to the r^2 in traditional regression analyses, was usually higher for models with more variables. The increases in McFadden's ρ^2 when conifer forest and snowfall were included were small relative to the loss of parsimony, or simplicity. Sensitivity and specificity are measures of the predictive power of the model. These measures are calculated against the data used to build the model. Thus they are optimistic, and are skewed toward high specificity because the ratio of absences to presences

was high (x = 6.99). Sensitivity, or the rate that presences were predicted correctly by the models, was moderate (x_{CPLFD} = 0.38; x_{CPLF} = 0.33), and the specificity was high (x_{CPLFD} = 0.91; x_{CPLF} = 0.90). The Hosmer Lemeshow P statistic, which is the probability that the data fit a logistic curve (Hosmer and Lemeshow 1989), was moderately high in most of the models (x_{CPLFD} = 0.59; x_{CPLF} = 0.56), but exhibited much variability (0.02 – 0.95) across the 20 replications (Appendix E), which was likely an artifact of small sample size. McFadden's ρ^2, sensitivity, specificity, and the Hosmer Lemeshow P were all consistent with the ΔAIC_c in indicating that models CPLFD and CPLF incorporated the best trade-off of goodness of fit and parsimony.

The probability π(x) of lynx occurrence in northwestern Maine was mapped by inserting the model coefficients into the logistic equation:

$$\pi(x) = \frac{\exp(\alpha + \beta_{CLEAR} + \beta_{PART} + \beta_{LREG} + \beta_{FWET} + \beta_{DEC})}{1 + (\exp(\alpha + \beta_{CLEAR} + \beta_{PART} + \beta_{LREG} + \beta_{FWET} + \beta_{DEC}))}$$

A broader-scale model (Chapter 2) indicated that much of southern and eastern Maine was not potential lynx habitat. Therefore, the parts of the state with less than 10% probability of lynx occurrence based on that broader analysis were not included in the modeling exercise for northwestern Maine. Within northwestern Maine, the highest probability of lynx occurrence occurred in the extreme northwest, with several isolated areas of potential habitat north and west of Moosehead Lake, and one isolated area of habitat in the Telos region west of Baxter State Park (Figure 4.1-4.2). The predictive models, when applied to the landscape of northwestern Maine, predicted that 41.6% (CPLFD) or 40.0% (CPLF) of the landscape had a probability of occurrence less than 10%. The distribution of probabilities decreased in a nonlinear fashion in both models (Figure 4.3-4.4). Only 0.2% (CPLFD) or 0.1% (CPLF) of the landscape had a probability of lynx occurrence greater than 90%, and 5.5% (CPLFD) or 4.3% of the landscape of northwestern Maine had a greater than 50% probability of lynx occurrence.

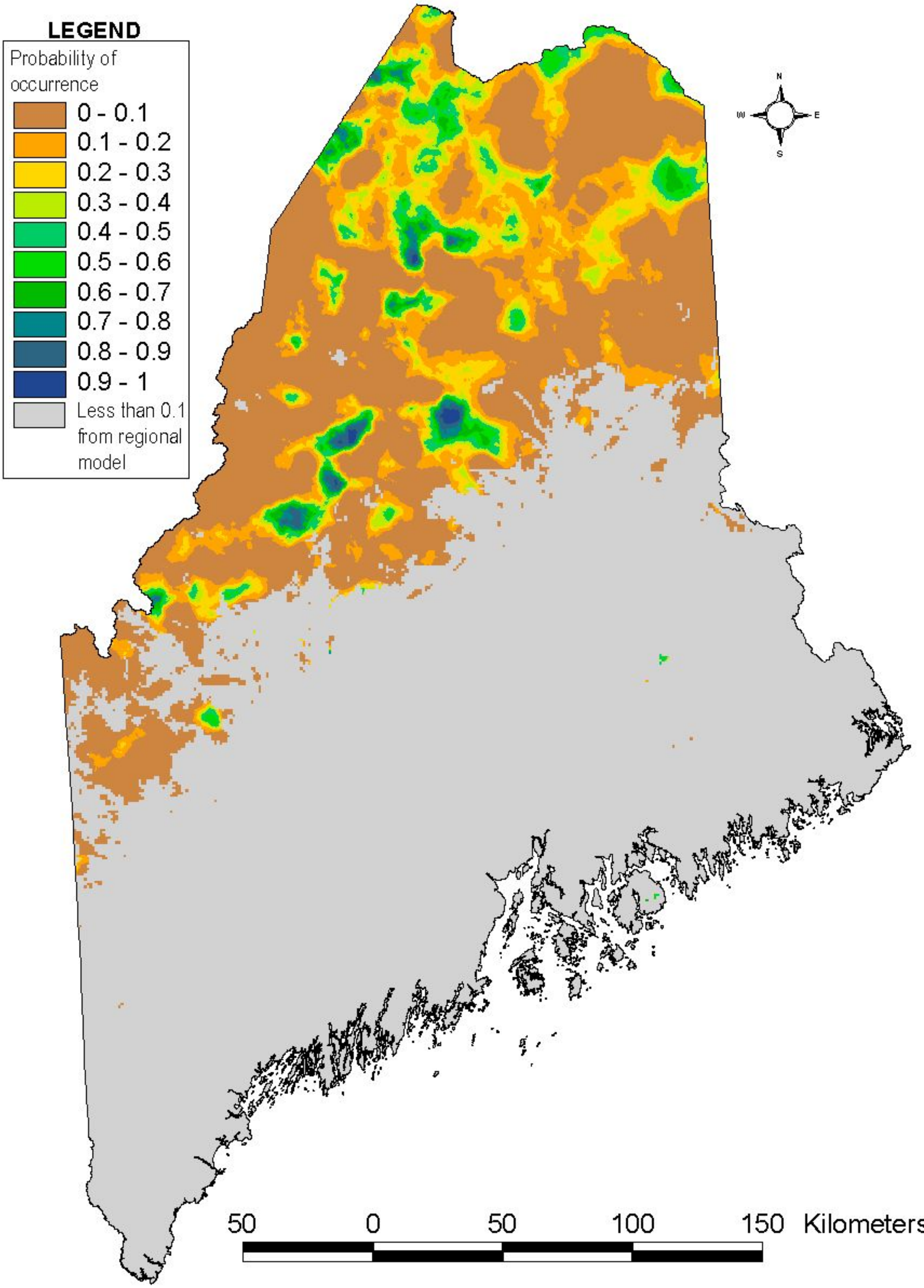

Figure 4.1. A probabilistic map of potential Canada lynx habitat in northwestern Maine, developed from logistic regression modeling of presence vs. absence of tracks along 2,241 km of snow track surveys conducted during 1994-1999. Probability of occurrence was predicted based on the proportion of late regeneration, partial harvest, clearcuts, forested wetlands, and mature deciduous forest (CPLFD) occurring within 100 km^2 of each 90 m^2 pixel.

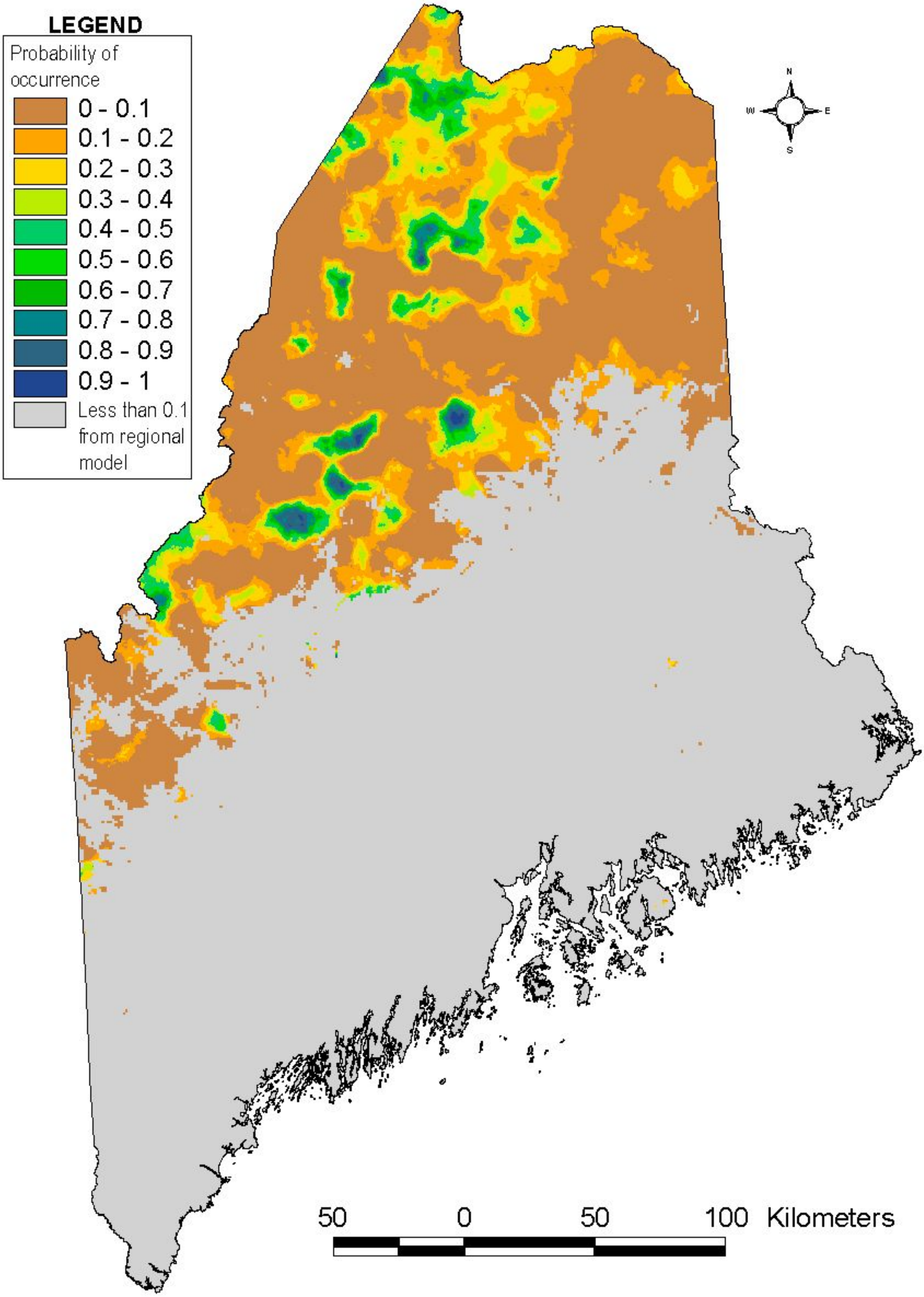

Figure 4.2. A probabilistic map of potential Canada lynx habitat in northwestern Maine, developed from logistic regression modeling of presence vs. absence of tracks along 2,241 km of snow track surveys conducted during 1994-1999. Probability of occurrence was predicted based on the proportion of late regeneration, partial harvest, clearcuts, and forested wetlands (CPLF) occurring within 100 km^2 of each 90 m^2 pixel.

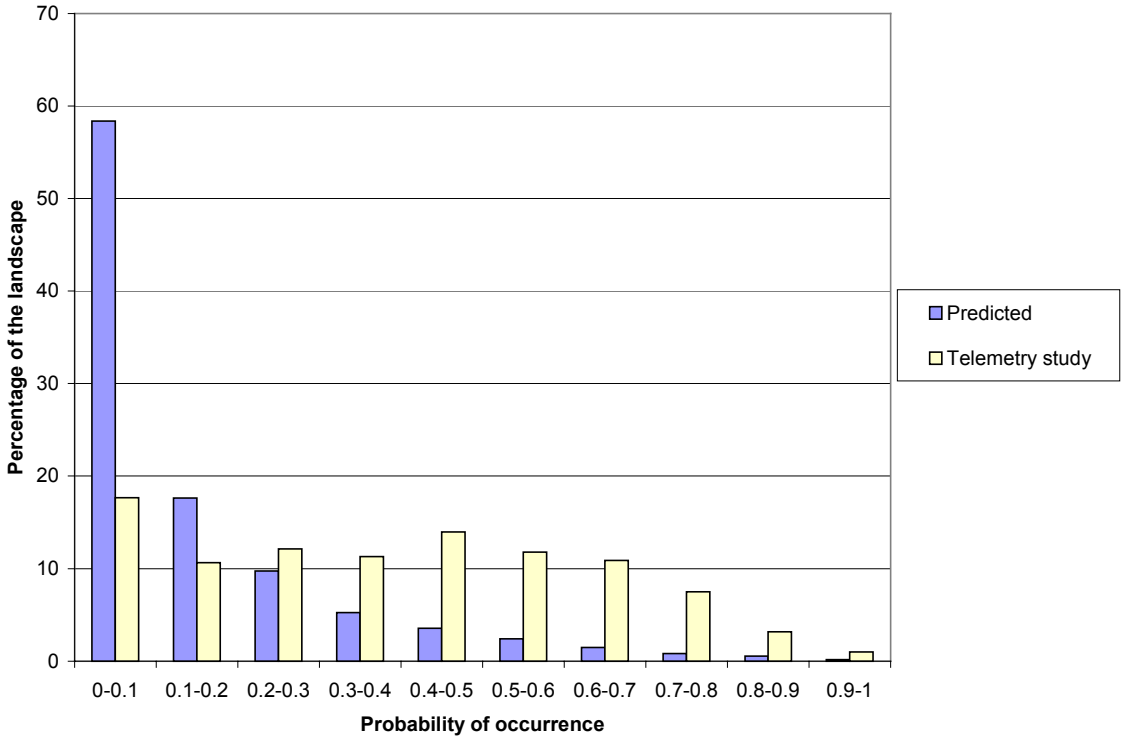

Figure 4.3. The distribution of probability of occurrence on the landscape relative to the distribution of probability of occurrence around locations where Canada lynx were known to occur from a MDIFW radio telemetry study. Because the distributions differ, the model appears to have predictive power. This model included clearcut, partial harvest, late regeneration, forested wetland, and mature deciduous forest (model CPLFD).

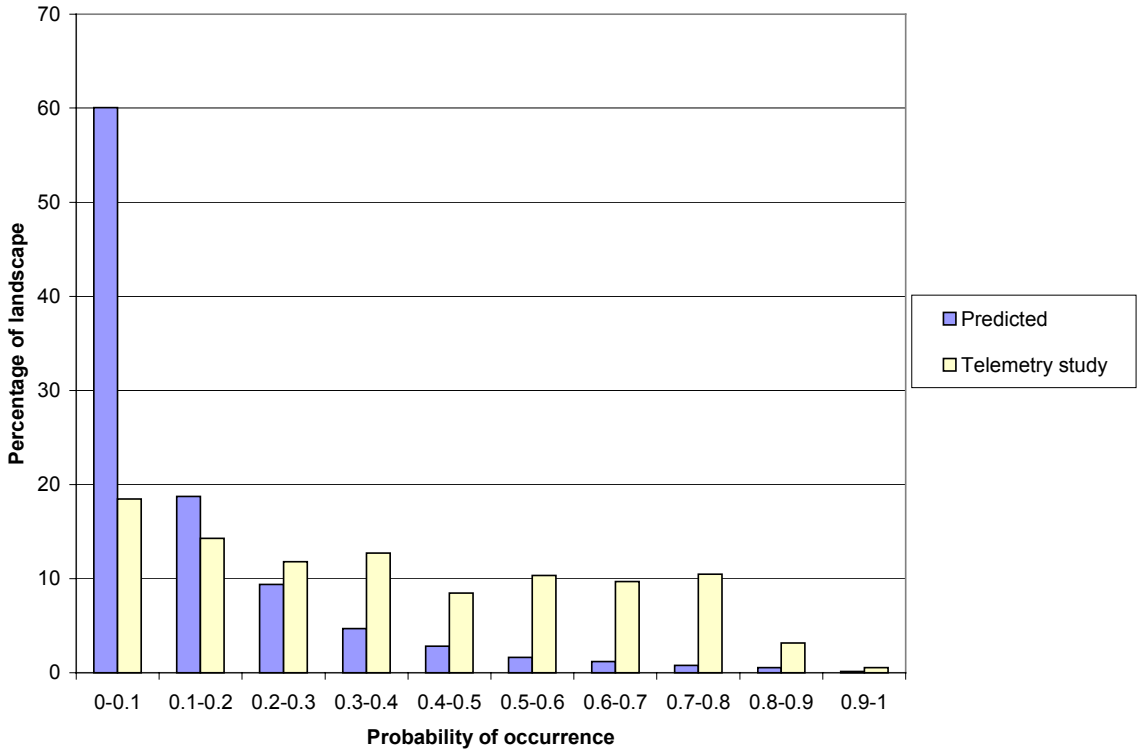

Figure 4.4. The distribution of probability of occurrence on the landscape relative to the distribution of probability of occurrence around locations where Canada lynx were known to occur from a MDIFW radio telemetry study. Because the distributions differ, the model appears to have predictive power. This model was applied to northwestern Maine, and included clearcut, partial harvest, late regeneration, and forested wetland (model CPLF).

The two models with the lowest ΔAIC_c accurately predicted capture points from an ongoing telemetry study (Figure 4.3-4.4). If observations of lynx were distributed at random on the landscape, one would expect that lynx would be distributed on the landscape in proportion to the amount of the landscape in that probability class. For example, one would predict that 5.5% of lynx observations should occur in areas with a greater than 50% probability of lynx occurrence because 5.5% of the landscape has a greater than 50% probability of lynx occurrence. However, if more lynx occur in high probability areas relative to their abundance on the landscape, the model has some predictive power. Lynx from the telemetry study (N = 25) occurred much more frequently in areas (Figure 4.5-4.6) with a predicted high probability of lynx occurrence relative to the amount of the landscape in those probability classes (Figures 4.3-4.4). The model does appear to have some power to predict capture points from the telemetry study. However, relative to the spatial extent of the model, the evaluation set was only for a small area where lynx were predicted to occur.

DISCUSSION

The two models with $\Delta AIC_c < 2$ were similar; the main difference was that one model included a small negative association with deciduous forest. Statistically, these models give an equally valid approximation of reality, based on the snow track data available. Thus, both were reported. The model that has a negative association to deciduous forest (model CPLFD), however, does not predict lynx habitat well outside of the forests of northwestern Maine. Parts of northeastern Maine have extensive areas of agricultural land (primarily potato fields). Because this area is mostly agricultural, it has little deciduous forest. Thus, it is predicted in model CPLFD as potential lynx habitat (Figure 4.1), which it is not. This is a result of extrapolating a model developed for a forested landscape to a largely agricultural landscape. The model without deciduous forest (model CPLF, Figure 4.2) is probably the better model for conservation and

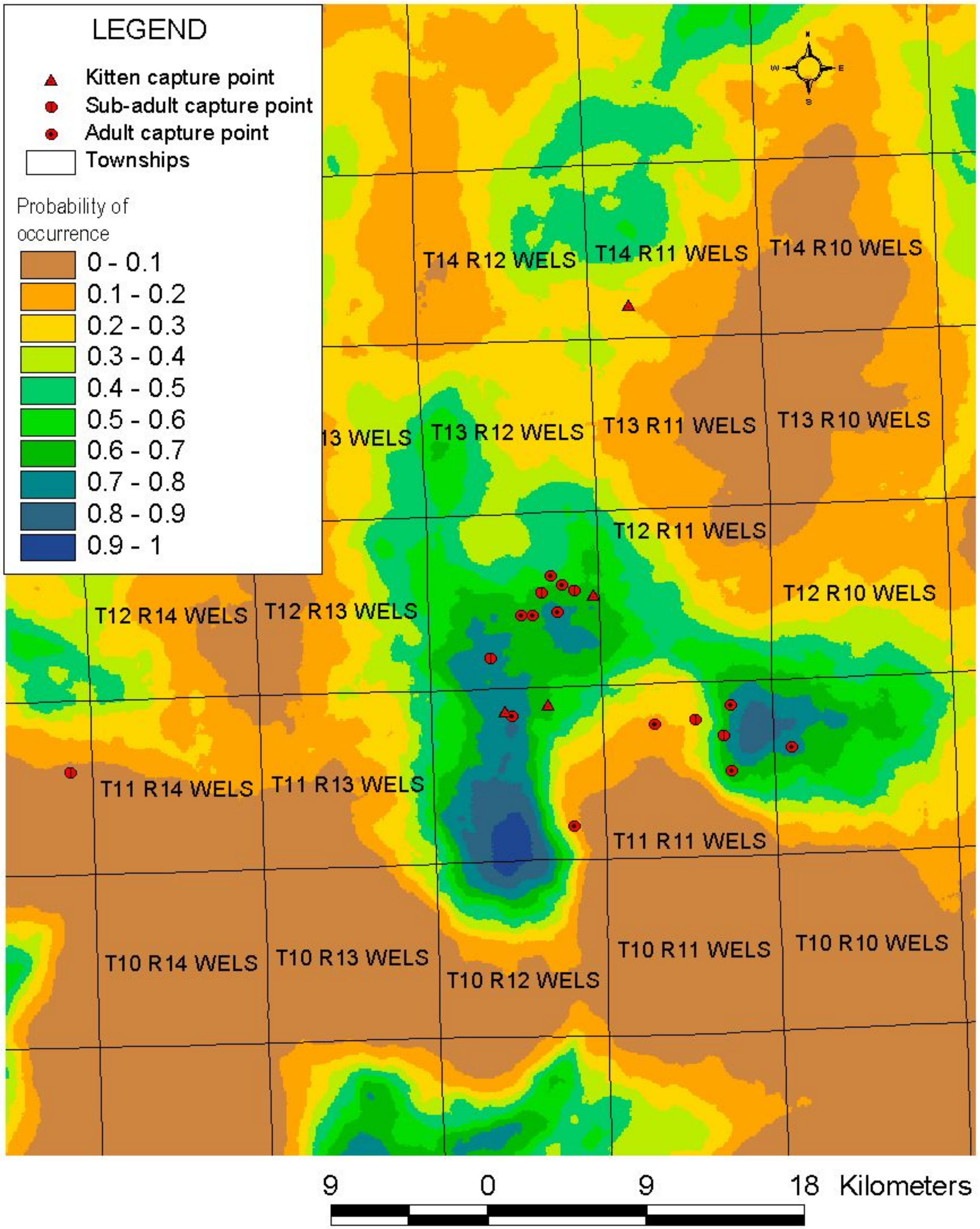

Figure 4.5. Capture points of Canada lynx from a Maine Department of Inland Fisheries and Wildlife radio-telemetry study, 1999-2000, superimposed on an independently derived logistic regression model predicting probability of lynx presence from snow track surveys conducted during 1994-1999 in northwestern Maine. Probability of occurrence was predicted from late regeneration, partial harvest, clearcuts, forested wetlands, and mature deciduous forest (CPLFD).

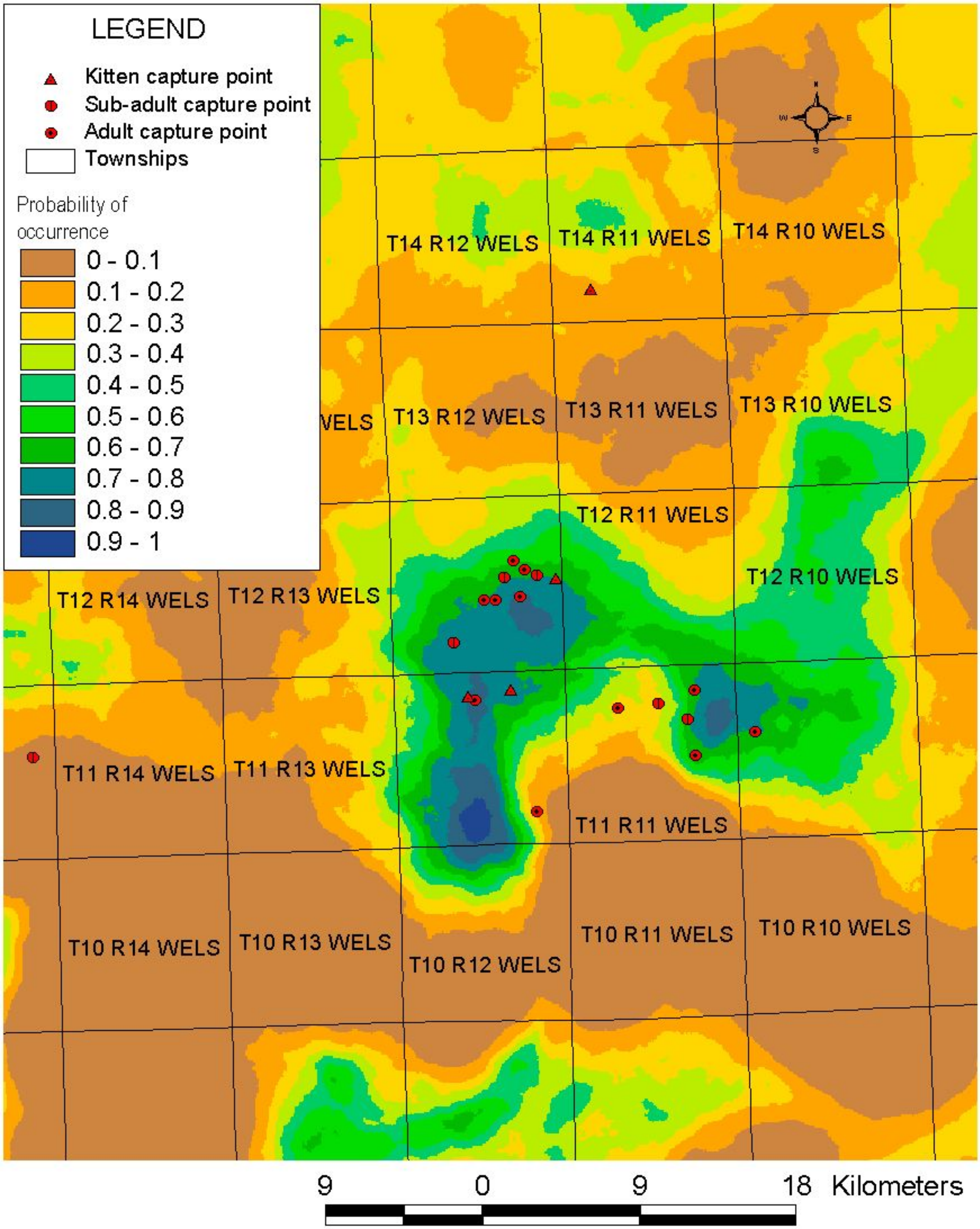

Figure 4.6. Capture points of Canada lynx from a Maine Department of Inland Fisheries and Wildlife radio-telemetry study, 1999-2000, superimposed on an independently derived logistic regression model predicting probability of lynx presence from snow track surveys conducted during 1994-1999 in northwestern Maine. Probability of occurrence was predicted from late regeneration, partial harvest, clearcuts, and forested wetlands (CPLF).

management because it accurately predicts non-forested areas in northern Maine as poor lynx habitat.

Track surveys

The lynx probabilities on the maps of potential habitat (Figure 4.1-4.2) likely underestimate the amount of lynx habitat in northwestern Maine. Ideally, track surveys should be conducted 3 days following a snowfall event (Golden 1994) and/or repeated several times throughout each winter (Halfpenny et al. 1995) to determine lynx presence or absence in a surveyed area. Many of the surveys available for this study were conducted 1 day following a snowfall event, and none were repeated within a season. Several areas surveyed may have had lynx, but survey effort was too low in those areas to ensure detection. Limited survey effort would increase the ratio of absences to occurrences, which would skew the logistic equation toward lower probabilities. Areas predicted to have a relatively low probability of lynx occurrence may be occupied by lynx.

Clearcuts, partial harvest, and lynx

Lynx in the mixed coniferous-deciduous forests of Maine occurred most frequently in 100 km^2 landscapes with a disproportionately high amount of regenerating forest relative to areas where lynx were absent. A similar pattern has been reported for lynx on Cape Breton Island (Parker et al. 1983) and other northern boreal forests (Kesterton 1988, Staples 1995, Mowat et al. 2000). Lynx presence was negatively associated with recent clearcuts, partial harvests, and with landscapes dominated by mature deciduous forest. Snowshoe hare showed the same positive associations with late regeneration and negative associations with clearcuts, partial harvests, and mature deciduous forest in 0.46 km^2 landscapes (Chapter 3), which suggests that lynx are exhibiting second order habitat selection (Johnson 1980) based primarily on the abundance of primary prey.

The proportion of partial harvest (which included thinning, selection cuts, and shelterwood cuts) within 100 km^2 landscapes was negatively associated with both the presence of lynx and the relative abundance of hare (Chapter 3). At the scale of the forest stand, Fuller (1999) reported that hare were two orders of magnitude less abundant in one type of partial harvest, 3-4 years post-harvest, relative to regenerating forests. In the logistic regression models, the mean model coefficients for partial harvests were nearly as great as the negative effect of recent clearcuts (Appendix D).

Though lynx presence was positively associated with regenerating clearcuts, lynx presence was negatively associated with recent clearcuts. Clearcutting was beneficial to lynx at one time scale because it produced regeneration and abundant snowshoe hare, but clearcutting had a negative effect at shorter time scales. In Maine, lynx appeared to be most likely to occur in 100 km^2 landscapes (approximately the size of a township) that experienced relatively intensive clearcutting in the past 15-25 years, but currently experience relatively little clearcutting. This suggests that in the eastern North America, extensive areas of even-aged management may mimic large-scale natural disturbances associated with lynx occurrences in boreal forest landscapes (Poole et al. 1996, Paragi et al. 1997).

The trend during the 1990s has been toward more partial harvesting, and less clearcutting in the Maine forest. In 1989, clearcuts accounted for 45% and partial harvests (including shelterwood) for 55% of the acres of forest harvested (Maine Forest Service 1995). During the past decade, forest practices have changed dramatically. In 1999, clearcuts accounted for only 3%, whereas partial harvest accounted for 96% of the acreage harvested in Maine (Maine Forest Service 2000). Much of the late regeneration on the landscape in the 1990s was a result of large-scale clearcutting in the 1970s and early 1980s associated with salvage harvesting from the spruce budworm (*Choristoneura fumiferana*) outbreaks. Recent trends away from clearcutting in favor of

partial harvest could have significant negative consequences on landscape scale densities of snowshoe hare, and may affect carnivores that depend on hare, such as lynx. Many types of forest practices are included under the term “partial harvest.” Different types of partial harvest, as well as the age of a partial harvests, were not available from the Maine Vegetation and Land Cover Map. Therefore, further study is needed to better understand the effects of partial harvest on snowshoe hare and lynx.

Old growth forest

A federal judge recently stated that Canada lynx were threatened by “forest clearing and current timber management” (U.S. Department of the Interior 1997), and a recent review of the scientific knowledge of Canada lynx hypothesized that old gap-phase forest may ensure more temporally stable habitat for lynx relative to earlier stages of forest succession (Buskirk et al. 2000). In xeric habitats of the western United States, current timber management might be harmful to lynx, depending on the structure that regeneration provides on these sites. In Maine, however, lynx are positively associated with certain types of timber management. Landscapes of 100 km^2 with much late regeneration forest (15-25 years after clearcutting) are more likely than mature or partial-cut forests to support lynx. The proportion of mature conifer forest in 100 km^2 was not associated with the occurrence of lynx, and the proportion of mature deciduous forest was weakly negatively associated with lynx presence. The current timber management in Maine that may have the greatest negative effect on lynx is partial harvesting. Recent partial harvests were poor habitat for hare (Fuller 1999), the lynx’s primary prey, and partial harvests are unlikely to regenerate into the dense regeneration that often follows clearcutting or fires. More study is needed to determine the short-term and long-term effects of different types of partial harvesting on snowshoe hare and lynx.

Canada lynx occurred in significant numbers in Maine prior to the large-scale clearcutting of the late twentieth century (Chapter 1). Though lynx occurred often in old burns (Audubon and

Bachman 1852, Thoreau 1893), the pre-settlement rate of fire return, or frequency of fires, appears to have been low in most of Maine (Coolidge 1963, Lorimer 1977) relative to more conifer dominated boreal forests to the north, with the exception of extreme northwestern Maine (C. Cogbill, unpublished manuscript). Epidemic insect infestations, such as spruce budworm outbreaks, may account for lynx occurrence in pre-settlement forest. Spruce budworm outbreaks generally cause extensive mortality in mature balsam fir (*Abies balsamea*) and lesser mortality in mature white spruce (*Picea glauca*), red spruce (*P. rubra*), and black spruce (*P. mariana*) (Blais 1985). Outbreaks in Canada appear to be cyclic with a period of 25–100 years, and occur over extensive areas (Blais 1983, Krause 1997). The most recent outbreak affected Ontario, Quebec, Maine, New Brunswick, Nova Scotia, and Newfoundland (Hardy et al. 1985). Though there is some disagreement as to the proximate causes and frequency of budworm outbreaks in Maine (Seymour 1992), spruce budworm and spruce bark beetle (*Dendroctonus rubipennis*), which affects mature spruce, likely caused mortality over relatively large parts of Maine (Seymour 1992). Snowshoe hare were more abundant in stands defoliated by the spruce budworm relative to mature forest in northcentral Maine (Lachowski 1997). Thus, regeneration following periodic mortality of mature forest following insect infestations may have increased densities of hare in pre-settlement forests in Maine.

Old growth forest was not surveyed by the MDIFW in their snow track surveys because it does not currently exist as a functional component on the landscape in Maine (Critical Areas Program 1980). As such, this study can determine little about Canada lynx associations, either positive or negative, with old growth forest. Lynx did occur in heavily managed forests of northwestern Maine where only a few, scattered small blocks of old growth forest were present. Thus, there are currently no benchmarks for evaluating the relative habitat quality of pristine versus managed forests for lynx in the northeastern USA.

Forested wetlands

Snowshoe hare were positively associated with forested wetlands (Chapter 3); however, lynx were negatively associated with forested wetlands in all models (Appendix D). The negative association of forested wetlands with lynx occurrence was weaker than the negative association with recent clearcuts or partial harvests, and stronger than the negative association with mature deciduous forest.

Forested wetlands were at relatively low elevation on the landscape, but fine scale exclusion by bobcats on an elevation or snowfall gradient could not explain avoidance of forested wetlands by lynx. On Cape Breton Island, lynx occurred at high elevations where snow is deep, and bobcats occurred at low elevation where snow is shallow, or more likely to form supporting crusts (Parker et al. 1983). Though snowfall strongly affects broad-scale lynx distributions (Chapter 2), it had little affect on lynx habitat associations at the sub-state scale (Table 4.1, Appendix D).

A possible explanation for negative associations of lynx presence with forested wetlands is that densities of hare in forested wetlands may have been inconsistent relative to consistently high densities of hare in regenerating forest over many years. As densities of snowshoe hare increased in Maine, they reached higher densities in late regeneration before forested wetlands, indicating that late regeneration may have been higher quality habitat for hare (Chapter 3). If hare were only abundant in forested wetlands when densities were also high in regeneration, forested wetlands may have held relatively little value across the several years that a lynx might occupy a given home range. Although lynx might have selected for forested wetlands within their home range (third order selection, Johnson 1980) during years that hare are abundant in forested wetlands; lynx appeared not to select their home range (second order selection, Johnson 1980) based on forested wetlands.

Another possible explanation is that the associations of hare and lynx with forested wetlands are confounded by scale. Large forested wetlands are relatively rare in northwestern

Maine, (Figure 4.7). Hare associations were calculated from 0.46 km^2 landscapes, whereas lynx associations were calculated on 100 km^2 landscapes. Forested wetlands usually occur in large patches relative to hare home ranges, but usually occur in small, isolated patches relative to the areas of lynx home ranges. Lynx may perceive forested wetlands as too rare to affect second order habitat selection (Johnson 1980). Further, forested wetlands are usually of relatively low site quality for forest harvest, and forested wetlands may act as a surrogate variable for little regenerating forest. Thus, surrogate variables may also be operating to cause a negative association of lynx presence with forested wetlands at the scale of 100 km^2 landscapes.

Spatial scales

At the multi-state and provincial scale, a simple model with a strong positive association with snowfall and a strong negative association with the proportion of deciduous forest within 100 km^2 predicted presence or absence of lynx; reserved data verified the model with a 94% correct classification rate (Chapter 2). At the sub-state scale, a model with the same variables performed very poorly, with the worst ΔAIC_c and a McFadden's ρ^2 of only 0.034 (Table 4.1). Relative to the region (Chapter 2, Figures 2.1 and 2.5), northwestern Maine has relatively uniform snowfall, but within that region the patterns of late regeneration, partial harvests, recent clearcuts, forested wetlands, and mature deciduous forest appear to most strongly influence occurrence of lynx.

Different patterns of habitat association are evident at different spatial scales, and a complete understanding of lynx habitat requires integrating knowledge from multiple scales. This is especially important for species such as lynx, which are at the edge of their geographic range. Lynx show some flexibility with regard to the broader scale model (Chapter 2); lynx occur north and west of Moosehead Lake, in areas of much regeneration and little partial harvest, but where the

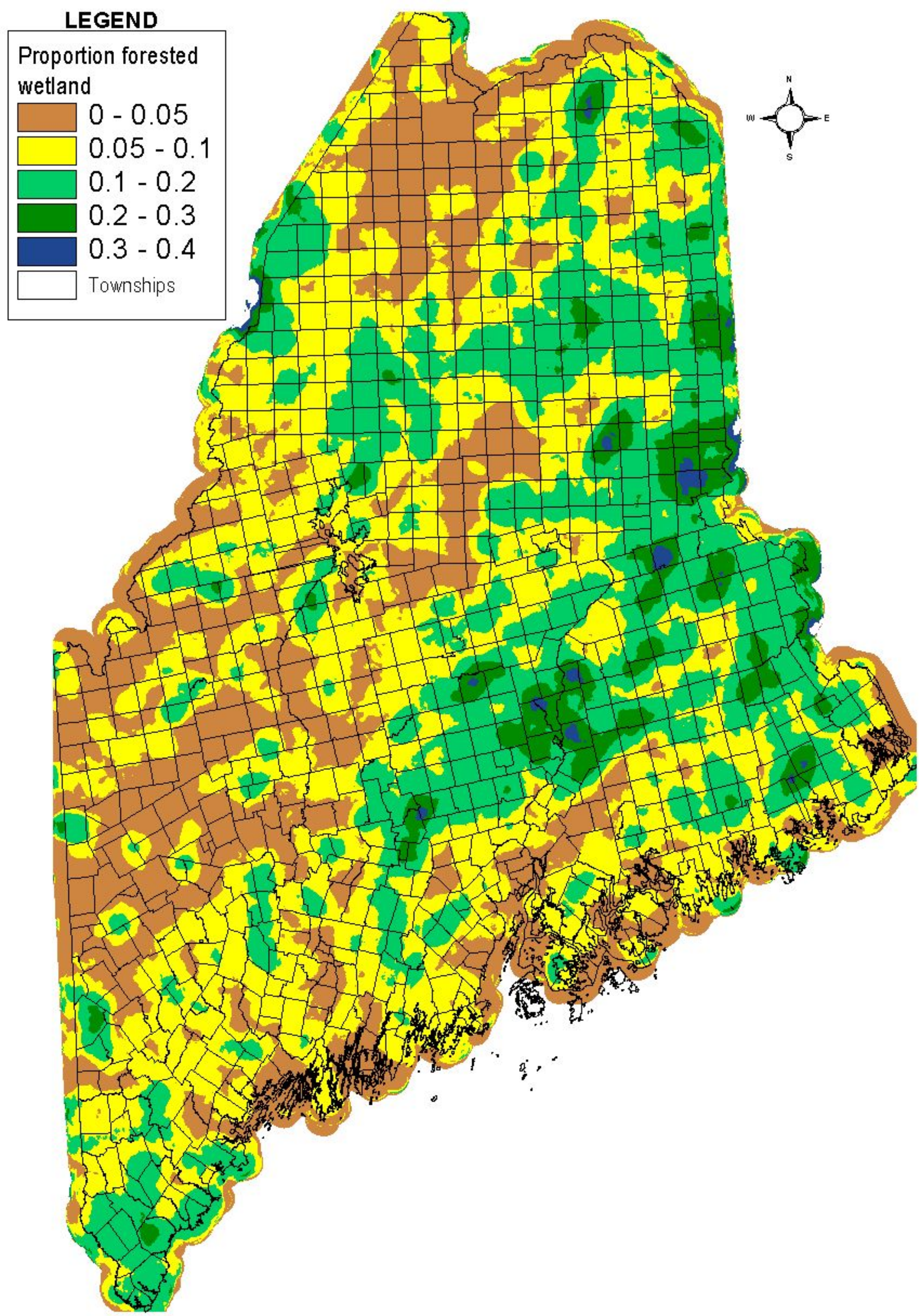

Figure 4.7. Proportion of forested wetlands from the Maine Vegetation and Land Cover Map of Maine (Hepinstall et al. 1999) within a 100 km circular moving window at a resolution of 90 m^2.

broader scale model yielded only a 33% probability of occurrence (Chapter 2). In contrast, the broader scale model predicts a greater than 50% probability of occurrence for much of northwestern Maine where a relative scarcity of extensive areas of late regeneration or a predominance of partial harvest may preclude lynx occurrence at finer spatial scales. Both climate and forest practices appear associated with the distribution of lynx in Maine, but at different spatial scales.

MANAGEMENT IMPLICATIONS

Lynx are listed as a federally threatened species. Therefore, lynx management should be based on the best available information. Maine is large (32,600 km^2), but lynx are rare and occur over a relatively small area of the state. Less than 3% of the state was predicted to have a higher than 50% probability of lynx occurrence. Thus, within this small area, mortality of lynx associated with human causes should be minimized.

Because little information is currently available regarding habitat associations of lynx at the scale of individual home ranges in Maine, management actions could be taken to avoid incidental mortality of lynx in areas with high probabilities of lynx occurrence. Neck snaring of coyotes could potentially cause unintended mortalities of lynx; therefore one possible application of these models would be to close deer wintering areas to snaring based on the probability of lynx occurrence. At a 50% probability level, only 0.4% of all DWAs would be closed (Figure 4.8). At a 10% probability level, 3.7 - 4.7% of all DWAs would be closed (Figure 4.9). Similar scenarios could be constructed evaluating the effects of changing forest harvest practices.

Short-term effects of partial harvesting can result in low densities of snowshoe hare (Fuller 1999, Chapter 3), and lynx are less likely to occur in areas with much partial harvesting, as it is delineated on the Maine Vegetation and Land Cover map developed by Hepinstall et al. (1999). Partial harvesting takes many forms, and the effects on snowshoe hare and lynx probably change

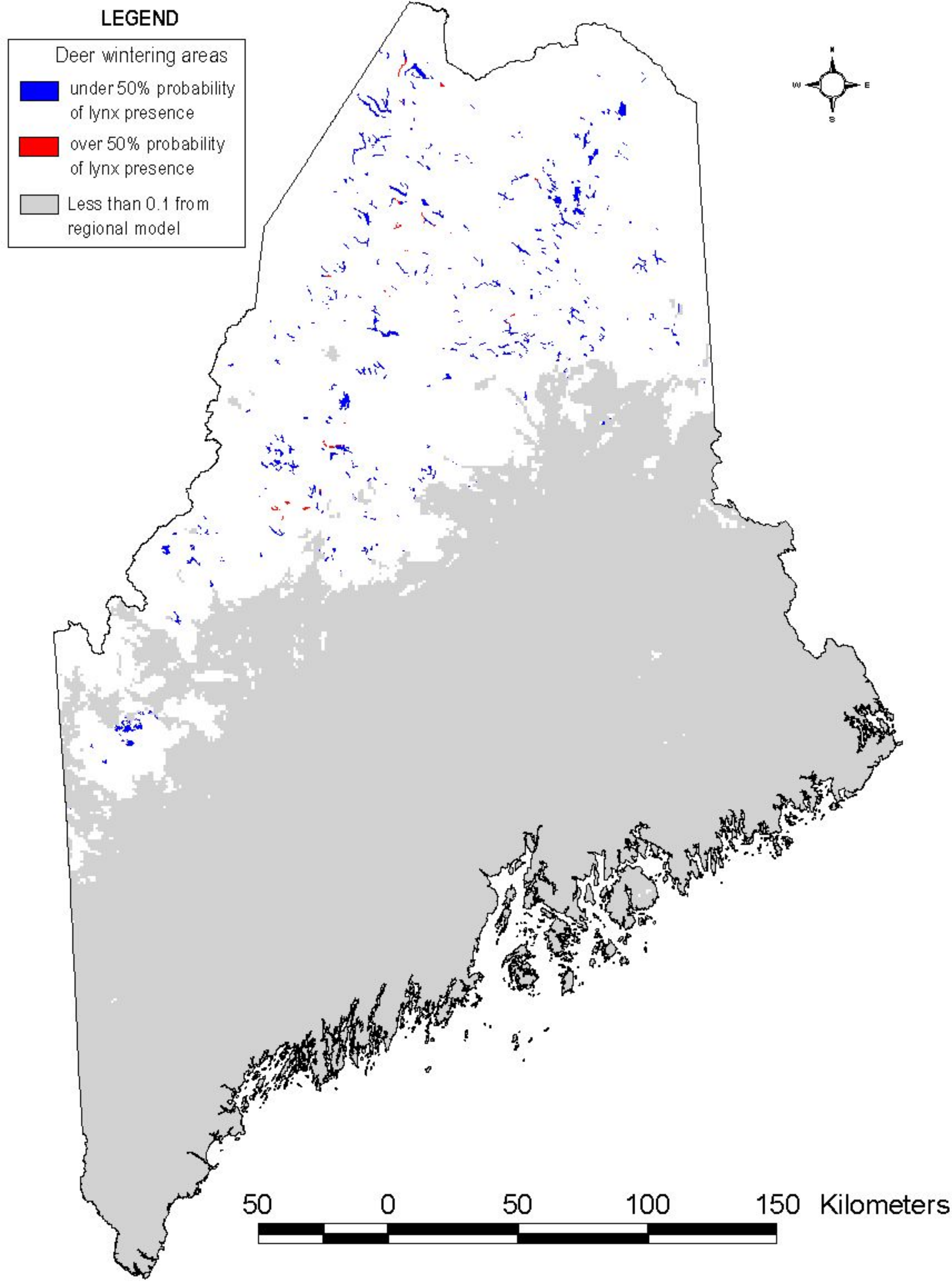

Figure 4.8. Distribution of deer wintering areas in relation to probability of lynx occurrence as predicted from a logistic regression model developed from snow track surveys conducted, 1994-1999, in northwestern Maine.

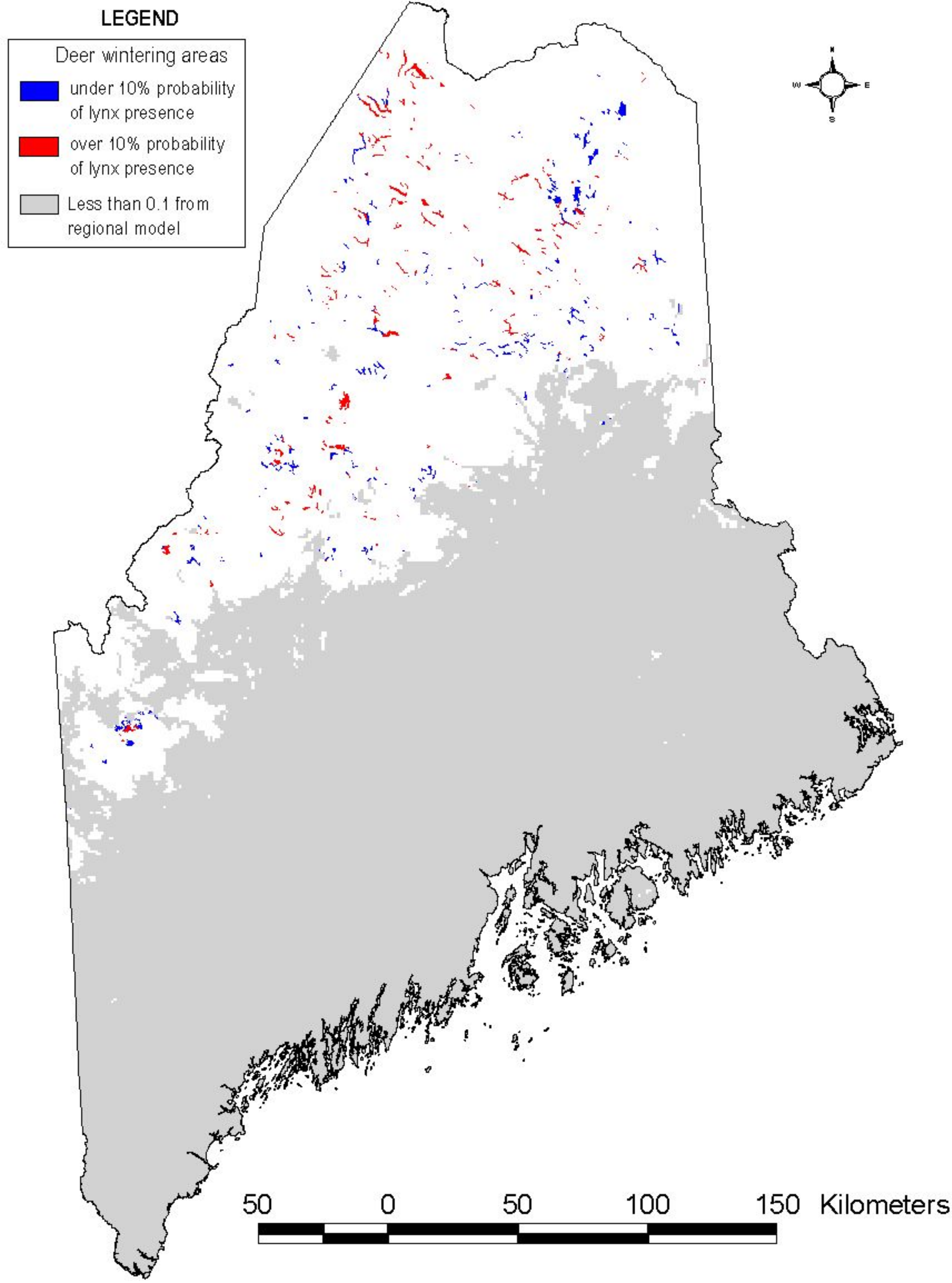

Figure 4.9. Distribution of deer wintering areas in relation to probability of lynx occurrence as predicted from a logistic regression model developed from snow track surveys conducted, 1994-1999, in northwestern Maine.

through time. Given the amount of partial harvesting currently occurring in Maine, further study is needed on the specific effects of different forms of partial harvesting on lynx and hare through time.

The utility of the habitat model presented herein has not been tested, and in this sense, it is an exploratory model. Capture points from an ongoing telemetry study of lynx (Maine Department of Inland Fisheries and Wildlife, unpublished data) were associated with areas predicted to have a high probability of lynx occurrence based on the model; however, a representative sample of lynx presence throughout northern and western Maine is needed to rigorously test the model. The easiest test may be a survey (via track transects, remote cameras, rubbing posts, etc.) stratified by areas predicted to have high, moderate, and low probabilities of lynx occurrence. If lynx are consistently verified to occur in areas predicted to have high probability of lynx occurrence, but are absent consistently from areas predicted to have low probability of occurrence, then the model could be a powerful tool for future conservation of lynx in Maine.

CONCLUSIONS

In northwestern Maine, lynx were most likely to occur in 100 km^2 landscapes with a high proportion of late regeneration, and a low proportion of forested wetlands, recent clearcuts and partial harvests. Snowfall and deciduous forest had little explanatory power at this scale because these variables were more uniform in northwestern Maine compared to all of eastern North America. In northwestern Maine, lynx were associated with ephemeral phenomena. Clearcuts (poor habitat) mature to regenerating forest (good habitat), which matures to mature forest (neutral habitat); all of these successional changes occur within a stand in approximately 50 years. In Maine, at the eastern part of the southern extreme of the lynx's geographic range, lynx have persisted on the landscape (Chapter 1) and continue to persist, especially in areas with much young regenerating forest. Potential climate warming (Chapter 2) and trends away from clearcutting are possible threats to the conservation of lynx in the eastern USA.

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APPENDICES

APPENDIX A
HISTORIC RECORDS OF CANADA LYNX (*Lynx canadensis*) OBSERVATIONS

Table A.1. Chronological listing of Canada lynx observed and reported at the township scale or finer with references, age, sex, and method of observation where available. Reference numbers match those in Figure A.1.

Ref. No.	Year	Observer	Reference	Age and sex	No. Lynx
1	1833	Anonymous	Norton (1930)	unknown	2
2	1834	Anonymous	Norton (1930)	unknown	1
3	1850	Portland Soc. Nat. Hist.	R. Palmer, unpublished	unknown	1
4	1851	Z.F. Durkee	Rich (1862)	1 adult	1
5	1859	M. Hardy and R. Philbrook	Palmer (1949)	2 adults	2
6	1860	J.G. Rich	Harvard MCZ[1] 1350, 1351	2 adults	2
7	1861	M. Hardy	Hardy (1903)	1 adult	1
8	1863	J.G. Rich	Harvard MCZ 1259	1 adult female	1
9	1864	J.G. Rich	University of Michigan, MZ[2] 62458 - 62461	1 adult, 3 juveniles	4
10	1864	J.G. Rich	Harvard MCZ 1271, 3805	2 juveniles	2
11	1865	J.G. Rich	Harvard MCZ 3612, 3613	2 juveniles	2
12	1865	J.G. Rich	Harvard MCZ 398, 1955	2 adults	2
13	1875	E.E. Thomas	Thomas (1923)	unknown	1
14	1876	J.A. Allen	Allen (1876a)	unknown	1
15	1877	F.C. Barker and J.S. Danforth	Barker and Danforth (1882)	unknown	9
103	1892	A.T. Mitchell	Ames (1893)	unknown	2
104	1893	A.T. Mitchell	Ames (1893)	unknown	1
16	1895	J.W. Strout	Strout (1895)	unknown	1

Table A.1. Continued

Ref. No.	Year	Observer	Reference	Age and sex	No. Lynx
17	1896	E. Ham	Ham (1963)	unknown	1
18	1896	A. Parker	Anonymous (1897)	unknown	1
19	1896	J. Darling	Darling (1896)	1 adult, 3 juveniles	4
20	1897	O. Stowe	Noyes (1998)	1 adult	1
21	1903	C.F. Batchelder	Harvard MCZ 47496	1 adult	1
22	1905	A.H. Norton	R. Palmer, unpublished	unknown	1
23	1905	Bowdoin College	R. Palmer, unpublished	unknown	1
24	1907	O. Sprague	Sprague (1972)	unknown	1
25	1911	E.H. Kenniston and E. Hewey	Anonymous (1911)	unknown	2
26	1912	P. Sayward	Sayward (1915)	unknown	1
27	1939	J. Kelly	Pers. com., R. Joseph 1998	1 adult, 1 juvenile	2
28	1940	L. Gardiner	Pers. com., R. Joseph 1998	unknown	1
29	1947	D. Priest	Pers. com., R. Joseph 1998	1 adult, 3 juveniles	4
30	1948	A. Nugent	Harvard MCZ 50522 - 50525	unknown	4
31	1948	D. Wing	Pers. com., R. Joseph 1998	unknown	1
32	1948	D. Priest	Pers. com., R. Joseph 1998	1 adult, 1 juvenile	2
33	1949	B. O'Leary	Pers. com., R. Joseph 1998	unknown	2
34	1949	A. Nugent and D. Priest	Pers. com., R. Joseph 1998	1 adult, 2 juveniles	3
35	1951	M. Pelletier	Pers. com., R. Joseph 1998	unknown	1
36	1954	L. Caron and L. Richie	Pers. com., R. Joseph 1998	unknown	1
37	1955	S.B. Covert	Gibbs (1961)	2 juveniles	2
38	1956	J. Robertson	Pers. com., R. Joseph 1998	unknown	1
39	1957	S.B. Covert	Gibbs (1961)	1 adult male	1

Table A.1. Continued

Ref. No.	Year	Observer	Reference	Age and sex	No. Lynx
40	1960	O. Gardiner	Pers. com., R. Joseph 1998	unknown	2
41	1962	K. Wentworth	Pers. com., R. Joseph 1998	1 adult, 1 juvenile	2
42	1964	M. Noble	Pers. com., R. Joseph 1998	3 juveniles	3
43	1965	J. Doucette	Pers. com., R. Joseph 1998	unknown	1
44	1965	M. Noble	Pers. com., R. Joseph 1998	1 adult, 2 juveniles	3
45	1967	J. Robertson	Pers. com., R. Joseph 1998	unknown	1
46	1967	B. Orcut	Pers. com., R. Joseph 1998	unknown	1
47	1967	A. Thibodeau	Letourneau (1967)	unknown	1
48	1969	L. Richie	Pers. com., R. Joseph 1998	unknown	1
49	1972	R. Pelletier	Pers. com., R. Joseph 1998	unknown	1
50	1972	L. Trafton and V. Moulton	Pers. com., R. Joseph 1998	unknown	1
51	1972	D. Laney	Pers. com., R. Joseph 1998	unknown	1
52	1975	D. Laney	Pers. com., R. Joseph 1998	unknown	1
53	1975	W.R. Lane and B. Wagg	Pers. com., R. Joseph 1998	unknown	1
54	1979	G. Donovan	Pers. com., R. Joseph 1998	unknown	1
55	1981	A. Theriault	Pers. com., R. Joseph 1998	unknown	1
56	1982	C. Bates	Pers. com., R. Joseph 1998	unknown	1
57	1982	L. Bonney	Pers. com., R. Joseph 1998	1 adult	1
58	1984	W. Hudson	Pers. com., R. Joseph 1998	unknown	1
59	1985	D. Livingstone	Pers. com., R. Joseph 1998	1 adult	1
60	1986	G. Wing	Pers. com., R. Joseph 1998	unknown	1
61	1986	D. Livingstone	Pers. com., R. Joseph 1998	2 juveniles	2
62	1987	J. Bartley and A. Theriault	Pers. com., R. Joseph 1998	unknown	1

Table A.1. Continued

Ref. No.	Year	Observer	Reference	Age and sex	No. Lynx
63	1988	R. Joseph and M. Favreau	Pers. com., R. Joseph 1998	unknown	1
64	1988	L. Pottle	Pers. com., R. Joseph 1998	1 adult, 1 juvenile	2
65	1988	B. Orcut	Pers. com., R. Joseph 1998	1 adult, 1 juvenile	2
66	1988	C. Atkins	Pers. com., R. Joseph 1998	3 adults	3
67	1989	B. Hanson	Pers. com., R. Joseph 1998	unknown	2
68	1990	B. Hanson	Pers. com., R. Joseph 1998	unknown	1
69	1990	R. Joseph	Pers. com., R. Joseph 1998	unknown	1
70	1990	D. Boston and C. Smalley	Pers. com., R. Joseph 1998	unknown	1
71	1990	W. Hudson	Pers. com., R. Joseph 1998	1 adult	1
72	1991	R. Dyer	Pers. com., R. Joseph 1998	unknown	1
73	1993	B. Orcut	Pers. com., R. Joseph 1998	unknown	1
74	1994	J. Guimond	Pers. com., R. Joseph 1998	unknown	2
75	1994	A. Later	Pers. com., R. Joseph 1998	unknown	1
76	1995	T. Kelly	Pers. com., R. Joseph 1998	unknown	1
77	1995	W. Noble	Pers. com., R. Joseph 1998	unknown	1
78	1995	J. Bartley	Pers. com., R. Joseph 1998	unknown	1
79	1995	C. Davis	MDIFW[3], unpublished data	unknown	4
80	1995	A. Stirling	MDIFW, unpublished data	unknown	4
81	1995	P. Dumond	MDIFW, unpublished data	unknown	3
82	1995	M. Noble	MDIFW, unpublished data	unknown	1
83	1995	C. Atkins	Pers. com., R. Joseph 1998	2 adults, 1 juvenile	3
84	1996	W. Hudson	Pers. com., R. Joseph 1998	unknown	1
85	1996	M. Noble	Pers. com., R. Joseph 1998	unknown	1

Table A.1. Continued

Ref. No.	Year	Observer	Reference	Age and sex	No. Lynx
86	1996	B. Carpenter	Pers. com., R. Joseph 1998	unknown	2
87	1996	N. Wade	Pers. com., R. Joseph 1998	unknown	1
88	1996	G. Wing	Pers. com., R. Joseph 1998	unknown	1
89	1996	C. Atkins and W. Davenport	Pers. com., R. Joseph 1998	unknown	1
90	1996	C. Davis	Pers. com., R. Joseph 1998	1 adult, 1 juvenile	2
91	1997	W. Hudson	Pers. com., R. Joseph 1998	2 adult, 2 juveniles	4
92	1998	A. Lovell	Pers. com., R. Joseph 1998	unknown	1
93	1998	W. Noble	Pers. com., R. Joseph 1998	unknown	1
94	1998	A. Stirling	MDIFW, unpublished data	unknown	1
95	1999	A. Vashon	MDIFW, unpublished data	9 adults, 2 juveniles	11
96	1999	J. Guimond	Pers. com., R. Joseph 1998	unknown	2
97	1999	G. Fenney	Pers. com., R. Joseph 1998	unknown	1
98	1999	A. Theriault	MDIFW, unpublished data	unknown	1
99	1999	M. Terra-Berns	MDIFW, unpublished data	unknown	1
100	1999	A. Vashon	MDIFW, unpublished data	unknown	3
101	1999	R. Joseph	R. Joseph	1 adult, 1 juvenile	2
102	1999	A. Stirling	MDIFW, unpublished data	adult	2

[1] Agassiz Museum of Comparative Zoology

[2] Museum of Zoology

[3] Historical bounty records were missing at the time of this study. In some years records of Canada lynx were separated from bobcat records. In other years both species were classified as "wildcats." Those records marked "bounty" were from wardens recollections or printed in the literature as bountied Canada lynx. Visual records represented sightings of lynx.

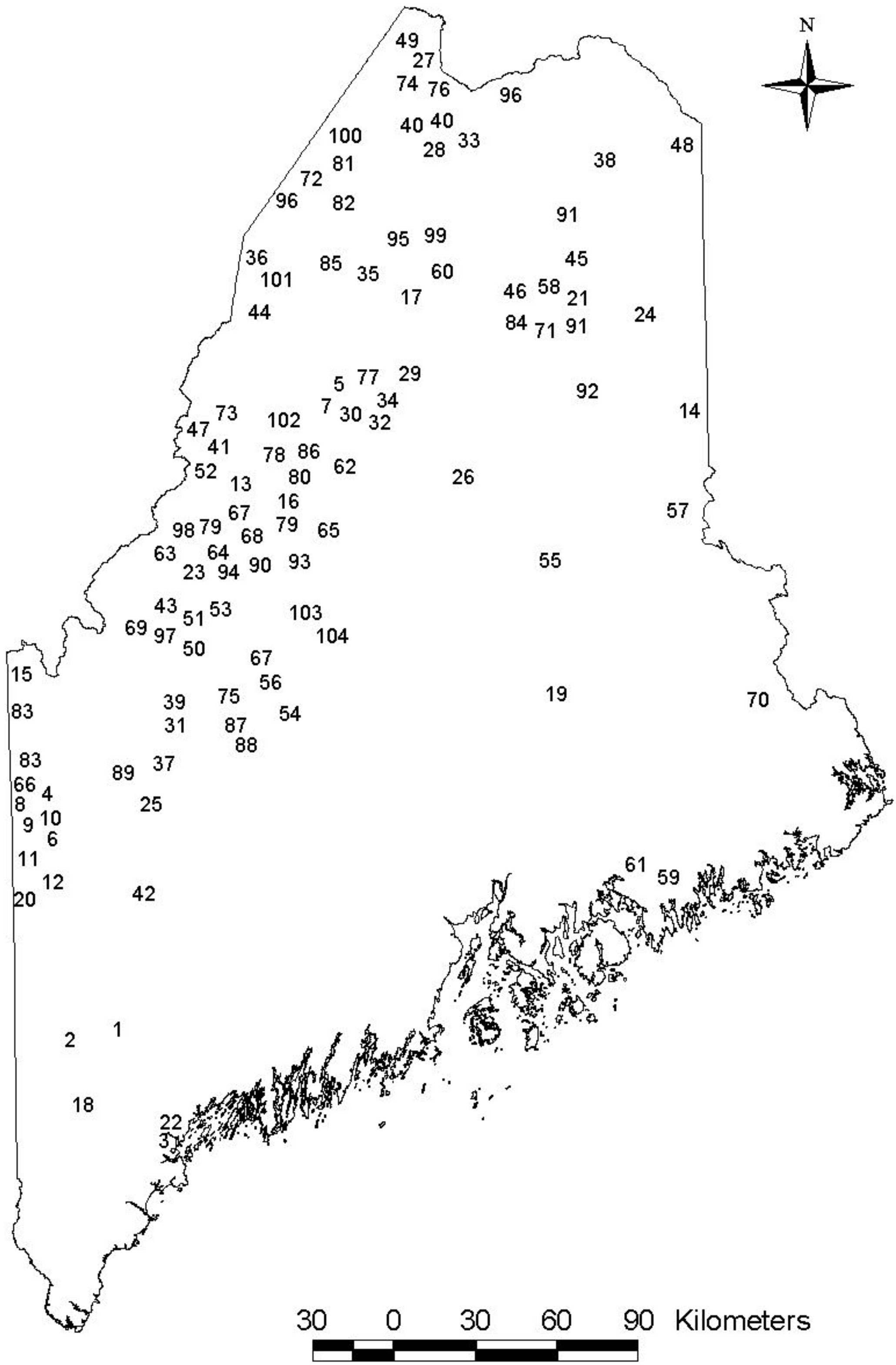

Figure A.1. Township-specific lynx observations in Maine, 1833-1999. Each reference matches the numbers listed in Table A.1. Locations are approximate due to clustering of locations. See Figure 1.1 for a temporal representation of these data.

Table A.2. A chronological listing of Canada lynx observed and reported at the regional scale with references, age, sex, and method of observation where available. Reference numbers match those in Figure A.2.

Letter	Year	Observer	Reference	Age and sex	No. Lynx
A	1840-1849	H.O. Stanley	Stanley (1906)	unknown	1
A	1843	J.G. Rich	Rich (1862)	unknown	49
B	1844-45	J. Simmons	Simmons (1845)	unknown	11
C	1848 - 1891	A. McLain	Anonymous (1891)	unknown	45
D	1860	A.P. Willard	Palmer (1949)	unknown	2
E	1860	R. Philbrook	Palmer (1949)	unknown	12
F	1861	M. Hardy	Palmer (1949)	unknown	20
G	1865	J.G. Rich	Harvard MCZ[1] 452-459	unknown	8
H	1865	J.G. Rich	Harvard MCZ 891	unknown	1
I	1868	H. Clapp	Clapp (1868)	unknown	9
J	1875	E.E. Thomas	Thomas (1923)	unknown	4
H	1897	C.H. Goldthwaite	Harvard MCZ B7259	female	1
K	1901	"M.S."	M.S. (1902)	1 adult, 3 juveniles	4
L	1947-1959	C. Beaulieu	Pers. com., R. Joseph 1998	unknown	12
M	1962	R. Dyer	Pers. com., R. Joseph 1998	unknown	7
N	1983	E. Cameron	Pers. com., R. Joseph 1998	unknown	1

[1] Agassiz Museum of Comparative Zoology

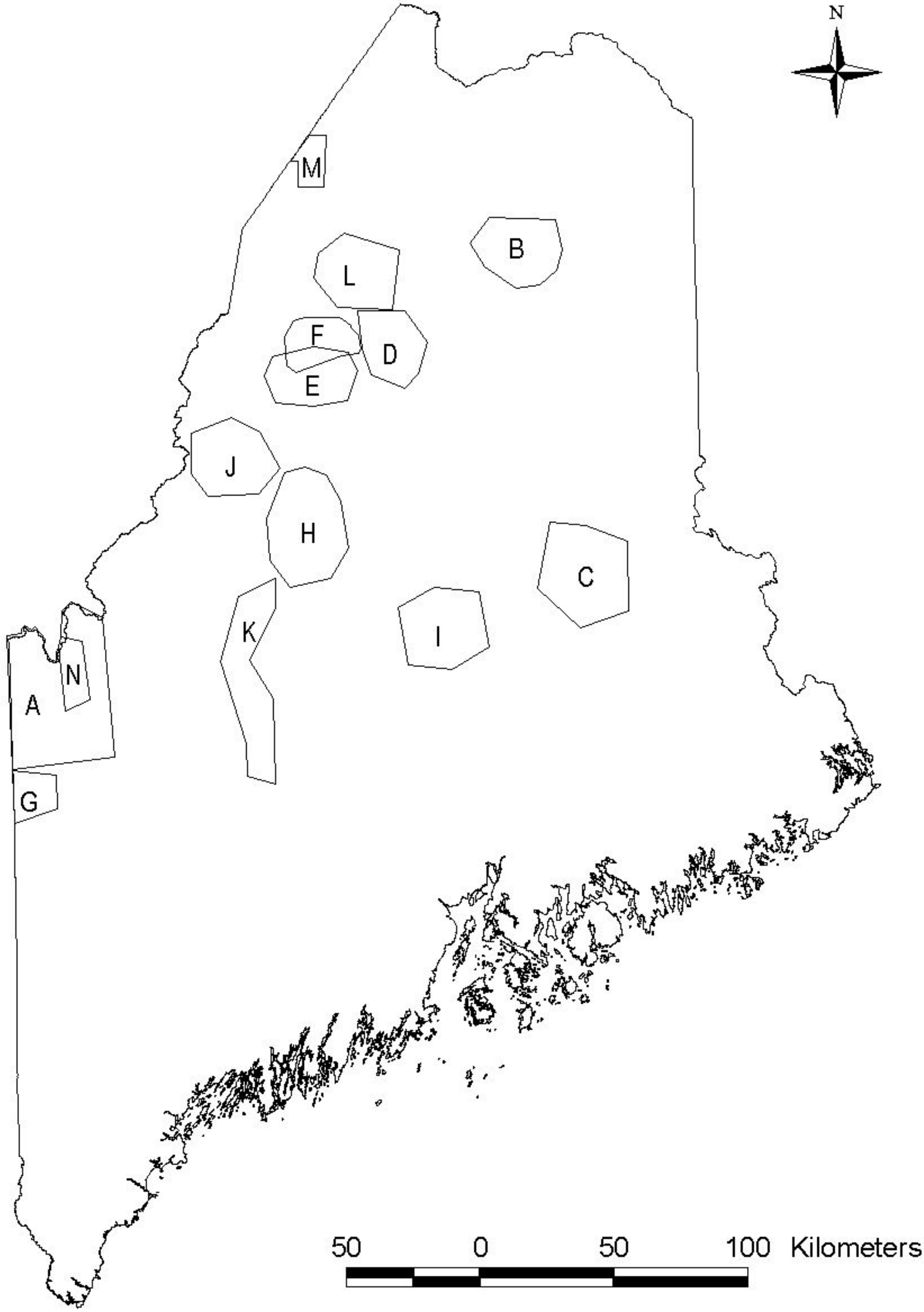

Figure A.2. Canada lynx observations from multi-township regions in Maine, 1843-1983. Most of these records are from traplines. Each letter matches the reference in Table A.2.

Table A.3. Chronological listing of other published comments regarding Canada lynx in Maine, and locations of lynx that were not specific to either year or region.

Reference	Year or Period	Comments
Whipple (1816)	~1816	present in Maine
Williamson (1832)	~1832	present in Maine
Emmons (1840)	~1840	present in Maine
Cram (1901)	~1845	common in southern Maine
Rich (1892)	1840 - 1850	common in western Maine
Verrill (1914)	~1850	"not uncommon" in south-western Maine
Audubon and Bachman (1852)	~1852	common in regenerating "burnt districts"
Thoreau (1893)	~1857	"plenty yet in the burnt grounds"
Hitchcock (1861)	1861	present in Maine
Hardy (1870)	1865 - 1870	about 100 per year though Bangor, decreasing
Stephens (1873) Appendix	~1873	about 200 per year trapped statewide
Hardy (1897)	~1873	"I was buying some 200 yearly…"
Hubbard (1884)	~1879	formerly common, becoming rare in Moosehead region
Penobscot (1879)	~1879	disappeared from lower and central Maine, common along north border
Hicks (1891)	~1891	present in Maine
Boardman (1892)	~1892	formerly abundant in eastern Maine, now rare
Rich (1892)	~1892	rare in western Maine
Anonymous (1897)	~1897	unusually plenty
Churchward (1898)	~1898	present in the "deep woods" of Maine
Allen (1904)	~1904	present in Maine
Hardy (1907a)	~1907	lynx absent from coast and near settlements, present elsewhere
Hardy (1907b)	~1907	"the number of lynx varies greatly"

Table A.3. Continued

Reference	Year or Period	Comments
Annual Reports of the Commissioners	1902	8 lynx trapped or shot in Maine
of Inland Fisheries and Game[1]	1911	5 lynx, 54 bobcat trapped or shot in Maine
" " " " "	1912	18 lynx, 93 bobcat trapped or shot in Maine
" " " " "	1913	18 lynx, 67 bobcat trapped or shot in Maine
" " " " "	1914	9 lynx, 36 bobcat trapped or shot in Maine
" " " " "	1915	7 lynx, 38 bobcat trapped or shot in Maine
" " " " "	1916	8 lynx, 88 bobcat trapped or shot in Maine
" " " " "	1917	8 lynx, 83 bobcat trapped or shot in Maine
" " " " "	1918	2 lynx 54 bobcat trapped or shot in Maine
" " " " "	1919	8 lynx, 192 bobcat trapped or shot in Maine
" " " " "	1920	22 lynx, 125 bobcat trapped or shot in Maine
" " " " "	1922	6 lynx, 155 bobcat trapped or shot in Maine
" " " " "	1924	1 lynx trapped or shot in Maine
" " " " "	1926	10 lynx trapped or shot in Maine
" " " " "	1928	11 lynx trapped or shot in Maine
Allen (1923)	~1923	formerly common, much depleted
Harvard MCZ 50520, 50521	~ 1954	present in Maine
Hunt (1964)	~1964	rare, present mainly in extreme northwestern Maine
Schemnitz (1966)	~1966	rare, restricted to the "northern wilderness"
Letourneau (1967)	~1967	has become rare in Maine

[1] The Commissioners' Reports did not distinguish between bobcat and Canada lynx, calling both "wildcat," in 1900 (19 caught), 1907 (19 caught) 1908 (30 caught), and 1910 (75 caught). Numbers in this appendix include only statistics reported for licensed hunters and trappers. Statistcis on licensed taxidemistists and fur dealers are not included, because fur dealers and taxidemists were likely handling lynx caught in Canada and imported to Maine.

APPENDIX B
MODEL COEFFICIENTS FOR THE BROAD-SCALE CANADA LYNX (*Lynx canadensis*) MODELS

Table B.1. Model coefficients and standard error for each variable from alternative logistic regression models describing the probability of Canada lynx occurrence in eastern North America.

	Constant		Deciduous		Snowfall		Conifer		Roads		Bobcat	
	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE
Deciduous, Snowfall, Conifer	-12.16	0.651	-0.058	0.007	0.048	0.002	-0.011	0.003				
Deciduous, Snowfall, Bobcat, Roads, Conifer	-12.32	0.776	-0.057	0.007	0.048	0.003	-0.011	0.003	0.007	0.289	8.504	8.221
Deciduous, Snowfall	-12.78	0.638	-0.052	0.007	0.049	0.002						
Deciduous, Snowfall, Roads	-12.98	0.722	-0.053	0.007	0.05	0.002			0.171	0.273		
Deciduous, Snowfall, Bobcat	-12.86	0.67	-0.052	0.007	0.049	0.002					3.637	8.857
Deciduous, Snowfall, Bobcat, Roads	-13.09	0.76	-0.053	0.007	0.05	0.003			0.184	0.274	4.254	8.83
Snowfall	-14.48	0.615			0.054	0.002						
Snowfall, Roads	-13.96	0.714			0.052	0.002			-0.364	0.27		
Snowfall, Roads, Bobcat	-14.21	0.742			0.053	0.003			-0.322	0.272	10.917	8.109

Table B.1. *continued*

	Constant		Deciduous		Snowfall		Conifer		Roads		Bobcat	
	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE
Conifer, Snowfall	-14.52	0.625			0.054	0.002	0.001	0.003				
Conifer, Snowfall, Roads	-13.97	0.745			0.052	0.002	0	0.004	-0.361	0.28		
Deciduous, Bobcat, Roads	2.189	0.1	-0.087	0.008					-2.675	0.227	-173.2	13.713
Deciduous, Roads	1.703	0.086	-0.079	0.008					-2.787	0.219		
Conifer, Bobcat, Roads	1.974	0.103					0.004	0.002	-4.291	0.201	-175.2	17.16
Deciduous	0.897	0.056	-0.109	0.008								
Conifer, Roads	1.983	0.1					-0.012	0.002	-4.561	0.201		
Roads	1.632	0.079							-4.256	0.189		
Bobcat	-0.005	0.044									-112.2	11.788
Conifer	-0.385	0.047					0.01	0.002				

APPENDIX C
MODEL COEFFICIENTS FOR THE SNOWSHOE HARE (*Lepus americanus*) MODELS

Table C.1. Model coefficients and standard errors for each habitat type[1] from alternative logistic regression models, describing abundant versus absent snowshoe hares on snow-track surveys in Maine. Vegetation types were from the Maine Vegetation and Land Cover map (Hepinstall et al. 1999).

Year	Model	constant		LREG		DEC		FWET		CLEAR		HPART		EREG	
		x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE
1995	DEC, LREG, HPART	-1.679	-0.022	0.051	0.011	0.000	0.008					-0.044	0.026		
1996	DEC, LREG, HPART	-1.240	0.244	0.011	0.016	-0.031	0.013					-0.189	0.071		
1998	DEC, LREG, HPART	-0.645	0.306	0.062	0.020	-0.045	0.012					-0.036	0.039		
1999	DEC, LREG, HPART	0.797	0.215	0.008	0.013	-0.036	0.006					-0.029	0.025		
ALL	DEC, LREG, HPART	-0.825	0.109	0.027	0.006	-0.014	0.004					-0.051	0.014		
1995	DEC, LREG	-1.836	0.207	0.052	0.011	-0.001	0.008								
1996	DEC, LREG	-1.542	0.232	0.006	0.015	-0.032	0.013								
1998	DEC, LREG	-0.769	0.279	0.063	0.020	-0.043	0.012								
1999	DEC, LREG	0.724	0.204	0.007	0.012	-0.036	0.006								

Table C.1. *continued*

Year	Model	constant		LREG		DEC		FWET		CLEAR		HPART		EREG	
		x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE
ALL	DEC, LREG	-0.982	0.102	0.027	0.006	-0.013	0.004								
1995	DEC, LREG, HPART, FWET	-2.267	0.283	0.060	0.012	0.007	0.008	0.070	0.017			-0.032	0.026		
1996	DEC, LREG, HPART, FWET	-1.905	0.324	0.022	0.017	-0.020	0.012	0.050	0.014			-0.171	0.071		
1998	DEC, LREG, HPART, FWET	-0.700	0.337	0.063	0.020	-0.043	0.013	0.008	0.021			-0.040	0.040		
1999	DEC, LREG, HPART, FWET	0.847	0.243	0.008	0.013	-0.036	0.006	-0.006	0.014			-0.029	0.025		

Table C.1. *continued*

Year	Model	constant		LREG		DEC		FWET		CLEAR		HPART		EREG	
		x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE
ALL	DEC, LREG, HPART, FWET	-1.071	0.129	0.030	0.006	-0.010	0.004	0.028	0.007			-0.049	0.014		
1995	DEC, LREG, EREG, HPART, FWET	-1.943	0.345	0.062	0.012	0.001	0.009	0.063	0.018			-0.037	0.026	-0.010	0.006
1996	DEC, LREG, EREG, HPART, FWET	-1.832	0.372	0.022	0.017	0.021	0.013	0.049	0.014			-0.169	0.071	-0.003	0.008
1998	DEC, LREG, EREG, HPART, FWET	-0.367	0.390	0.072	0.022	-0.051	0.014	0.004	0.021			-0.047	0.041	-0.014	0.009
1999	DEC, LREG, EREG, HPART, FWET	0.477	0.337	0.010	0.013	-0.030	0.007	-0.001	0.014			-0.027	0.025	0.010	0.006

Table C.1. *continued*

Year	Model	constant		LREG		DEC		FWET		CLEAR		HPART		EREG	
		x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE
ALL	DEC, LREG, EREG, HPART, FWET	-1.187	0.164	0.030	0.006	-0.008	0.004	0.029	0.007			-0.048	0.014	0.003	0.003
1995	DEC, FWET	-1.606	0.189			-0.002	0.008	0.056	0.016						
1996	DEC, FWET	-2.025	0.238			-0.023	0.012	0.052	0.013						
1998	DEC, FWET	-0.206	0.262			-0.048	0.012	-0.002	0.019						
1999	DEC, FWET	0.839	0.196			-0.037	0.006	-0.007	0.013						
ALL	DEC, FWET	-0.890	0.095			-0.014	0.004	0.025	0.007						
1995	CLEAR, DEC, LREG, EREG, HPART, FWET	-1.853	0.352	0.059	0.012	0	0.009	0.062	0.018	-0.026	0.027	-0.031	0.027	0.0	0.006

Table C.1. *continued*

Year	Model	constant		LREG		DEC		FWET		CLEAR		HPART		EREG	
		x	SE	x	SE	x	SE	x	SE	x	SE	x	SE	x	SE
1996	CLEAR, DEC, LREG, EREG, HPART, FWET	-1.794	0.383	0.021	0.017	-0.022	0.013	0.048	0.014	-0.021	0.054	-0.168	0.071	-0.003	0.008
1998	CLEAR, DEC, LREG, EREG, HPART, FWET	-0.376	0.401	0.072	0.022	-0.051	0.014	0.004	0.021	0.003	0.035	-0.048	0.042	-0.014	0.009
1999	CLEAR, DEC, LREG, EREG, HPART, FWET	0.721	0.359	0.006	0.013	-0.032	0.008	-0.003	0.014	-0.039	0.019	-0.028	0.025	0.008	0.006
ALL	CLEAR, DEC, LREG, EREG, HPART, FWET	-1.122	0.168	0.028	0.006	-0.009	0.004	0.029	0.008	-0.018	0.013	-0.046	0.015	0.004	0.003

[1] DEC = Mature deciduous forest

LREG = Late regeneration forest harvested before 1991, sapling to poletimber with greater than 50% canopy closure

EREG = Early regeneration forest harvested before 1991, seedling to sapling size trees

Table C.1. *continued*

HPART = Heavy partial cut, greater than 50% of canopy removed

CLEAR = Clear-cut between 1991 and 1993, greater than 90% canopy removed

FWET = Deciduous or coniferous scrub-shrub or forested wetlands

APPENDIX D

MODEL COEFFICIENTS FOR CANADA LYNX (*Lynx canadensis*) IN NORTHWESTERN MAINE

Table D.1. Model parameters and standard error for each habitat type[1] from the each logistic regression model, describing the probability of lynx occurrence in northwestern Maine, from snow track survey data, 1994-1999. Vegetation types were from the Maine GAP Vegetation and Land Cover map (Hepinstall et al. 1999).

Model	α		β_{CLEAR}		β_{PART}		β_{LREG}	
	x	SE	x	SE	x	SE	x	SE
CLEAR, PART, LREG, FWET, DEC	1.81	1.59	-56.33	26.57	-45.59	20.34	34.42	12.06
CLEAR, PART, LREG, FWET	-0.36	1.00	-50.26	26.06	-44.07	17.07	40.77	11.63
CLEAR, PART, LREG, FWET, DEC, CON	1.68	2.32	-50.28	26.73	-46.04	20.64	35.12	13.89
CLEAR, PART, LREG	-1.39	0.82	-51.86	25.56	-40.54	17.48	34.88	10.39
PART, LREG, FWET, DEC	0.06	1.34	N/A	N/A	-40.25	18.10	33.77	11.53
CLEAR, PART, LREG, FWET, DEC, CON, SNOW	1.19	7.01	-56.33	26.93	-46.69	22.03	35.28	13.97
CLEAR, LREG, FWET	-1.77	0.88	-37.73	22.82	N/A	N/A	22.76	8.40
LREG	-3.28	0.67	N/A	N/A	N/A	N/A	19.33	7.88
DEC, SNOW	0.76	5.10	N/A	N/A	N/A	N/A	N/A	N/A

Table D.1. continued

	β_{FWET}		β_{DEC}		β_{CON}		β_{SNOW}	
	x	SE	x	SE	x	SE	x	SE
CLEAR, PART, LREG, FWET, DEC	-23.78	12.17	-8.34	4.86	N/A	N/A	N/A	N/A
CLEAR, PART, LREG, FWET	-19.42	12.18	N/A	N/A	N/A	N/A	N/A	N/A
CLEAR, PART, LREG, FWET, DEC, CON	-24.19	12.59	-8.02	6.25	0.75	7.76	N/A	N/A
CLEAR, PART, LREG	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
PART, LREG, FWET, DEC	-24.33	11.83	-6.41	4.57	N/A	N/A	N/A	N/A
CLEAR, PART, LREG, FWET, DEC, CON, SNOW	-24.11	12.74	-8.03	6.31	0.83	7.81	0	0.04
CLEAR, LREG, FWET	-12.38	10.06	N/A	N/A	N/A	N/A	N/A	N/A
LREG	N/A	N/A	N/A	N/A	N/A	N/A	N/A	N/A
DEC, SNOW	N/A	N/A	-5.01	3.31	N/A	N/A	-0.01	0.02

Table D.1. continued

[1] CLEAR = Clear-cut between 1991 and 1993, greater than 90% canopy removed.

PART = Heavy and light partial cut, includes selection harvest, shelterwood, and improvement thinning.

LREG = Late regeneration forest harvested before 1991, sapling to poletimber with greater than 50% canopy closure.

FWET = Deciduous or coniferous scrub-shrub or forested wetlands.

DEC = Mature deciduous forest.

CON = Mature coniferous forest.

SNOW = predicted 10 year mean annual snowfall from weather station data, 1980-1990, from Chapter 2.

APPENDIX E
VARIABILITY OF MODEL PARAMETERS FROM 20 RANDOM SAMPLES OF TRACK TRANSECTS

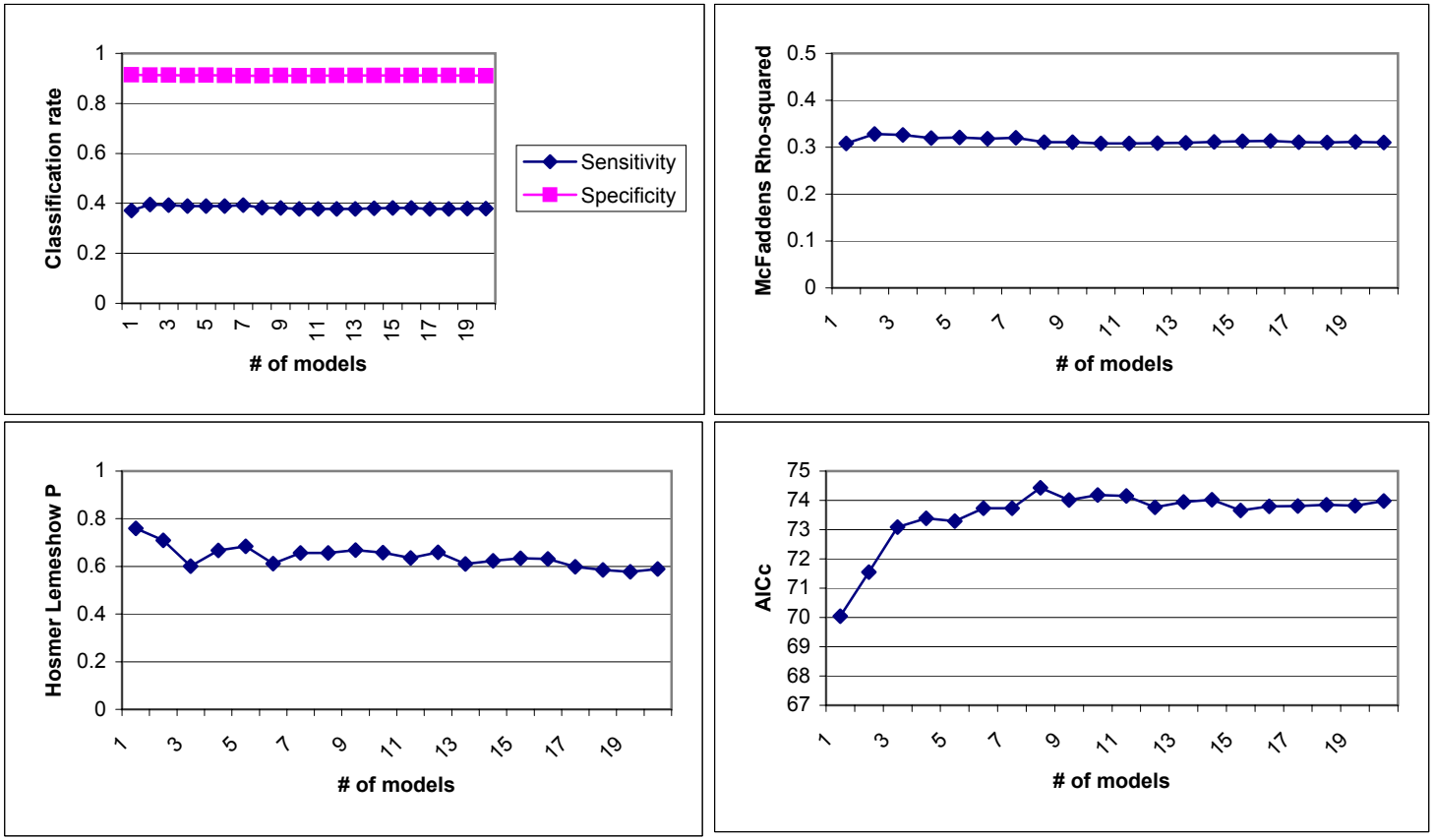

Figure E.1. Cumulative average of model parameters as a function of the number of models considered. Models were constructed from 20 random selections of track transects on which Canada lynx were detected or not detected. Variables in the models were proportion of a 100 km^2 circle in recent clearcut, partial harvest, regenerating forest, forested wetland, and mature deciduous forest.

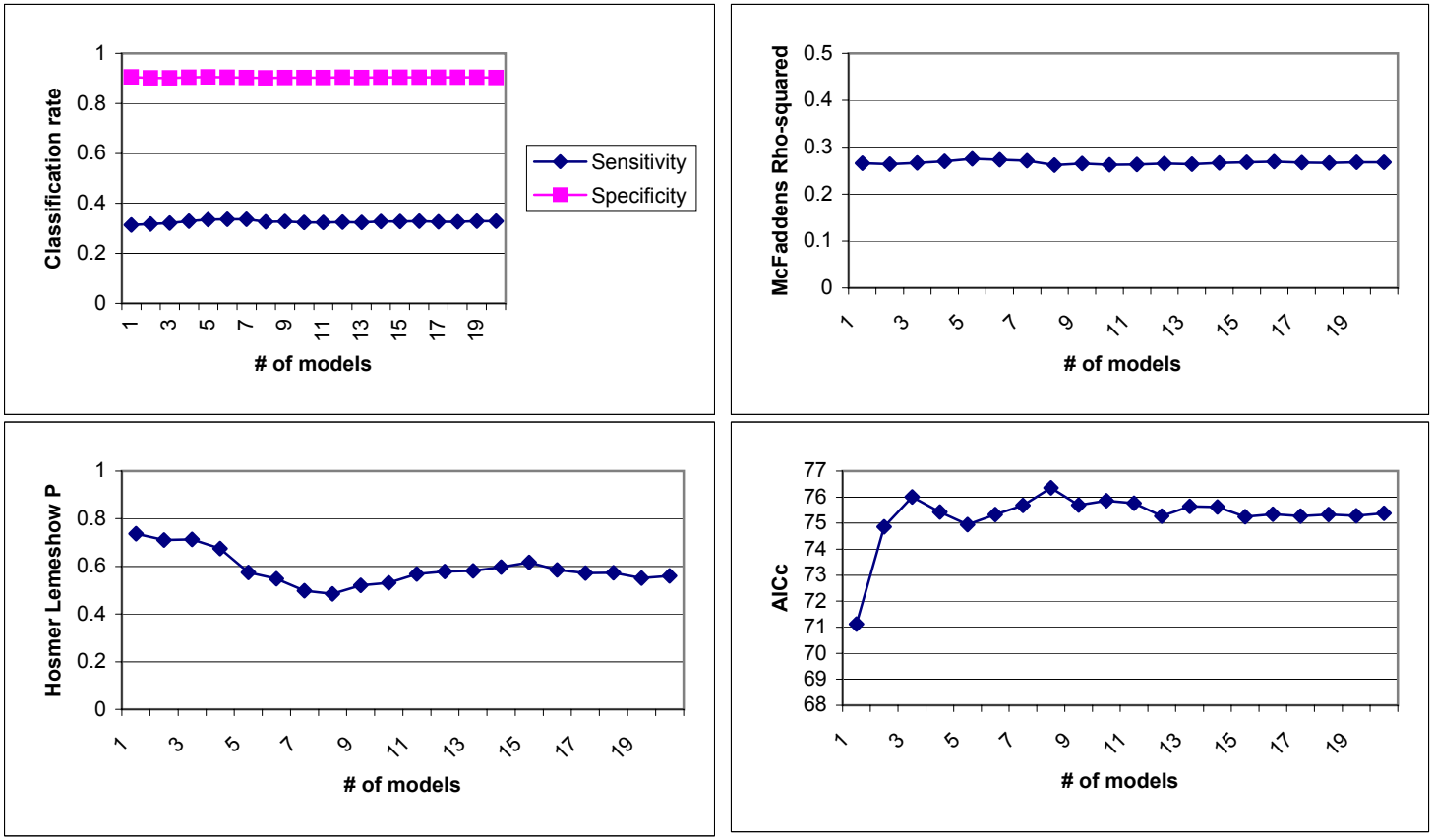

Figure E.2. Cumulative average of model parameters as a function of the number of models considered. Models were constructed from 20 random selections of track transects on which Canada lynx were detected or not detected. Variables in the models were proportion of a 100 km^2 circle in recent clearcut, partial harvest, regenerating forest, and forested wetland.

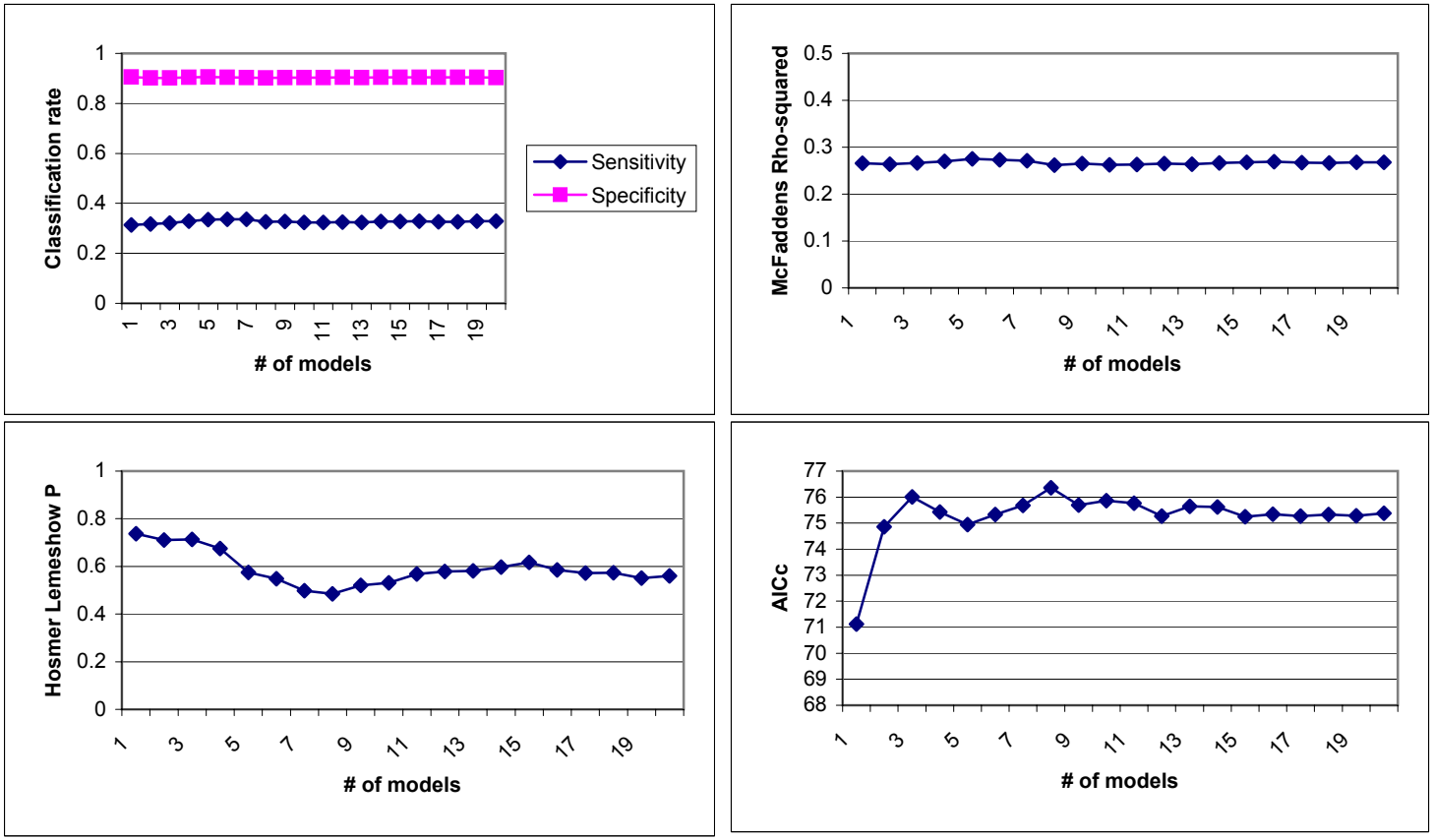

Figure E.2. Cumulative average of model parameters as a function of the number of models considered. Models were constructed from 20 random selections of track transects on which Canada lynx were detected or not detected. Variables in the models were proportion of a 100 km^2 circle in recent clearcut, partial harvest, regenerating forest, and forested wetland.

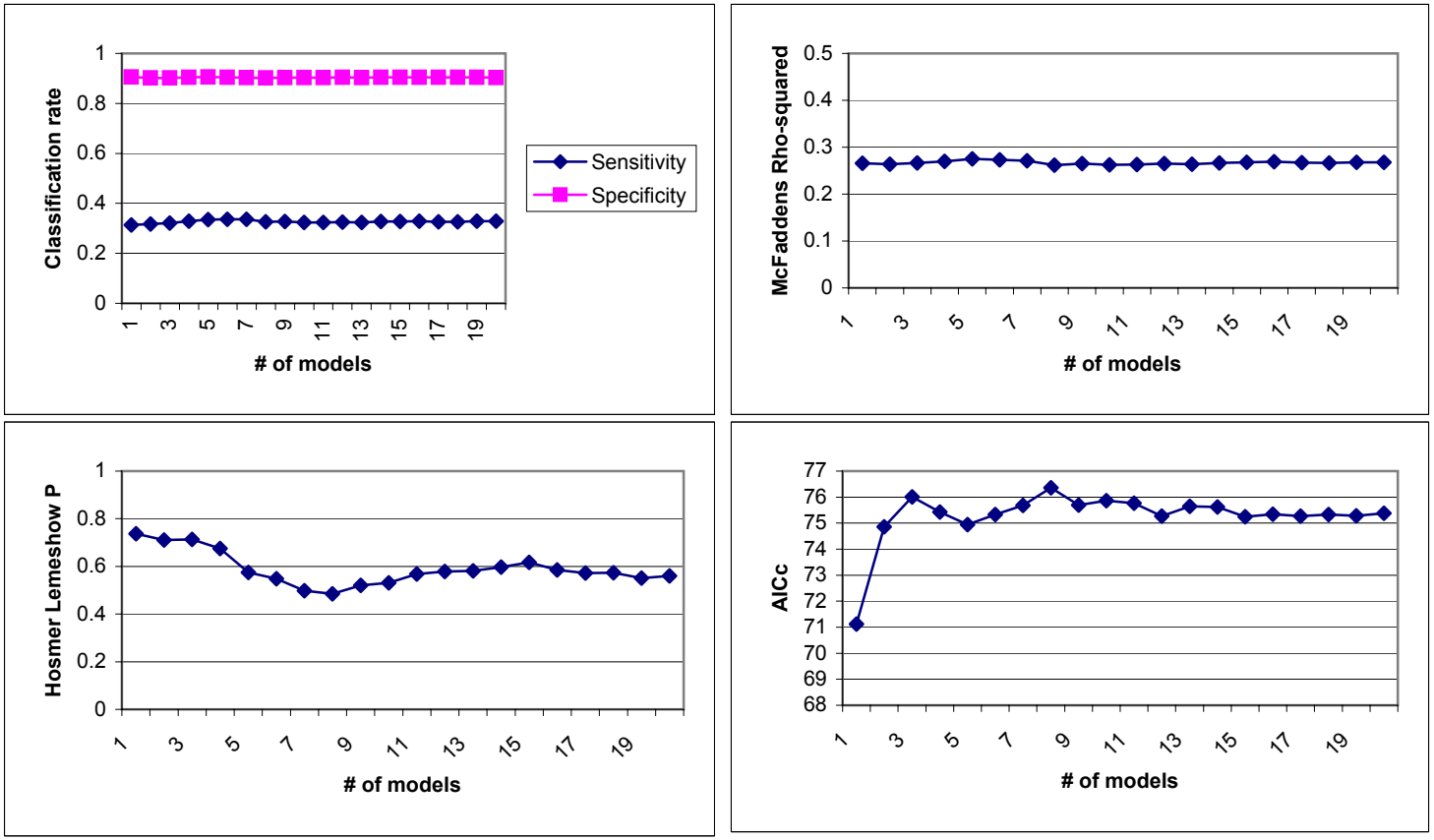

Figure E.2. Cumulative average of model parameters as a function of the number of models considered. Models were constructed from 20 random selections of track transects on which Canada lynx were detected or not detected. Variables in the models were proportion of a 100 km^2 circle in recent clearcut, partial harvest, regenerating forest, and forested wetland.

APPENDIX F

CANADA LYNX (L*ynx canadensis*) AND SNOWSHOE HARE (*Lepus americanus*) MODELING USING CLASSIFICATION AND REGRESSION TREE (CART)

Classification and regression tree (CART) is a modeling technique that is becoming more common in ecology (De'ath and Fabricius 2000). CART trees are constructed by repeatedly splitting the data into homogenous, mutually exclusive sets using a rule that finds the best possible split at each branch or "node" in the tree. Thus, CART does not assume that the data fits a particular form (such as a straight line or the logistic curve). CART also reveals hierarchical or contingent relationships among variables (Clark and Pregibon 1992, De'ath and Fabricius 2000). The number of nodes in the final tree can be determined in several ways.

Because I was only using CART as an exploratory tool, nodes were created when they resulted in a greater than 0.01 improvement in the r^2 of the final model. I chose to model lynx and hare habitat in Chapters 2-4 using logistic regression because logistic regression, results in a probability of occurrence. By contrast, CART predicts a binary variable as binary outcome.

After completing the analyses for Chapters 2-4, I analyzed the same data using CART (SYSTAT 9.0, SPSS Inc., Chicago, Illinois, USA). The models from the CART analysis were remarkably similar to the results of the logistic regression models with the best Akaike's Information Criterion (AIC) scores (Figures J.1-3). The CART model for lynx presence in eastern North America had a r^2 of 0.768, and snowfall explained 68.1% of the variance. Lynx presence was explained exclusively by snowfall and deciduous forest, despite the fact that bobcat harvest density, conifer forest, and road density were input to the model. The CART model for hare habitat in northern Maine first subset the model by year, and then by the amount of late regeneration, deciduous forest, and forested wetland. This model had a relatively low r^2 of 0.195. Again, results

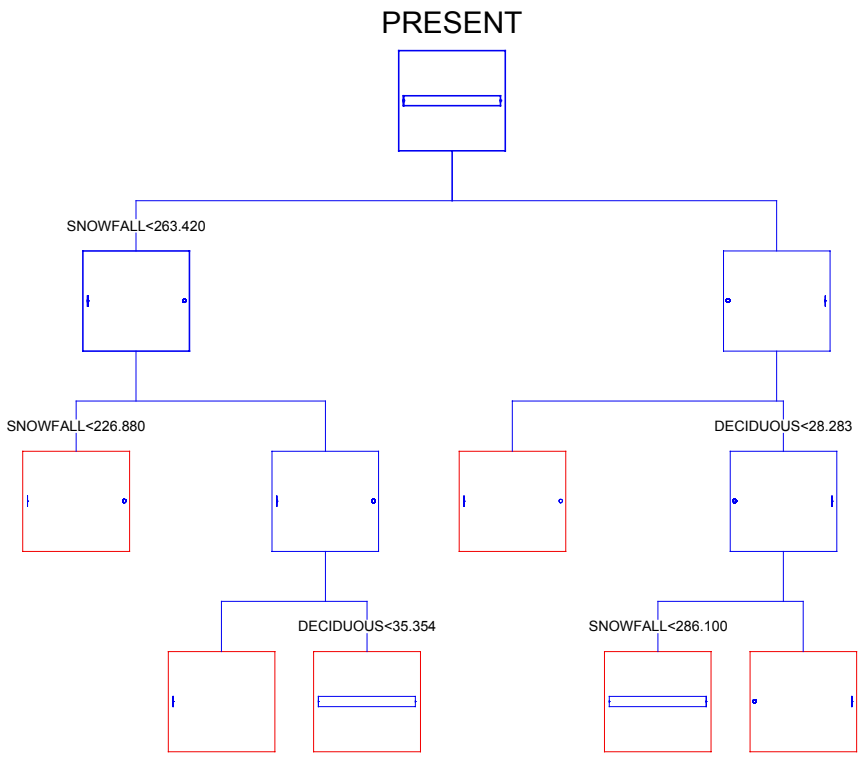

Figure F.1. Tree of Canada lynx presence in eastern North America, using the data from Chapter 2. Boxes to the right of each split indicate presence. Lynx presence was predicted using only snowfall and deciduous forest.

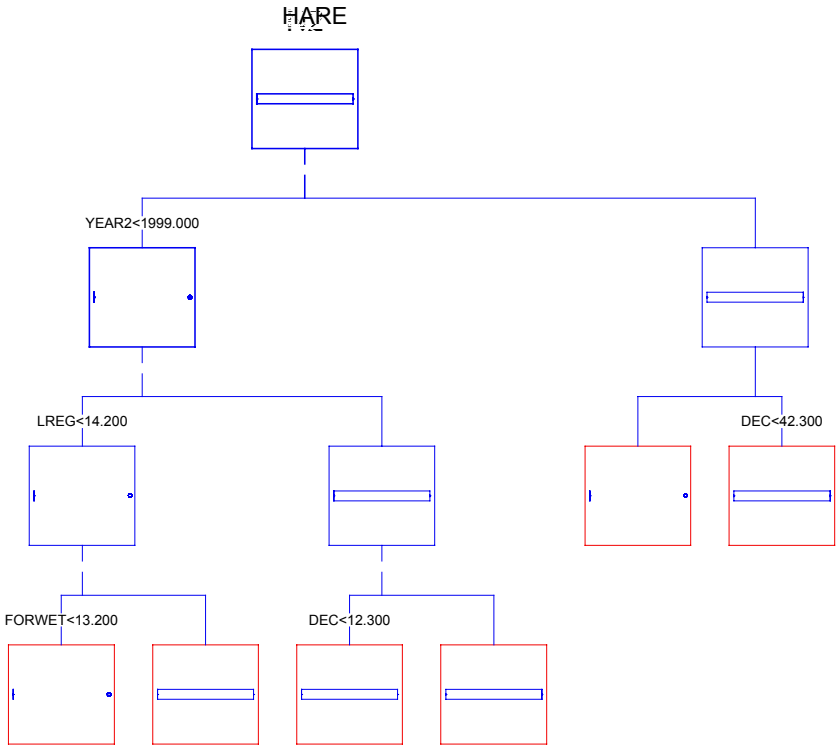

Figure F.2. Tree of snowshoe hare abundance in northern Maine, using the data from Chapter 3. Boxes to the right of each split indicate presence. Hare abundance was first subset by year. Hare were most abundant in 1999, especially where the area surrounding each transect was less than 42.3% mature deciduous forest. For 1995-1998, hare abundance was associated with late regeneration and forested wetlands.

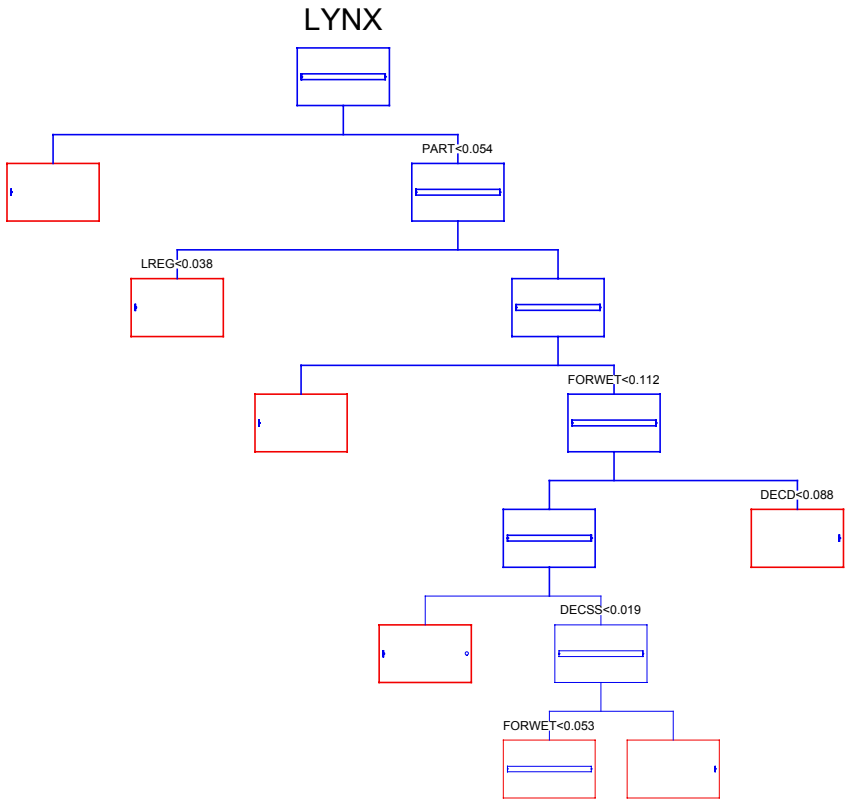

Figure F.3. Tree of Canada lynx occurrence in northwestern Maine, using the data from Chapter 4. Boxes to the right of each split indicate presence. Lynx presence was predicted for areas with less than 5.4% of a 100 km^2 landscape in partial harvest, and more than 3.8% of the landscape in late regeneration.

were similar to those in Chapter 3, even to the degree that temporal effects dominated the model. The CART model for lynx presence in northwestern Maine was similar to the results in Chapter 4, but the CART model did not include a prediction based on recent clear-cuts. The directions of associations were the same, and this model had a r^2 of 0.766.

The results of this exploratory analysis suggested that the patterns of habitat association reported in Chapters 2-4 were not artifacts of the assumptions inherent to logistic regression analysis, but gave similar results when other modeling methodologies were used.

BIOGRAPHY

Christopher Lee Hoving was born on a hot day in a condemned Army hospital at Fort Gordon, Georgia. Shortly thereafter Christopher relocated to Michigan, and did not return to Georgia for 20 years. In Grand Rapids, Michigan, Mr. Hoving attended Creston High School where he served proudly on a soccer team that lost most of its games and a debate team that was placed second in the city of Grand Rapids. After graduating from Creston in 1992, Chris wisely shunned an athletic career and enrolled at Michigan State University in East Lansing, Michigan. During the summers between his undergraduate years, Mr. Hoving worked in the factory of a multinational office products corporation, assisted a graduate student in northern Michigan studying deer damage to agricultural fields, and assisted another graduate student studying bats and small mammals in rural Idaho. After graduating *cum laude* with a Bachelor of Science degree in Fish and Wildlife in 1996, Chris worked one summer as a naturalist for a summer camp for physically handicapped children from inner city New York, and then volunteered in St. Louis, Missouri with the Mennonite Voluntary Service. In St. Louis Chris was an office manager, webmaster, and program assistant for the Missouri Coalition for the Environment. After St. Louis, Christopher spent a winter in Traverse City, Michigan before moving to Old Town, Maine in 1998. In Maine, Chris learned the art of GIS. His models of snowfall, 1950-1990, have been used in posters and presentations on fisher, marten, and lynx. He has been a member of The Wildlife Society since 1993. Christopher is a candidate for the Master of Science degree in Wildlife Ecology from The University of Maine in May, 2001.