INFLUENCES OF PAST AND FUTURE FOREST MANAGEMENT ON THE SPATIOTEMPORAL DYNAMICS OF HABITAT SUPPPLY FOR CANADA LYNX AND AMERICAN MARTENS IN NORTHERN MAINE

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

An Abstract of the Thesis Presented
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I evaluated the effects of past and future forest management on habitat supply and probability of occurrence for Canada lynx (*Lynx canadensis*) and American martens (*Martes americana*). I used timber harvest and forest composition information derived from Landsat satellite imagery to develop spatially-explicit time series of habitat for lynx and martens (1970-2007) across 1.62 million hectares of commercial forestland in Maine. Timber harvesting was widespread with 55% of the forestlands receiving a harvest 1970-2007, which ultimately resulted in the broad-scale loss of marten habitat (>435,000 ha) and the increase of lynx foraging habitat (~189,000 ha). Rapid declines in habitat supply and probability of occurrence for martens occurred 1975-1991, as large blocks of spruce-fir forest were salvage logged in response to the 1973-1985 spruce budworm (*Choristoneura fumiferana*) outbreak. As regenerating forest created during this period began to reach 16 years post-harvest there was a rapid increase in lynx foraging habitat

and the mean density of snowshoe hares (*Lepus americanus*) within potential lynx home ranges, 1985-2007. Probability of occurrence for lynx increased during this period in areas of increased hare density. Marten habitat continued to decline in the 1990s and 2000s, which coincided with shifts in timber harvesting patterns that resulted from new forest policies implemented in 1991.

To provide a better understanding of how past forest management legacy (1970-2007) will influence outcomes of future forest management, I developed alternative forest management scenarios to model the effects on habitat supply and population density for lynx and martens, 2007-2032, across 14 townships with diverse legacies. The worst scenario for future lynx and marten habitat was a continuation of recent (2001-2007) trends in harvest rates, including an aspatial limit (~4% of total acreage harvested) on clearcut harvesting to mimic the effects of current forest policies in Maine. Removing the limit on clearcut harvesting provided some limited benefit to both species; under all harvest scenarios, however, habitat supply and densities for both species are expected to decline from current levels as a result of past forest management legacies. Conservation planning for these species needs to incorporate the anticipated loss of habitat supply in the future.

PREFACE

Understanding the spatial and temporal dynamics of landscape change and its influence on habitats and species occurrence patterns is essential to predicting and mitigating the effects of land-use activities. In the Acadian Forest of Maine, timber harvesting is currently the dominant driver of landscape change, and over the last 40 years timber harvesting rates and patterns have been strongly influenced by natural disturbance events and changes in forest policy and forestland ownership. The rate and the extent of clearcut harvesting increased significantly during the periods of preemptive and salvage logging in the 1970s and 1980s, which occurred in response to the infestation of spruce-fir forest during the 1973-1985 spruce budworm (*Choristoneura fumiferana*) outbreak. During this salvage period, there were no legislative definitions or standards in place to regulate the size or arrangement of clearcuts in Maine, and eventually the public outcry over the large scale of salvage clearcuts lead to the passage of the Maine Forest Practices Act (MFPA) in 1989 (12 MRSA §8867-A to §8888 & MFS Rules Chapter 20). The immediate effects of the MFPA were that the first year after the legislation was passed the number of acres harvested by clear-cut declined by ~40%. In the 10 years following passage, the total annual acreage harvested from commercial forestlands increased from ~250,000 acres to ~500,000 acres, and the percentage of the acreage clearcut declined from 40% to 4%. The partial harvests that have replaced the clearcuts in northern Maine include a variety of silivicultural treatments, including both even-aged (e.g., shelterwood) and uneven-aged (e.g., selection) management techniques that result in a wide range of residual stand conditions (Robinson 2006).

Forest management creates landscape patterns that are persistent and that differ significantly from those that develop under natural disturbance regimes (Franklin and Forman 1987, Li et al. 1993, Mladenoff et al. 1993, Wallin et al. 1994, James et al. 2007), and species-level responses to habitat disturbance can be complex and can take time to emerge (Ewers and Didham 2006). Little attention, however, is generally directed at documenting the processes that contribute to habitat distribution or the associated species-habitat relationships (Knick and Rotenberry 2000). Although numerous studies have evaluated species distributions and abundance in landscapes degraded or fragmented by timber harvesting (e.g., McGarigal and McComb 1995, Cushman and McGarigal 2003, Betts et al. 2006), few attempt to also understand the spatial and temporal structure of the habitat changes that have previously occurred. Methods are needed that can provide insight into how landscape change affects the spatiotemporal variability in habitats and species occurrence. Thus, my dissertation research evaluated the influence of past and future forest management on the spatial and temporal dynamics of habitat supply and probability of occurrence for Canada lynx (*Lynx canadensis*) and American martens (*Martes americana*) across 1.62 million hectares of commercial forestland in northern Maine. My overall goal was to understand the process and the cumulative effects of forest management as an agent of broad-scale landscape change using two species that represent a range of ecological conditions.

Umbrella species have been proposed as a single-species approach that can be used for simplifying biodiversity conservation by targeting the protection of habitat for species whose protection should also maintain the viability of an array of other species with similar habitat associations (Murphy and Wilcox 1986, Noss 1990). Lynx and

martens have shown great potential as umbrella species for conservation planning in the Acadian forest (Hepinstall and Harrison *In preparation*), and because the two species have different habitat associations, early- and mid-to-late successional forests respectively, they also represent complementary groups of species for which they can serve as umbrella species (Lambeck 1997). Lynx (Poole 1994, Slough and Mowat 1996, Ward and Krebs 1985) and martens (Bissonette et al. 1997, Chapin et al. 1998) also have large spatial requirements, which make them good umbrella species for understanding how broad-scale habitat conditions have changed over the last 40 years as a result of the timber harvesting rates, patterns, natural disturbance events, and changes in forest policy and forestland ownership.

In Chapter 1, I used timber harvest and forest composition information derived from Landsat satellite imagery to develop a spatially-explicit time series of marten habitat supply (1975-2007), and used the time series to quantify the changes in marten habitat quantity, configuration, and spatial distribution. I documented the reduction in marten habitat resulting from habitat loss and fragmentation to better understand how these processes contributed to overall declines in marten habitat. I used previously developed models based on landscape metrics for predicting the probability of occurrence (POC) for male and female martens (Hepinstall et al. *In preparation*) to develop a time series of POC for each sex, and used Empirical Orthogonal Functions (EOFs) to quantify the underlying spatiotemporal patterns. I also determined the cumulative percentage, within all potential marten home ranges, of the remaining marten habitat ca. 2007 that was affected by partial harvesting. These analyses provided insight into the interacting effects

of forest management and forest policy on marten habitat, and the potential for partial harvesting to compound the effects of habitat loss and fragmentation.

In Chapter 2, I modeled landscape-scale lynx occurrence (2nd-order selection; Johnson 1980) using presence/absence data provided by snow track surveys conducted across townships in northern and western Maine 2003-2006. I used the presence/absence data to simulate occupied and non-occupied home ranges and developed a 2004 forest cover type map, based on timber harvest and forest composition information from Landsat satellite imagery, to derive habitat-based predictor variables. I evaluated whether lynx selected habitat based on home range composition, landscape-scale density of snowshoe hares (*Lepus americanus*), and/or habitat configuration. Using the resulting top-ranked model, I calculated the POC for lynx and estimated the density of resident adults, which allowed me to make recommendations about the importance of maintaining regenerating forest to support habitats with high snowshoe hare density and lynx occurrence.

In Chapter 3, I documented and quantified the effects of forest management (1988-2007) on the ecological factors, identified in Chapter 2 (i.e., snowshoe hare density and percent mature conifer), that drive lynx occurrence at the home range-scale. I generated a spatially-explicit time series of lynx POC using the top-ranked model identified in Chapter 2, and quantified spatiotemporal trends in the time series by calculating the area of forestland within probability categories and by estimating and comparing the density of adult resident lynx in 1991 and 2007. Finally, I estimated the future supply of high-quality hare habitat 2007-2022 based on timber harvesting patterns in the 1990s and 2000s and compared the spatial distribution of habitat in 2007 and 2022,

which allowed me to demonstrate how the distribution of habitat that can support high snowshoe hare densities will shift away from areas currently occupied by lynx in the near future.

In Chapter 4, I used the Remsoft Spatial Planning System to model the outcomes of alternative forest management scenarios on habitat supply for lynx and martens over the next 25 years. I applied the scenarios to 14 townships with a diverse legacy of past forest management to provide a better understanding of how past forest management will influence the outcomes of future forest management. I developed scenarios to simulate realistic timber harvesting rates and patterns, and applied specific modifications to management plans including aspatial and spatial constraints of clearcut harvesting. I compared volume harvested, habitat supply for lynx and martens, and estimates of lynx and marten densities to evaluate the long-term effects of past and future forest management. I ranked each of the scenarios based on the total percent change in habitat quantity or density across all 14 townships between 2007 and 2032 to determine if any scenario provides some benefit for both lynx and martens, and also compared the percent change between the 14 townships across legacy and scenario using repeated measures Analysis of Variance. These analyses provided insight into the likely future of habitat supply for lynx and martens in northern Maine over the next 25 years, as well as potential strategies for maintaining habitat in the future.

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CHAPTER 1

SPATIOTEMPORAL DYNAMICS OF AMERICAN MARTEN HABITAT 1975-2007 ON COMMERICAL FORESTLANDS IN NORTHERN MAINE

ABSTRACT

The American marten (*Martes americana*) prefers habitats with complex physical structure associated with mature, closed-canopy forest, which provides protection from predators, resting sites, and access to prey. Previous research has concluded that timber harvesting can negatively influence marten density, and clearcut harvesting has been implicated in local population declines. Studies also suggest that martens may be particularly sensitive to habitat loss, predicting a steep decline in probability of home range occupancy in response to a small decline in percent suitable habitat. Little is known, however, about the cumulative effects of habitat loss and fragmentation on habitat supply for martens or the spatiotemporal dynamics of probability of occurrence for martens in a managed landscape. I developed a spatially-explicit time series of marten habitat, derived from satellite imagery, to evaluate effects of forest management on quantity and distribution of marten habitat, on spatiotemporal patterns of marten occurrence, and on estimated densities of martens in a dynamic forest landscape 1975-2007. Timber harvesting was widespread during this period and habitat that previous research has defined as suitable by martens declined by 434,978 ha (32%) as a result of stand-replacing harvests 1975-2007. Declines in probability of occurrence followed two spatiotemporal trends. The majority of loss occurred in the first 16 years of the time series (1975-1991), resulting from salvage logging that occurred in response to the 1973-1985 spruce budworm (*Choristoneura fumiferana*) outbreak. Rapid declines in

probability of occurrence for both male and female martens occurred where large blocks of mature spruce-fir forest were salvaged. Salvage logging also contributed to fragmentation of marten habitat with a 5.6-fold increase in the number of suitable habitat patches 1975-1991. Declines in habitat supply and probability of occurrence continued 1991-2007, coinciding with the broad-scale changes in timber harvesting patterns, which resulted from the implementation of new forest policies that contributed to a reduction in clearcut harvesting but a widespread increase in partial harvesting and total acreage harvested. The cumulative effects of loss and fragmentation of marten habitat 1975-2007 negatively influenced the percent suitable habitat and habitat configuration at the scale of a marten home range. These changes resulted in widespread declines in probability of occurrence for males and female martens and a substantial reduction in the number of townships with a potential marten density of $\geq$1 martens/km^2. Additionally, 307,862 ha (33%) of marten habitat received a partial harvest 1988-2007, which cumulatively affected >90% of potential marten home ranges. Partial harvesting may increase the spatial requirements of martens, suggesting that declines in potential marten densities are conservative. Further, based on previously published structural thresholds for marten habitat use, it is likely that some proportion of the areas that have received a partial harvest no longer represent suitable habitat for martens. Preliminary estimates suggest that in many partially-harvested stands the residual basal area is less than published thresholds for marten habitat use. This indicates that the actual loss of habitat 1975-2007 was between 32% and 54%, and strongly suggests that additional research is needed to determine the extent that partial harvesting is affecting habitat for martens, and

potentially compounding the effects of habitat loss and fragmentation that are reported herein.

INTRODUCTION

Reliable knowledge about the spatiotemporal distribution of habitat is essential to understand the cumulative effects of landscape change on patterns of species occurrence (Turner 1989, Turner et al. 2003). Patterns of habitat selection and occurrence for many species are influenced both by the amount and configuration of habitat (e.g., McGarigal and McComb 1995, Trzcinski et al. 1999), and for those species assessing how land use activities influence processes of habitat loss and fragmentation is also an important prerequisite to effectively predict population-level responses to habitat change (Schmiegelow and Mönkkönen 2002). Further, land management recommendations to conserve species will differ when both habitat configuration and habitat loss influence species persistence (Trzcinski et al. 1999, Boutin and Hebert 2002, Schmiegelow and Mönkkönen 2002). Predicting the outcome of landscape change when forest management is the dominant form of disturbance also requires an understanding of how land management decisions can scale-up to have large-scale impacts on the composition and configuration of forested landscapes (Wickham et al. 2007). Although forest management does not generally result in static landscape configurations in the same way as land use conversion (Schmiegelow and Mönkkönen 2002), it still can create persistent patterns that differ significantly from those that develop under natural disturbance regimes (Franklin and Forman 1987, Li et al. 1993, Mladenoff et al. 1993, Wallin et al. 1994, James et al. 2007). Thus, it is important to know the relevant spatial and temporal scales and patterns associated with land use activities and species habitat use in order to mitigate

potential conflicts between the objectives of resource management and habitat management (Bissonette et al. 1989, Thompson and Harestad 1994).

The American marten (*Martes americana*) has been identified as a species that "epitomizes" the potential conflicts between resource and wildlife habitat objectives (Sturtevant et al. 1996). Martens have large individual area requirements relative to their body mass (Buskirk and McDonald 1989) and select habitat types with complex physical structure, which provide protection from predators (Hargis and McCullough 1984, Hodgman et al. 1997), resting sites (Buskirk et al. 1989, Bull and Heater 2000), and access to prey (Sherburne and Bissonette 1994, Thompson and Curran 1995). Throughout much of the southern parts of the marten's geographic range, clearcut harvesting has become a common land management practice (Buskirk and Ruggerio 1994) and along with trapping is thought to have contributed to the northern contraction of the geographic range of marten in North America (Laliberte and Ripple 2004). Extensive clearcutting has been implicated in local declines and reduced landscape-scale carrying capacities because clearcuts lack the structure (e.g., coarse woody debris, low hanging branches, multi-storied canopies) martens are thought to require (Soutiere 1979, Snyder and Bissonette 1987, Phillips 1994, Payer 1999, Poole et al. 2004; but see Payer and Harrison 2004). Research has indicated that marten are considerably less likely to occupy landscapes with greater than 25-40% open areas or regenerating forest (Chapin et al. 1998, Hargis et al. 1999, Povin et al. 2000). Studies have further suggested that martens may be particularly sensitive to the effects of habitat loss, with the probability of home range occupancy by martens declining steeply as soon as the percent of suitable habitat declines below 100% (Fuller 2006). Little is known, however, about the cumulative

effects of habitat loss and fragmentation on habitat supply for martens or the spatiotemporal dynamics of probability of occurrence for martens in a managed landscape.

Because of their sensitivity to habitat loss and its effects on landscape pattern, researchers have investigated the effects of landscape composition and configuration on the landscape-scale (2nd-order *sensu* Johnson 1980) habitat selection of martens (Fuller 2006, Hepinstall et al. *In preparation*). Fuller (2006) used an information-theoretic approach (Burnham and Anderson 2002) to evaluate the relationship between home range occupancy and habitat composition and configuration for Newfoundland martens (*Martes americana atrata*), and concluded that occupancy was most influenced by the amount of suitable habitat within marten home ranges and, consequently, that habitat loss was the most important factor determining species persistence. A similar approach to evaluate home range occupancy by female and male martens separately on commercial forestlands in north-central Maine, under the assumption that male and females might be differentially influenced by landscape composition and configuration (Hepinstall et al. *In preparation*). How male and female martens are affected by changes in habitat amount and configuration will be determined by the interaction between the scale(s) at which landscape change and habitat selection occur, and male home ranges are larger than female home ranges (Buskirk and McDonald 1989). Fuller (2006) compared the extent of suitable habitat with a probability of occurrence ≥90% separately for male and female martens, but the data used to model home range occupancy was pooled across sex. Modeling results in Maine indicated that home range occupancy for males and females in Maine was influenced by the amount of suitable habitat and the configuration of habitat

(landscape shape index and patch density, respectively), and concluded that occupancy was negatively affected by both habitat loss and fragmentation (Hepinstall et al. *In preparation*). These results suggest that a habitat-based approach that considers both habitat amount and configuration will be necessary to conserve marten populations in managed landscapes.

Regional habitat conditions for martens in Maine have likely changed significantly over the last 30-40 years. In the 1970s and 1980s, large areas of spruce-fir forest were preemptively and salvage logged in response to the 1973-1985 spruce budworm (*Choristoneura fumiferana*) outbreak. In the 1990s, timber harvesting rates and patterns changed in response to the end of the budworm outbreak and the statewide implementation of new policies, which increased regulatory standards and requirements associated with clearcut harvesting (Maine Forest Service 1995). Acreage harvested by clearcut declined quickly in the 1990s, however, total acreage harvested approximately doubled as an increasing number of acres were partially harvested (Maine Forest Service 1994, 1997, 2003). Since the late 1990s, 500,000-560,000 acres have been harvested annually from commercial forestlands in Maine, and >94% of those acres have been partially harvested (Maine Forest Service 2003, 2005, 2007). Previous research has suggested that, in addition to being sensitive to the habitat loss created by clearcut harvesting, partially harvested forest may represent lower quality habitat compared to mature, second growth forest (Fuller and Harrison 2005), but little is known about the extent to which marten habitat has been reduced or degraded by timber harvesting in Maine.

Remotely-sensed data greatly contributes to our understanding of how forest management influences landscape pattern and forest fragmentation. Satellite-derived data, particularly from Landsat Thematic Mapper (TM) and enhanced Thematic Mapper Plus (ETM+), are increasingly being used to evaluate changes in land cover composition and configuration (e.g., Turner et al. 1996) or to map forest disturbance directly (Sader et al. 2003, Jin and Sader 2006, Kuemmerle et al. 2007) using a time-series approach that compares image data from consecutive satellite images. Few studies have, however, used a similar approach to evaluate habitat change for wildlife (Osborne and Suárez-Seone 2007, Viña et al. 2007, Mueller et al. 2008), despite the widespread availability of satellite data and methodologies. The main goal of my research was to increase understanding of how forest management influences marten habitat supply and landscape-scale occurrence; so, I used information derived from Landsat satellite imagery that depicted the changes in timber harvesting rates and patterns that have occurred over the last 30-40 years in Maine (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*) to develop a spatially-explicit time series of marten habitat supply across ~1.62 million hectares (4 million acres) of commercially-managed forestland. The objectives of this study were to: 1) document the effects of forest management on forest conditions associated with marten occurrence 1975-2007; 2) evaluate changes in landscape-scale probability of occurrence 1975-2007 using a previously developed predictive model (Hepinstall et al. *In preparation*); and 3) estimate the changes in potential marten densities on commercial forestlands in northern Maine 1975-2007.

STUDY AREA

The study area included ~1.62 million hectares (4 million acres) of commercial forestland (Figure 1.1) within the Acadian forest ecoregion, an ecological transition zone in the northeastern U.S.A. between the southern temperate deciduous-dominated forests and the northern boreal forests (Seymour and Hunter 1992). Boundaries of the study area were defined by the area of overlap between the Landsat Multispectral Scanner (MSS), Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) satellite imagery (Landsat Worldwide Reference System path 12, row 28) used to construct the harvest detection time series (see Methods below) and by the northwestern political boundary between Maine and the province of Quebec, Canada. This area included all or part of 174 unorganized townships that are primarily privately-owned. Forest ownership types (e.g., industrial forest products companies, family-owned corporations, investment entities) and the recent history of ownership change within this region broadly represent the unorganized townships of northern Maine (Hagan et al. 2005, Jin and Sader 2006). Interspersed among these townships were some state owned-parcels and reserve areas managed by the Maine Bureau of Parks and Lands, as well as the largest of Maine's state forest reserves, Baxter State Park, which was located along the eastern edge of the study area (Figure 1.1). Commonly occurring species include: balsam fir (*Abies balsamea*), white (*Picea glauca*), red (*P. rubens*) and black (*P. mariana*) spruce, white pine (*Pinus strobus*), white (*Betula papyrifera*) and yellow (*B. alleghaniensis*) birch, red (*Acer rubrum*) and sugar (*A. saccharum*) maple, and American beech (*Fagus grandifolia*). Forest harvesting was the primary form of forest disturbance within this area (Seymour 1992, McWilliams et al. 2005) and forest harvesting practices are regulated under the

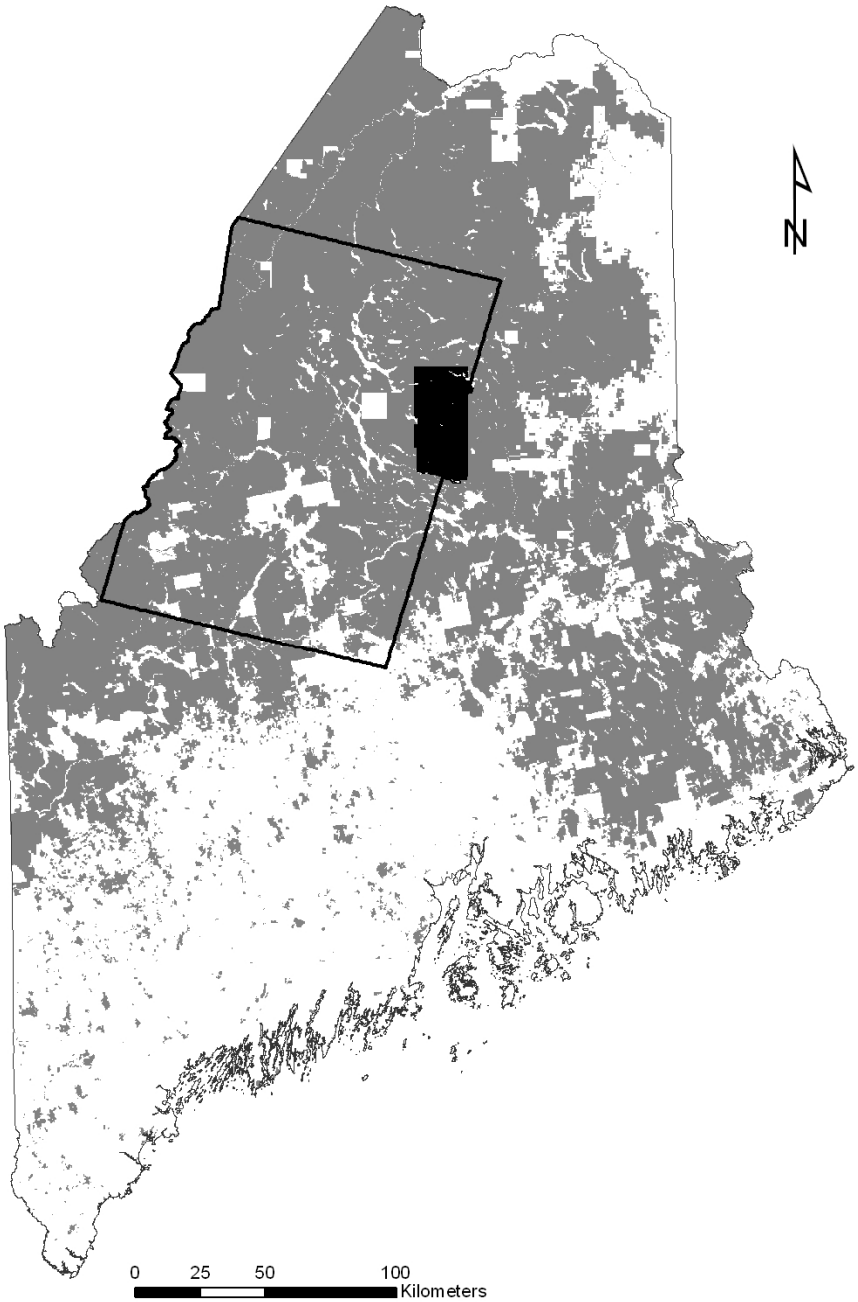


Figure 1.1. The study area (black outline) encompassed ~1.62 million hectares of commercial forestland (shown in gray), and was defined by the overlap between the Landsat satellite imagery used to construct the harvest detection time series and the Maine border. This area also included the majority of Maine's largest forest reserve, Baxter State Park (shown in black).

Maine Forest Practices Act (12 MRSA §8867-A to §8888 & MFS Rules Chapter 20). Urban and residential development is minimal and concentrated in a few townships in the southeastern corner of the region (Hepinstall et al. 1999).

METHODS

Marten habitat time series

The marten habitat time series was derived using a timber harvest detection time series (1970-2007) that was assembled from five Multispectral Scanner (MSS) and ten Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) images (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*). Consecutive leaf-on (May-September) images with the lowest cloud cover and at the shortest temporal interval available were acquired to maximize the detection of harvest events based on the Normalized Difference Vegetation Index (NDVI) or Normalized Difference Moisture Index (NDMI). Extensive investigations into the use of vegetation indices to map forest change in northern Maine have indicated that NDMI-based methodology is capable of detecting timber harvests with good accuracy, provided Landsat TM images are acquired 1-3 years apart (Wilson and Sader 2002, Jin and Sader 2005). After co-registration (RMS error <15 m), to improve the consistency of image interpretation during subsequent analyses, all images were transformed into a common radiometric scale using a relative radiometric normalization procedure (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*). NDMI images were calculated from the radiometrically normalized images using the TM near infrared (NIR) band 4 (0.76-0.90 μm) and mid-infrared (MIR) band 5 (1.55-1.75 μm): NDMI = (NIR - MIR) / (NIR + MIR).

A series of three-date RGB-NDMI classification sequences (Wilson and Sader 2002, Jin and Sader 2005) were performed to produce a time series of 9 harvest maps based on the TM and ETM+ imagery: 1988-1991, 1991-1993, 1993-1995, 1995-1997, 1997-1999, 1999-2000, 2000-2001, and 2001-2004. Harvests detected within each interval were classified into two intensity classes based on the magnitude of NDMI change: heavy or light. This classification scheme was not designed to match current regulations in Maine that classify harvests based on the residual structure as "clearcut" (currently defined any timber harvest greater than 5 acres in size that results in a residual basal area of trees over 4 ½ inches in diameter measured at 4 ½ feet above the ground of less than 30 ft^2/ac; 12 MRSA §8867-A to §8888 & MFS Rules Chapter 20) or "partial harvest" (i.e., all other harvests greater than 5 acres that retain >30 ft^2/ac). The heavy harvest class represented stand-replacing or regeneration harvests targeted at initiating the next cohort of growing stock, which I expected would include both clearcut and heavy partial harvests. Light harvests represented partial harvests and tending operations targeted at the current growing stock, which I expected would retain >50% of the live basal area. A similar process was used to detect heavy harvest entries using the MSS imagery based on NDVI, expanding the time series by 5 additional intervals: 1973-1975, 1975-1978, 1978-1982, 1982-1985, and 1985-1988. NDVI, based on NIR and the red band (0.63-0.69 μm), was used in place of NDMI because Landsat MSS does not record reflected radiation in the mid-infrared range (1.55-1.75μm). Additionally, areas disturbed ca. 1970-1973 were mapped directly from the 1973 MSS image. Light harvests were not mapped 1970-1988 because they could not be reliably classified using Landsat MSS imagery. Additional details about the image processing and timber harvest detection will

be presented in Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono (*In preparation*).

The harvest detection time series was subsequently combined with the Maine GAP Vegetation and Land Cover map (MEGAP) (Hepinstall et al. 1999) to create a time series of forest cover maps. According to the MEGAP, approximately 89% of the 1.62 million hectare (4.0 million acre) study area was comprised of forestland ca. 1993, which as a superclass the Maine GAP program mapped with omission and commission accuracies of 92% and 94% respectively (Hepinstall et al. 1999). Forestland pixels in the MEGAP were classified as one of seven classes: four mature forest classes (Coniferous Forest, Coniferous/Deciduous Forest, Deciduous/Coniferous Forest, and Deciduous Forest), two forested wetland classes (Coniferous Forested Wetland and Deciduous Forested Wetland), three harvest classes (Clearcut, Light Partial Cut, and Heavy Partial Cut), and two forest regeneration classes (Early Regeneration and Late Regeneration). The harvest and regeneration subclasses were originally classified with poor user accuracies (4.4 - 54.5% commission error), so they were replaced with updated information. The harvest classes (6.5% of the Forestland pixels) were the result of timber harvests that occurred 1991-1993 (Hepinstall et al. 1999) and were replaced with ca. 1991 mature forest cover types (Coniferous Forest, Mixed Forest, Deciduous Forest, Coniferous Forested Wetland, Deciduous Forested Wetland) from an unsupervised classification of the 1991 TM image. The regeneration classes (19.2% of the Forestland pixels) were the result of timber harvests that occurred 1975-1991, and were replaced with ca. 1975 mature forest cover types (Coniferous Forest, Mixed Forest, Deciduous Forest, Coniferous Forested Wetland, Deciduous Forested Wetland) from an

unsupervised classification of the 1975 MSS image using the 1991 TM as a reference dataset for classification (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*). By replacing the harvest and regeneration classes, which contributed negatively to the overall accuracy of the forestland superclass, the commission accuracy of mature forest in the revised MEGAP is expected to be >94%.

At the scale of the forest patch, suitable habitat for martens was defined *a priori* based on the results of previous studies in Maine (Chapin et al. 1998, Payer 1999, Payer and Harrison 2003, Fuller and Harrison 2005) as patches ≥2.7 ha with tree height >6 m. Using this definition, I developed the first map in the marten habitat time series, reflecting habitat conditions ca. 1975, by first recoding the mature forest classes (Coniferous Forest, Mixed Forest, Deciduous Forest) and Coniferous Forested Wetland in the revised MEGAP as suitable habitat for martens (1) and all remaining land cover classes as unsuitable (0). By this definition, suitable marten habitat ca. 1975 was characterized by pole- to sawtimber sized trees ca. 1975 and leaf-on canopy closure of >75% (Hepinstall et al. 1999). I then generated a map identifying all 1975 habitat patches to selectively re-class small islands in lakes and inland waterways and patches of suitable habitat <2.7 ha as unsuitable (0).

Using the 1975 marten habitat map as the first in the time series, I developed the remainder of the marten habitat series using a two step procedure for each time step. First, I used the harvest detection time series to remove any previously intact marten habitat (e.g., ca. 1975) that was affected by heavy harvests (e.g., 1975-1978) from the subsequent marten habitat map (e.g., 1978). I retained areas affected by a light harvest as marten habitat because the magnitude of the biomass change did not suggest that these

disturbances were stand-replacing, but instead represented various forms of tending or uneven aged management operations in which the majority of live basal area was retained for future operations (e.g., selection harvest, shelterwood establishment). Based on previous research indicating that martens occupied home ranges in landscapes with high proportions (maximum = 73% leaf-on) of partially-harvested forest with mean residual basal area 13 m^2/ha (Fuller and Harrison 2005), I assumed in the creation of the initial time series that these areas retained sufficient structure to support marten use. Finally, I generated a map of habitat patches and removed patches of suitable marten habitat <2.7 ha (Chapin et al 1998). I repeated these two steps for each of the harvest intervals to create a marten habitat time series comprised of 14 time steps (1975, 1978, 1982, 1985, 1988, 1991, 1993, 1995, 1997, 1999, 2000, 2001, 2004, and 2007) that allowed me to quantify the accumulating change in marten habitat supply across the interval 1975-2007.

Habitat change

I documented and quantified the changes in marten habitat quantity, configuration, and distribution directly from the marten habitat time series. For each of the 14 time steps, I calculated the total area in marten habitat, the total area of habitat patches >2.7 ha, the amount of habitat change between time steps and cumulative habitat change since 1975, and the patch size frequency distribution at each time step. When calculating the patch size frequencies, I combined patches into bins based on previous research in Maine that has determined the minimum patch area requirements for male and female martens (Chapin 1995, Chapin et al. 1998). Chapin (1995) calculated the percent of a marten's home range that was composed of a single, contiguous forest (>6 m) patch, which I then used to calculate the size of the largest patch (ha) within the home range

based on the individual's home range size. Patches were collapsed into five bins representing: habitat patches below the minimum size recorded to support a female marten (2.7 - 80 ha), habitat patches within the 50th percentile for female home ranges and the 25th percentile for male home ranges (80 - 150 ha), habitat patches within the 75th percentile for female home ranges and the 50th percentile for male home ranges (150 - 247 ha), habitat patches within the 75th percentile for male home ranges (247 - 382 ha), and patches large enough to support ≥75% of a male marten's home range (>382 ha). It is important to note that, although based on the definition of suitable habitat (see above *Marten habitat time series*) the overall accuracy of the binary class is expected to be high, the estimated quantity of habitat ca. 1975 should be considered an overestimate because, since no harvest information was available prior to 1970, the maps of suitable habitat likely included some degree of commission error. This source of error would also be reflected in subsequent time steps, which would affect the overall range of values estimated by the dataset but not the calculated rates or magnitudes of change 1975-2007 in either habitat quantity or patch size distribution.

To account for the growth of regenerating stands into marten habitat I also modeled future habitat recruitment using site index curves for the eastern U.S. (Carmean et al. 1989). For this analysis, I assumed uniform, moderate tree growth conditions (i.e, site index = 50) and optimistic starting stand conditions (i.e., initial stand height = breast height (bh) or 4.5 ft) when determining the time lags associated with growth of balsam fir, red spruce, red maple and sugar maple. Beginning with the harvest interval (1975-1978), I divided the harvested acreage from each interval by the number of years included in the interval to create an estimate of annual acreage harvested. I then

referenced the site index curves to identify the age at bh at which dominant trees would be expected to reach 6 m and 9 m, and determined what year that would occur for areas harvested during each time step. Six meters represents the threshold height above which martens no longer avoid regenerating forest (Katnik 1992), and 9 m is the height above which marten show positive stand-level habitat selection (Payer 1999).

Probability of marten occurrence time series

In a previous study, Hepinstall et al. (*In Preparation*) investigated the influences of habitat amount and habitat configuration on marten landscape-scale occurrence (2nd order habitat selection; Johnson 1980) in north-central Maine based on radiotelemetry locations collected over an 11-year field study (Katnik 1992, Phillips 1994, Chapin et al. 1998, Phillips et al. 1998, Payer 1999, Fuller and Harrison 2005). The original MEGAP served as the base map for developing year-specific habitat maps for their study area that were used to calculate landscape metrics for occupied home ranges (95% minimum convex polygons; n = 121) and simulated unoccupied home ranges areas (n=86). Landscape metrics were selected for inclusion as predictor variables in a logistic regression analysis *a priori* based on previous studies in Maine (Katnik 1992, Chapin et al. 1998) and elsewhere (Hargis et al. 1999) to reflect measures of landscape composition and habitat configuration thought to be important determinants of marten occurrence. For example, a metric that quantifies the proportion of suitable habitat within a marten's home range (PHR) was included because of the important role habitat amount appears to play in marten occurrence (Katnik 1992, Chapin et al. 1998, Hargis et al. 1999). Metrics of landscape configuration were selected to capture various aspects of habitat patch size, shape, and spatial distribution within the home range (Hepinstall et al. *In preparation*). *A*

priori models representing biological hypotheses about landscape-scale marten occurrence were constructed and evaluated for male and female martens separately using model selection criteria to rank logistic regression model performance based on AIC_c (Burnham and Anderson 1998). See Hepinstall et al. (*In preparation*) for a more detailed description of model development.

The top-ranked models for females and males included measures of both habitat amount and habitat configuration (Tables 1.1 and 1.2). The top-ranked model for predicting female marten occurrence (Table 1.1) included the proportion of suitablehabitat within home range (PHR), patch density (PD), and the interaction term (PHR*PD). PD is calculated as: the number of patches divided by home range area. The top-ranked model for predicting male marten occurrence (Table 1.2) included the proportion of suitable habitat within home range (PHR), landscape shape index (LSI), and the interaction term (PHR*LSI). LSI is calculated from the total length of class edge (or perimeter) divided by the minimum length of class edge (or perimeter) possible for a maximally aggregated class.

Using the top-ranked models developed by Hepinstall et al. (*In preparation*) and the marten habitat time series, I created a time series (1975-2007) to depict the probability of occurrence (POC) surfaces for male and female martens across the 1.62 million hectare study area. I calculated continuous surfaces for each of the metrics for each time step in the marten habitat time series using a circular moving window approach. Moving window functions derive a value for each cell of an input map (e.g., marten habitat map) within a specified neighborhood surrounding the cell (e.g., circle with a specified radius). I based the radius of the circular moving window for males

Table 1.1. Parameter estimates and associated odds ratios for the top-ranking female marten model (Hepinstall et al. *In preparation*). Model included the predictor variables: percent suitable habitat in home range (PHR), suitable habitat patch density (PD), and the interaction (PHR*PD).

Parameter	**Estimate**	**95% Lower**	**95% Upper**	**Odds Ratio**
Constant	0.113	-4.927	5.153	
PHR	-0.001	-0.066	0.064	0.999
PD	-7.558	-14.742	-0.374	0.001
PHR*PD	0.111	0.008	0.213	1.117

Table 1.2. Parameter estimates and associated odds ratios for the top-ranking male marten model (Hepinstall et al. *In preparation*). Model included the predictor variables: percent suitable habitat in home range (PHR), landscape shape index (LSI), and the interaction (PHR*LSI).

Parameter	**Estimate**	**95% Lower**	**95% Upper**	**Odds Ratio**
Constant	-25.835	-54.253	2.583	
PHR	0.187	-0.061	0.436	1.206
LSI	-0.867	-3.769	2.035	0.420
PHR*LSI	0.073	0.006	0.140	1.076

(1025 m) and females (876 m) on the median home range sizes for males and females (3.3 km^2 and 2.4 km^2 respectively) in northern Maine (Hearn 2007). I used FRAGSTATS version 3.3 (McGarigal et al. 2002) to calculate LSI (male radius) and PD (female radius) surfaces for each marten habitat map, and ArcGIS 9.0 to calculate PHR surfaces to better control the treatment of non-habitat (e.g., water bodies). Before calculating metric surfaces I divided each of the 14 marten habitat maps into 6 large tiles based on the major rivers that transverse the study area. I did this to ensure that metric values reflected realistic potential home range placement on the landscape associated with the dominant geophysical barriers to marten movement. The 6 tiles were then mosaiced after metric calculation and prior to subsequent analyses. I also used ArcGIS 9.0 to derive the final probability surfaces for each time step, applying the logistic regression parameter coefficients to the appropriate metric surface and then calculating the corresponding probability value for each available cell in the study area.

Spatiotemporal analyses

I quantified the changes in habitat amount and configuration using the landscape metric (PHR, PD, and LSI) and POC surfaces. Using the 1975 and 2007 metric surfaces, I calculated and compared the area within binned (e.g., 10% classes) values of PHR and of PD and LSI to assess the broad-scale temporal shifts in metric distributions. I also calculated the pairwise difference (i.e., each time step as compared to 1975 baseline) for all potential home ranges (i.e., center pixel of moving window) and the overall median change for each metric to assess the magnitude and directionality of spatiotemporal shifts in composition and configuration of marten habitat for males and females at the scale of the home range. Finally, I compared the cumulative area within 10% POC classes (0-

100%) across the endpoints of the time series to quantify total change between 1975 and 2007.

To evaluate the complex spatiotemporal patterns in POC for male and female martens, I used Empirical Orthogonal Functions (EOFs). EOF analysis is commonly used in the atmospheric (e.g., Aldrian and Djamil 2008) and oceanographic sciences (e.g., Legaard and Thomas 2007), but based on a review of peer-reviewed literature has never been used to evaluate terrestrial wildlife habitat change. The EOF method finds both time series and spatial patterns in a single scalar field (Björnsson and Venegas 1997). In the S-mode of EOF analyses data (e.g., probability values at location x_i at time t_j) are organized into a matrix where each row represents a map of all values at time t_j (i.e., one of the 14 time steps in the series) and the columns represent a time series of values for each location x_i (Björnsson and Venegas 1997). The EOF analysis, which is very similar to a Principal Components Analysis, then partitions the total variance of the two-dimensional matrix into a series of orthogonal functions that maximize the amount of variance explained with the fewest number of functions (Björnsson and Venegas 1997). I used EOF analysis to decompose the data into a set of temporal EOFs describing the characteristic patterns in the time series of probability values across all locations and a set of spatial amplitude functions describing the relative contribution of each EOF to the predicted POC at each location (i.e., pixel or cell). I performed this analysis on the series of POC surfaces for males and females separately. Prior to analysis, each POC map was normalized by its standard deviation and pixels experiencing <10% change in probability were removed as a data reduction technique. The statistical significance of each EOF mode was evaluated using a Monte Carlo approach.

Finally, I derived a surface describing the cumulative percent of habitat within a potential marten home range affected by *light* harvest entries for males and females as of 2007. Although martens have been shown to maintain home ranges in areas with moderate to relatively high proportions of partially harvested forest (range = 10-73% during the summer), Fuller and Harrison (2005) also concluded that the mean area for martens whose home ranges were comprised of >10% partial harvest (males = 6.29 km^2, and females = 3.25 km^2) were nearly double the area of home ranges of martens without partial harvest (males = 3.54 km^2, and females = 1.77 km^2). During winter, these martens also exhibited reduced relative selection for partially-harvested forest within their home ranges. Additionally, a 3rd-order selection study in Maine concluded that marten prefer areas within their home ranges with >18 m^2/ha basal area (of residual trees ≥7.6 cm dbh) and with overstory CC >50% (leaf-on) (Payer and Harrison 2003). Consequently, it was important to consider the degree to which marten habitat has been impacted by all timber harvesting since some partially harvested forest may represent lower quality habitat compared to mature, second growth forest (Fuller and Harrison 2005). To consider these effects, I identified those areas of marten habitat ca. 2007 that received one or more *light* partial harvests according to the harvest detection time series (1988-2007). I then generated a surface that quantified for all potential marten home ranges the percentage of the available marten habitat ca. 2007 that received at least one *light* partial harvests.

Predicted marten density

The final way that I measured the effect of the spatiotemporal changes in marten habitat was to investigate the change in potential marten density. In order to estimate marten density at the township-scale, I calculated average POC using a lattice. A similar

method was previously evaluated along with six other methods to estimate potential density of Newfoundland martens (*Martes americana atrata*) across ~2,755 km^2 of managed forest (Fuller et al. 2007). Estimates of potential marten density calculated by summation of probability values within a fixed grid representing marten home ranges (0.055 martens/km^2) corresponded closely with the density estimated based on a companion DNA hair snare study in conjunction with program MARK (0.061 martens/km^2). I determined the appropriate grid size for males through an analysis of the intrasexual spatial overlap patterns from previous research conducted in Baxter State Park (BSP) (Payer 1999). Using 95% minimum convex polygons (MCPs) calculated with radio-telemetry location data collected for male martens in 1995 (N = 16) and 1996 (N = 17), I calculated the proportion of each home range that was exclusive to that individual marten. I then screened individual MCPs on the basis of whether or not the trapping grid used to catch marten to attach radio collars was sufficient to capture spatial overlap on all sides of each marten's home range. I calculated the proportion of each MCP that was within 1,025 m of the trapping grid and excluded a home range from subsequent analysis if >65% of the home range age was outside the 1,025 m radius. Consequently, all home ranges (N = 33) contributed to calculating the exclusive areas, but only those home ranges for which the spatial access was such that potential overlap with neighboring males could be adequately addressed were retained for further analyses. With the remaining MCPs I calculated the median exclusive percentage of a male's home range (51%) and used that value to determine the grid cell size for males based on the median male home range size (3.3 km^2; 1,297 m). Because the grid size is based on the estimated exclusive area and not the mean or median home range area, the aggregation of

probability values should be appropriately scaled to estimate male marten density. An estimate based on the 95% MCP area would result in an underestimate of the estimated number of males present at any point in the time series because it would not consider home range overlap.

Previous research in Maine has shown that female martens tolerate very little intrasexual overlap (0-1.6%; Phillips 1994). A comparable MCP dataset was unavailable for assessing the effect of intrasexual overlap on the percentage of a female's home range that is exclusive to an individual. Consequently, because the sex ratio of resident, nonjuvenile martens in Maine has been found to be 1:1 (Payer 1999), I used the same grid size (1,297m) for estimating female marten densities. I aligned the grid with the south-west/north-east orientation of my study area to retain the maximum amount of surface data and used the square grids to calculate the average POC for each grid cell in 1975 and 2007. Grid cell values were then summed by township and divided by the township area to estimate the township-scale marten density.

RESULTS

Habitat change

Results indicated that there were 1,381,956 ha (3,414,887 ac) of suitable habitat for martens within the study area in 1975, which was comprised of mixed (44%), coniferous (28%), deciduous (22%), and wetland coniferous (6%) stands of pole- to sawtimber-sized forest. Between 1975 and 2007, the loss of habitat directly attributable to heavy harvest of mature forested stands ranged from a low of 6,155 ha/yr (2000-2001) to a high of 21,941 ha/year (1985-1988), and resulted in a total cumulative loss of 376,906 ha (27%) of the marten habitat present in 1975 (Table 1.3). An additional 58,072 ha was

Table 1.3. Amount of marten habitat, amount of marten habitat in patches ≥ 2.7 ha, annual marten habitat decline attributable directly to timber harvesting effects, and cumulative habitat loss for the period 1975-2007.

Period	Habitat (ha)	Habitat (≥ 2.7 ha)	Annual Direct Loss (ha)	Annual Patch-size Loss[a]	Cumulative total loss (ha)
1975-1978	1,343,846	1,342,893	12,703	318	39,063
1978-1982	1,291,002	1,288,729	12,973	568	93,227
1982-1985	1,237,616	1,233,975	17,038	1,214	147,981
1985-1988	1,168,151	1,162,495	21,941	1,885	219,461
1988-1991	1,118,149	1,110,980	14,782	2,390	270,976
1991-1993	1,095,437	1,087,699	7,772	3,869	294,257
1993-1995	1,076,468	1,068,182	5,616	4,143	313,774
1995-1997	1,062,516	1,053,762	2,833	4,377	328,194
1997-1999	1,040,525	1,031,018	6,618	4,754	350,938
1999-2000	1,018,560	1,018,123	12,458	4,368	363,833
2000-2001	1,011,968	1,011,652	6,155	316	370,304
2001-2004	975,270	973,535	12,127	578	408,421
2004-2007	948,585	946,978	8,317	536	434,978

[a] Habitat loss attributable to the formation of residual habitat patches following a *heavy* harvest that were too small (i.e.,<2.7 ha; Chapin et al. 1998) to contribute marten habitat requirements. Patches <2.7 ha were identified and area calculated at the end of each period.

lost due to fragmentation of residual forest into patches too small to receive marten use (i.e., <2.7 ha). The magnitude of loss created by this fragmentation effect increased in each harvest interval 1975-1999, with a peak annual loss of 4,754 ha/yr (1997-1999) (Table 1.3). Since 1999, the trends in direct loss and fragmentation-related loss have reversed as direct loss has increased in magnitude as fragmentation loss has declined. In total, 32% of the marten habitat in 1975 (434,978 ha) was lost as a result of the combined effects of habitat loss and minimum patch size requirements (Table 1.3).

Additional to the fragmentation losses caused by creation of patches <2.7 ha, the total number of habitat patches ≥2.7 ha increased 9.5-fold from 379 in 1975 to 3601 in 2007 (Table 1.4). The majority of this increase in the total number of habitat patches occurred in the smallest size classes that I evaluated (2.7 - 80 ha). In 1975, there were 356 patches 2.7 - 80 ha in size, but by 1991, there were 2014 patches, and by 2007, the number of patches had increased to 3414. Although the greatest increase in the number of patches occurred in that smallest size class, the number of patches in all patch size classes increased between 1975 and 2007 (Table 1.4), indicating a general trend towards broad-scale habitat fragmentation.

Based on site index curves (index = 50), balsam fir, red spruce, and sugar maple can be expected to reach 6 m bh at ages 15, 17, and 15, and 9 m bh at age 25, 27, and 24, respectively. Using these values, stands harvested 1975-1995 were recruited back into marginal marten habitat starting in 1988 using the 6 m height threshold. This included a total of 278,058 ha of habitat ca. 2007. Using the 9 m threshold, stands harvested 1975-1987 were recruited back into suitable marten habitat starting in 1997, which included a total of 172,293 ha ca. 2007. The effect of accounting for habitat recruitment based on the

Table 1.4. Number of habitat patches (≥ 2.7 ha) present within the study area after each harvest interval.

Year	2.7 - 80	80 - 150	150 - 247	247 - 382	> 382	Total
1975	356	7	3	1	12	379
1978	583	14	6	2	14	619
1982	928	30	10	4	19	991
1985	1226	38	14	9	22	1309
1988	1680	42	17	12	25	1776
1991	2014	54	24	9	29	2130
1993	2161	56	27	8	29	2281
1995	2290	60	25	10	30	2415
1997	2407	67	25	12	29	2540
1999	2589	63	28	13	33	2726
2000	2700	63	30	14	33	2840
2001	2749	63	30	17	35	2894
2004	3105	78	34	14	46	3277
2007	3414	89	34	14	50	3601

above assumptions reversed the trend in area of suitable habitat 1975-2007 (Figure 1.2); however, even the most optimistic assumptions (i.e., forest is suitable marten habitat when trees >6 m) there was a sustained loss of >150,000 ha of marten habitat ca. 2007.

Spatiotemporal analyses

At the scale of the marten home range, the distributions of landscape metrics included in the top-models developed to predict marten landscape-scale occurrence in northern Maine (Hepinstall et al. *In preparation*) shifted significantly 1975-2007. Forboth male and female martens, there was a broad-scale shift in the distribution of PHR within potential home ranges towards increased prevalence of lower PHR values (Figure 1.3). Between 1975 and 2007 the median PHR value was reduced from 95% to 64% for both sexes. In 1975, >1 million hectares (70%) of marten habitat had ≥90% PHR available for both female (1,070,593 ha) and male (1,060,663 ha) martens. This area was reduced to 218,200 ha and 188,860 ha, respectively, by 2007 (Figure 1.3). Based on a pairwise comparison between 1975 and 2007, 27% of potential female home ranges and 24% of potential male home ranges experienced a reduction in PHR of only 0-10% over the 32 year period. However, 43% of potential female home ranges and 43% of potential male home ranges experienced a reduction in PHR of ≥30%. Further, 12% of females ranges and 10% of male ranges had PHRs which declined by ≥60% from 1975-2007. The median change in PHR at the home-range scale was -24% for all potential female home ranges and -25% for all potential male home ranges.

The negative shifts in PHR were accompanied by significant distributional shifts in configuration metrics 1975-2007 (Figure 1.4). The spatial distribution of PD for potential female home ranges shifted towards increased prevalence of higher metric

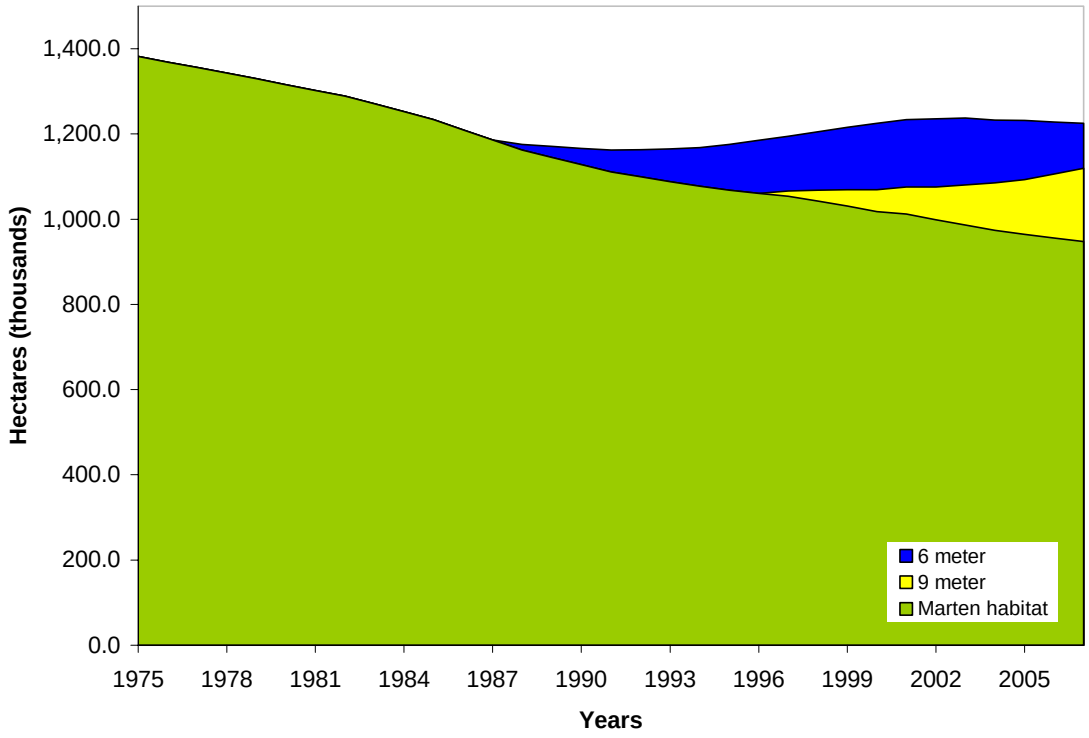
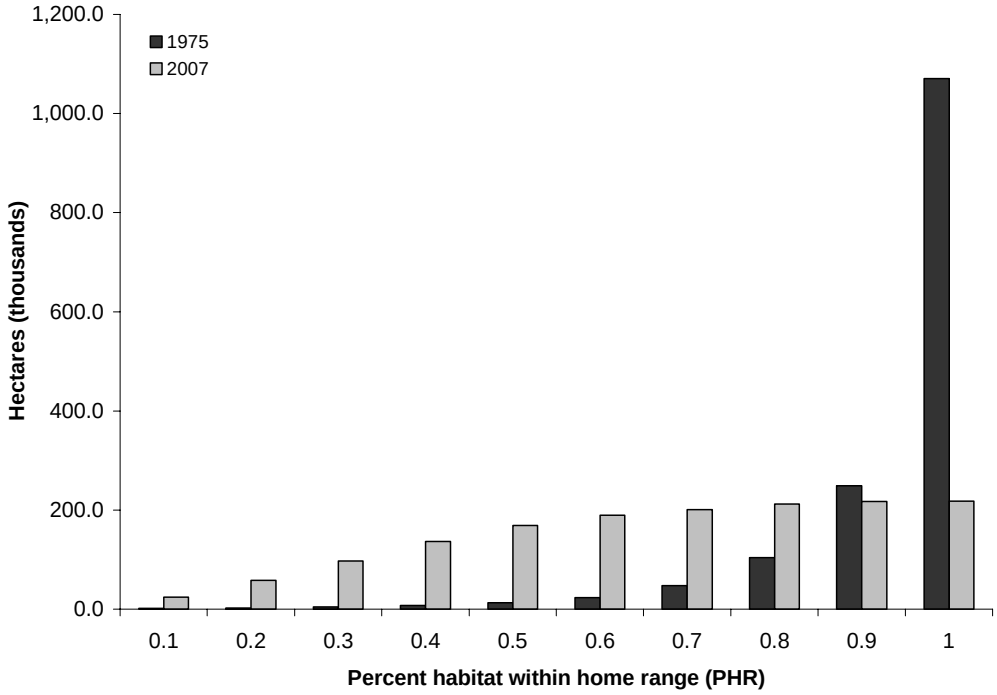


Figure 1.2. Total marten habitat amount (1975 - 2007) and predicted habitat recruitment at six and nine meters. Six meters represents the threshold height above which martens no longer avoid regenerating forest (Katnik 1992), and 9 m is the height above which marten show positive stand-level habitat selection (Payer 1999).

a)



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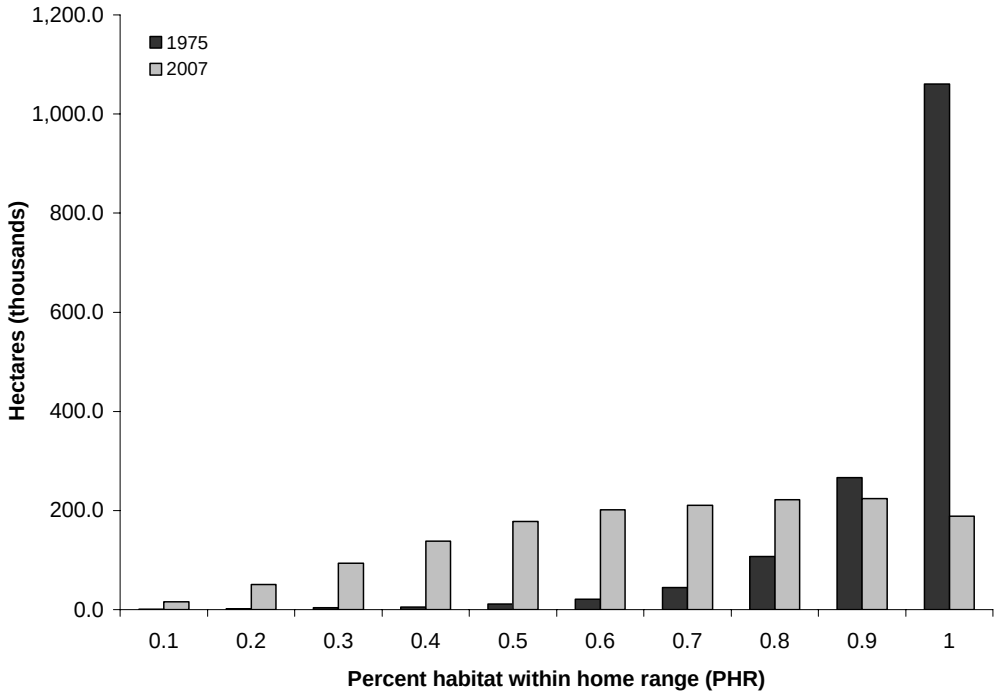
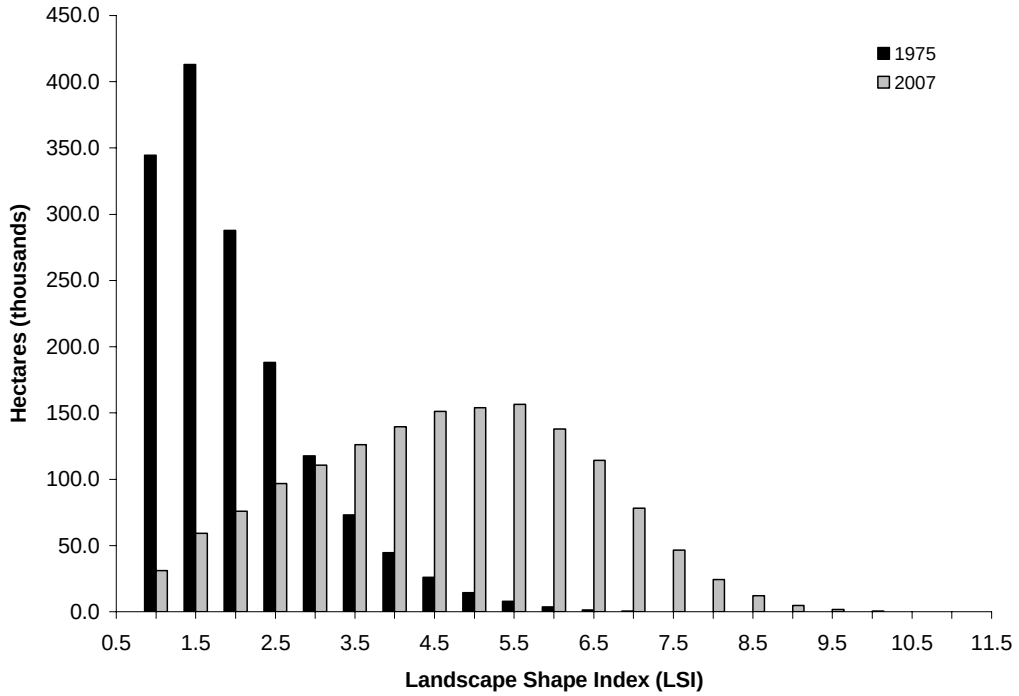


Figure 1.3. Area distribution of marten percent suitable habitat in home range (PHR) (y-axis) within 10% classes (x-axis) for a) females and b) males in 1975 and 2007.

a)



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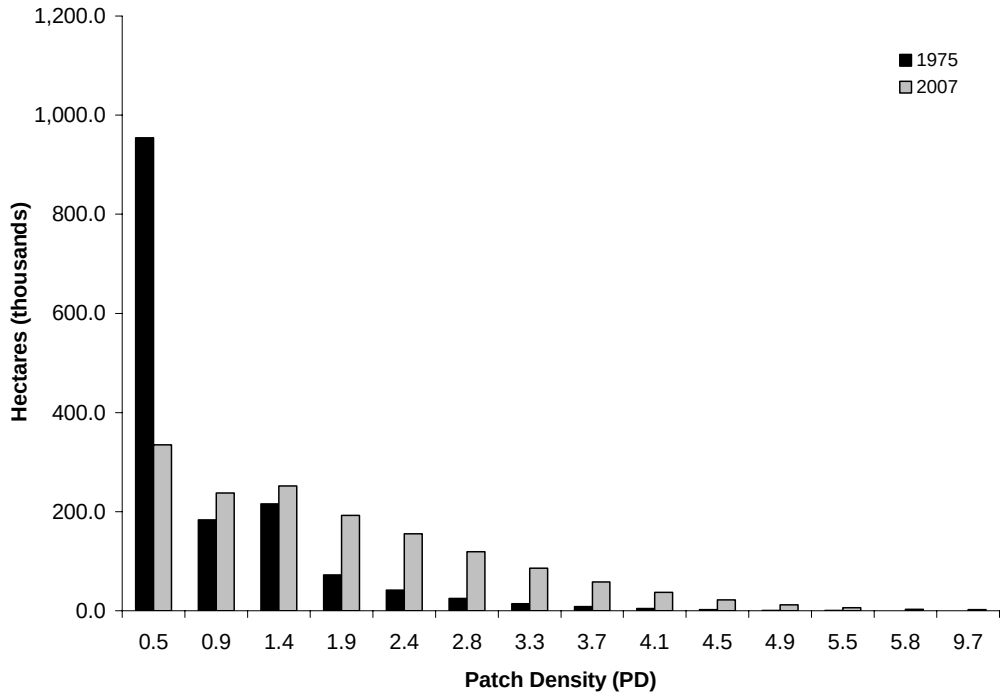


Figure 1.4. Area distribution of a) Patch Density (PD; females) and b) Landscape Shape Index (LSI; males) within potential home-range areas in 1975 and 2007. Median change in metric value at the home-range scale (1975-2007) was +0.87 (mean = +0.99) for PD and +2.6 (mean = +2.7) for LSI.

values (Figure 1.4a), and the median value of PD for potential female home ranges shifted from 0.43 (i.e, 1 patch per home range) in 1975 to 1.3 (i.e., 3 patches per home range) in 2007. A pairwise comparison indicated that the median change in the PD index at the home-range scale was +0.87. This increase corresponds to an approximate increase of 2 patches per home range, suggesting that there has been a broad-scale disaggregation of marten habitat and increase in patch density within potentially occupied home ranges. An even more pronounced shift was detected in the spatial distribution of LSI for potential male home ranges (Figure 1.4b), which shifted from a heavily right-skewed distribution to a more uniform distribution centered on intermediate LSI values (Figure 1.4b). The median value of LSI for potential male home ranges increased from 1.99 in 1975 to 4.89 in 2007. A pairwise comparison indicated that the median change in the LSI at the home-range scale was +2.6; LSI values in only 7% of potential male home ranges were unchanged 1975-2007. Consequently, for the majority of potential home ranges the 1975 LSI was less than the 2007 LSI, further indicating that there has been a broad-scale increase in level of disaggregation and the length of edge associated with marten habitat in northern Maine.

The EOF analysis successfully identified the dominant trends that describe the spatiotemporal changes in the time series of probability of occurrence (POC) for females and males 1975-2007 (Figure 1.5). For females, two significant temporal EOF modes explained 83.1% of the variance in the POC time series (Figure 1.6a). The first mode accounted for 70.9% of the variability in the dataset and described the effect of the interacting processes of habitat loss and habitat fragmentation on the overall broad-scale decline in female marten POC 1975-2007. The shape of temporal mode 1 indicated that

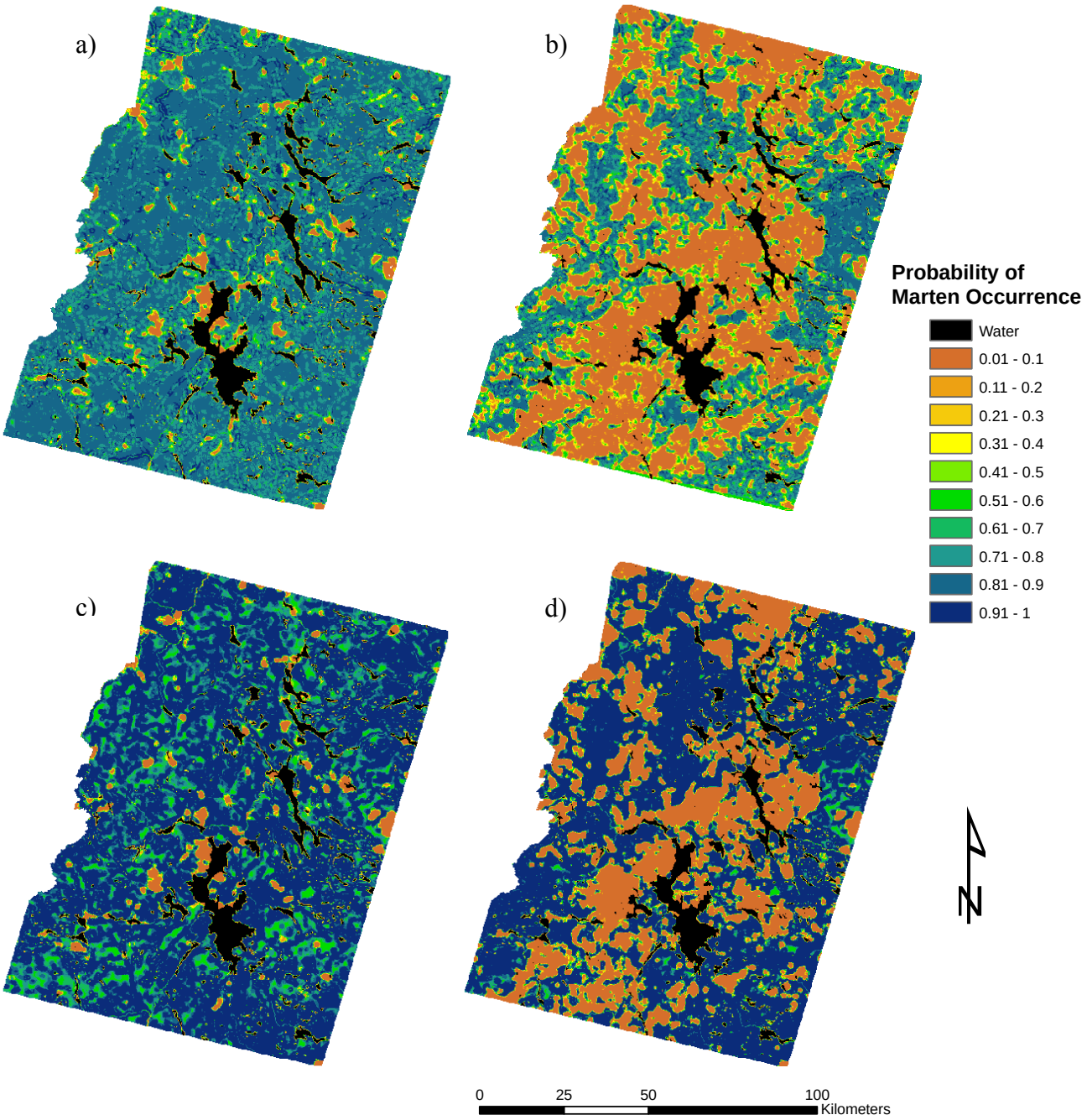
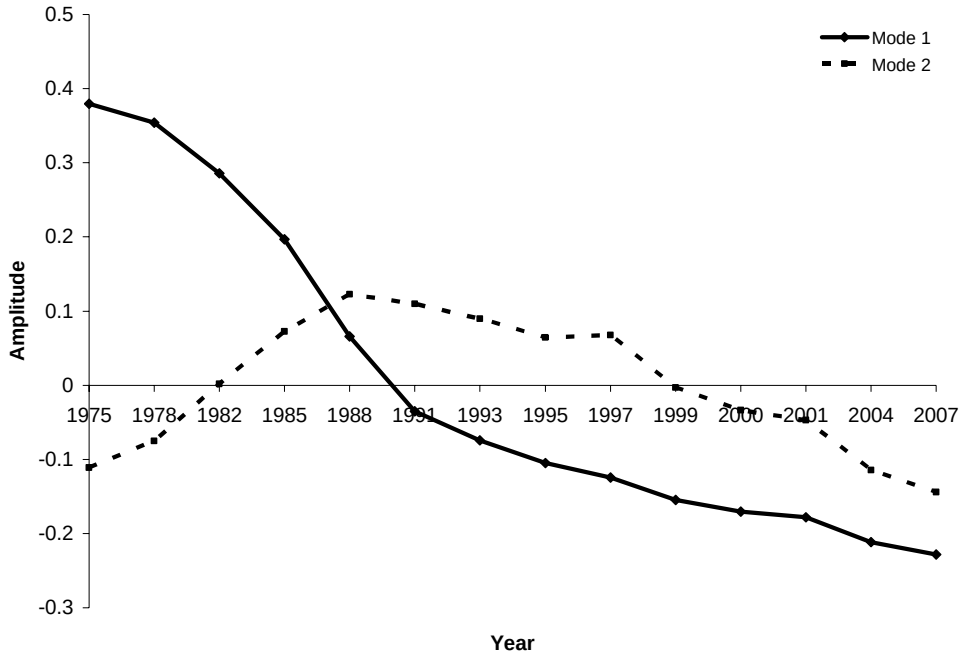


Figure 1.5. Probability of occurrence for a) female martens in 1975, b) female martens in 2007, c) male martens in 1975, and d) male martens in 2007. Values were derived using a previously developed model (Hepinstall et al. *In preparation*) for predicting occurrence at the scale of a marten home range based on habitat amount and configuration.

a)



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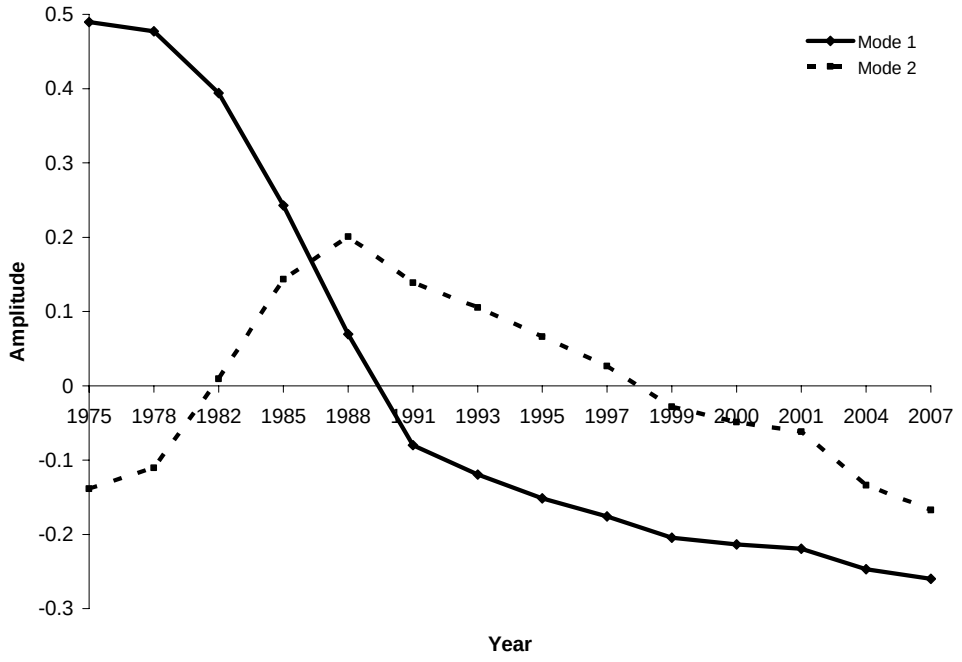

Figure 1.6. Significant temporal EOF modes 1 (black line) and 2 (dashed line) identified from the a) female (variance explained = 83.1) and b) male (variance explained = 82.0%) probability of occurrence time series.

the initial decline in POC in most areas was initiated early in the time series (1978-1988); that the rates of decline tapered off in the mid- to late-1990s; and that rates of decline have increased since 2001 (Figure 1.6a). Additionally, three primary patterns were captured by the spatial EOF weighting surface associated with temporal mode 1 (Figure 1.7). First, in those areas with strongly positive spatial weighting (value ≥1) PHR decreased 1975-2007 and PD increased 1975-2007 in the expected pattern, accelerating the rate and increasing the magnitude of the decline of female POC. Second, in those area with weakly positive weighting (value = 0-1), PHR decreased but PD also decreased, dampening the decline in POC and highlighting the role of the interaction term (PHR*PD) in the female marten model. In these areas the process of habitat loss was near complete; consequently, as PHR approached zero, PD also declined towards zero as all habitat patches were removed. Third, areas with negative spatial weighting effectively did not follow the dominant trend of strong POC decline 1975-2007, instead experiencing little habitat loss and, thus, little to no POC decline.

The second EOF mode describing the female POC time series accounted for an additional 12.2% of the variance and captured patterns related to the localized timing and magnitude of habitat loss (Figure 1.6a). The pattern of temporal mode 2 must be interpreted as modifying the magnitude of mode, rather than interpreted directly, and in the case of the female POC time series mode 2 had one of two primary effects on the predominant spatial pattern associated with mode 1. In those areas where the spatial weightings associated with mode 2 were negative (Figure 1.8), the rate of POC decline was significantly elevated 1975-1988, quickly approaching zero. Where spatial weightings associated with mode 2 were positive (Figure 1.8), POC decline was initiated

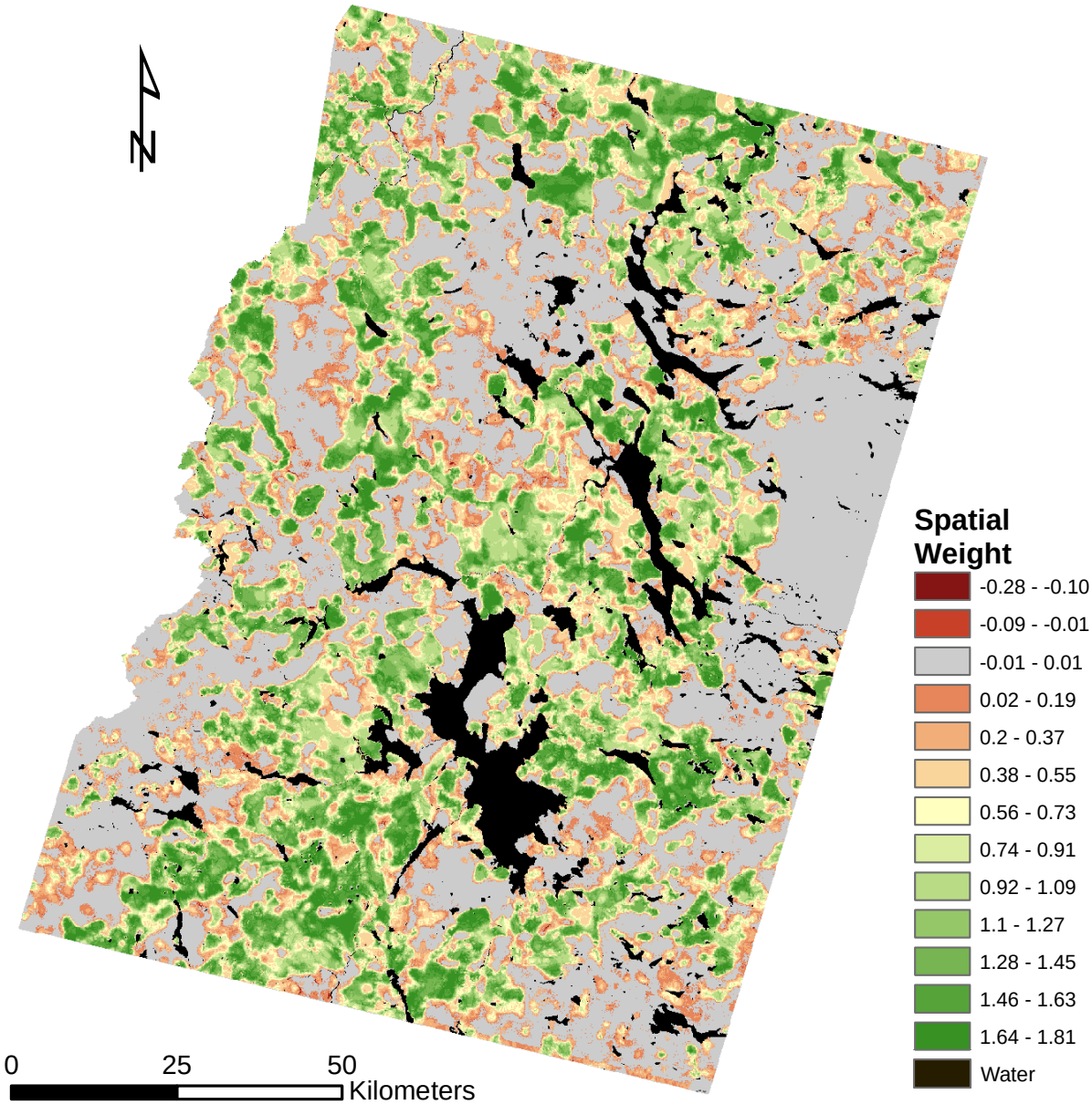

Figure 1.7. Surface describing the spatial EOF weighting associated with female temporal mode 1. In areas with strongly positive spatial weighting (value ≥1) PHR decreased 1975-2007 and PD increased 1975-2007 in the expected pattern. In areas with weakly positive weighting (value = 0.1-1) the process of habitat loss was near complete and both PHR and PD decreased. Areas with zero and negative spatial weighting experienced little to no habitat loss and so did not follow the dominant trend of strong POC decline 1975-2007.

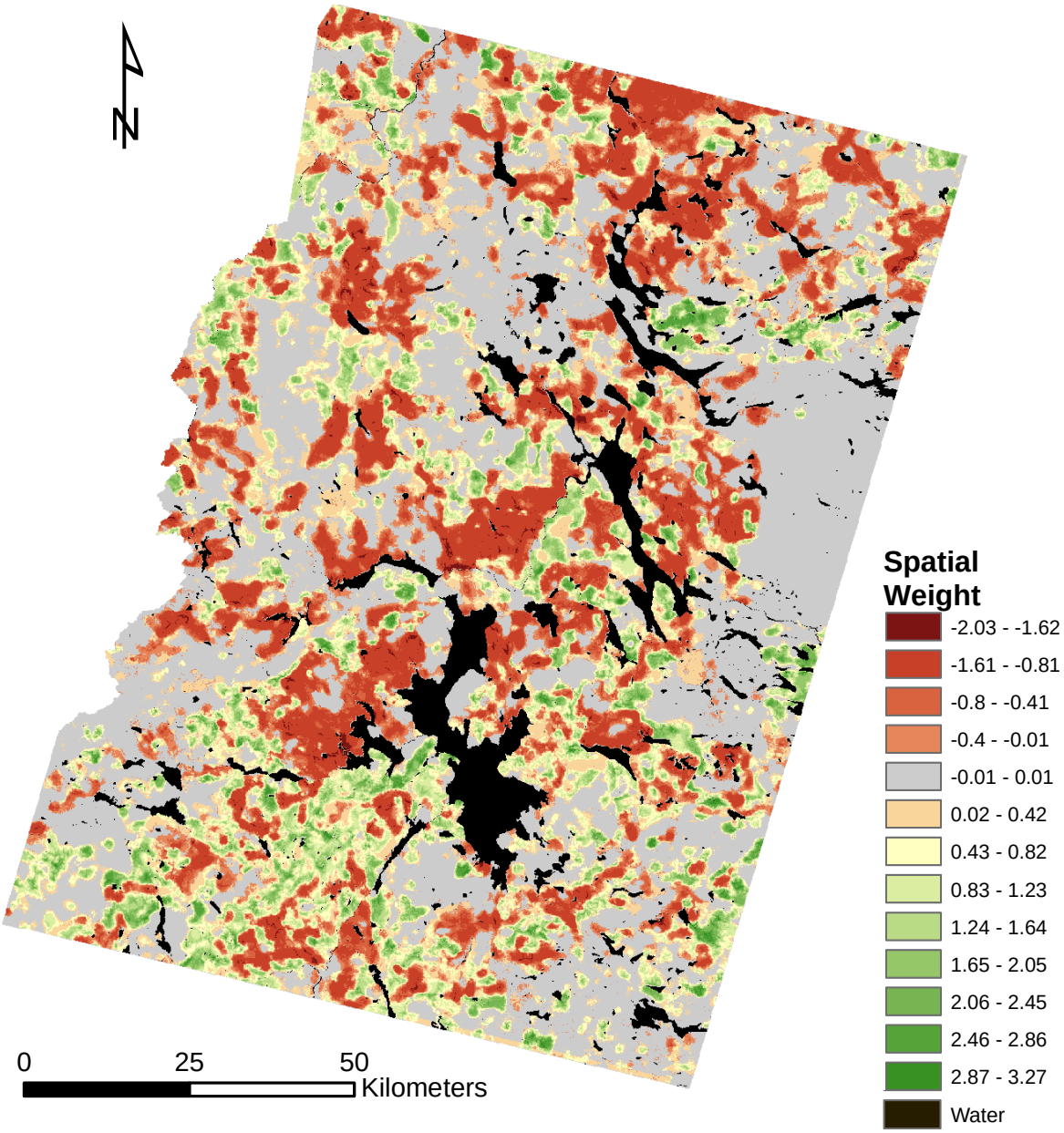

Figure 1.8. Surface describing the spatial EOF weighting associated with female temporal mode 2. In areas where the spatial weightings associated with mode 2 were negative, the decline in POC started at the beginning of the time series (1975-1988) and quickly approached 0%. In areas where the spatial weightings were positive, the POC decline was initiated after 1985 and continued to decline through the rest of the time series.

later than the dominant temporal trend, signifying a significant change in the temporal and spatial pattern of marten habitat loss and fragmentation. Although very infrequent, in areas where the spatial amplitudes associated with both mode 1 and mode 2 were weakly negative (i.e., between -1.0 and 0) the POC actually increased slightly 1975-2007 and was associated with a decrease in PD.

The EOF analysis also identified two significant temporal modes in the male POC time series, which explained 82.0% of the variance in the dataset (Figure 1.6b). The first mode accounted for 69.7% of the variance and had a similar shape as the mode 1 for the female POC time series (Figure 1.6b). One notable difference was that the rate associated with the initial POC decline (1978-1988) was steeper in the male POC time series, but the rate of decline after 1991 was reduced compared to the female POC time series; consequently, the two temporal trends converged at a very similar value ca. 2007. The spatial weights surface associated with mode 1 for the male POC time series (Figure 1.9) was also quite similar to that of the female POC time series (Figure 1.7), suggesting similar interacting processes. One interesting difference to note is the reduction in frequency of negative weightings in the male POC time series, which in the female POC time series correlated with areas that did not follow the dominant trend of POC decline 1975-2007. The second mode accounted for an additional 12.3% of the variance and the spatial patterns associated with the second EOF describing the male POC time series (Figure 1.10) were also similar to the female mode 2 (Figure 1.8). In those areas that followed the dominant pattern associated with mode 1(i.e., positive spatial weights where PHR decreased and PD increased), the effect of mode 2 when spatial weightings were negative was an increase in the rate of decline 1975-1988 to an even greater degree than

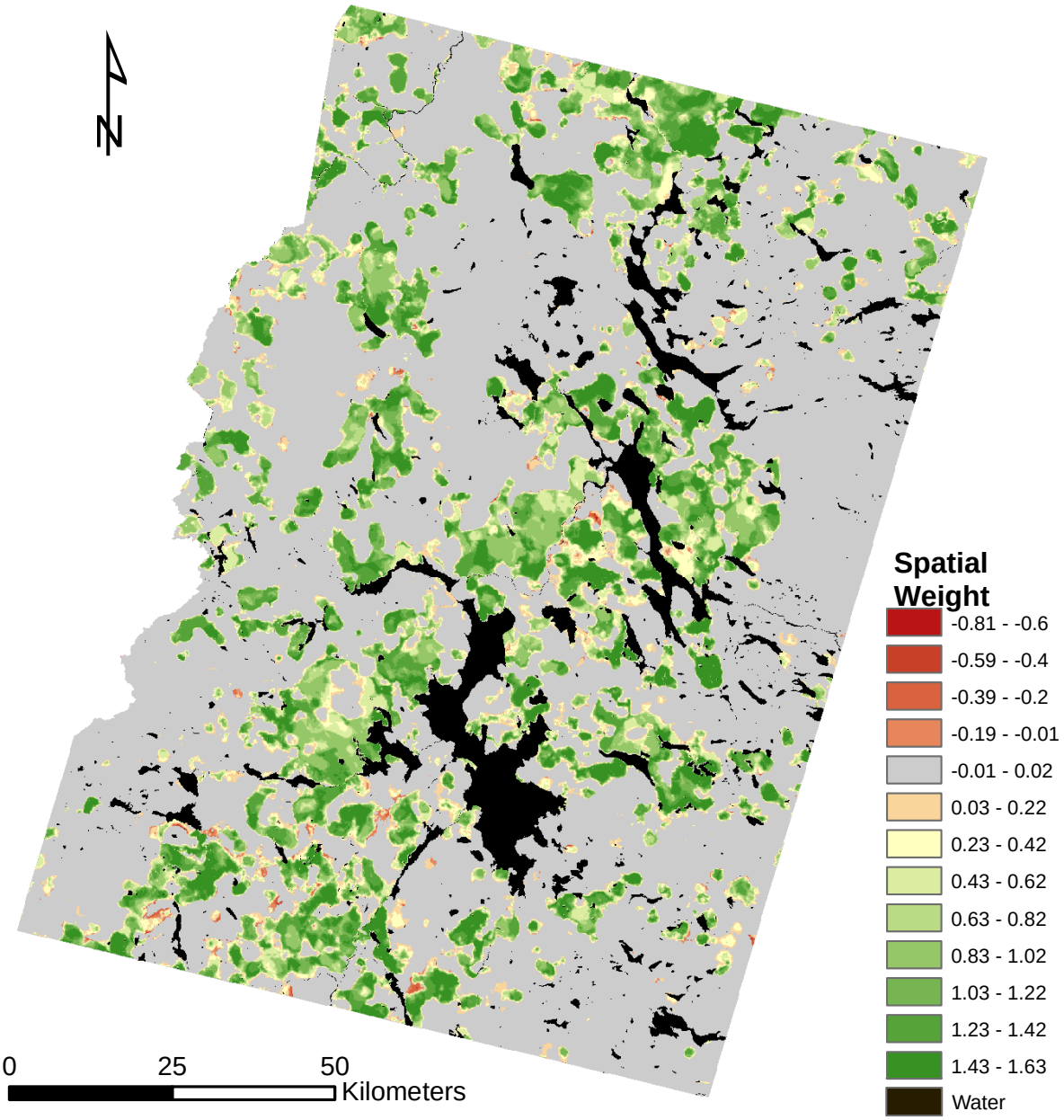

Figure 1.9. Surface describing the spatial EOF weighting associated with male temporal mode 1. In areas with strongly positive spatial weighting (value ≥1) PHR decreased 1975-2007 and LSI increased 1975-2007 in the expected pattern. Areas with zero and negative spatial weighting experienced little to no habitat loss and so did not follow the dominant trend of strong POC decline 1975-2007.

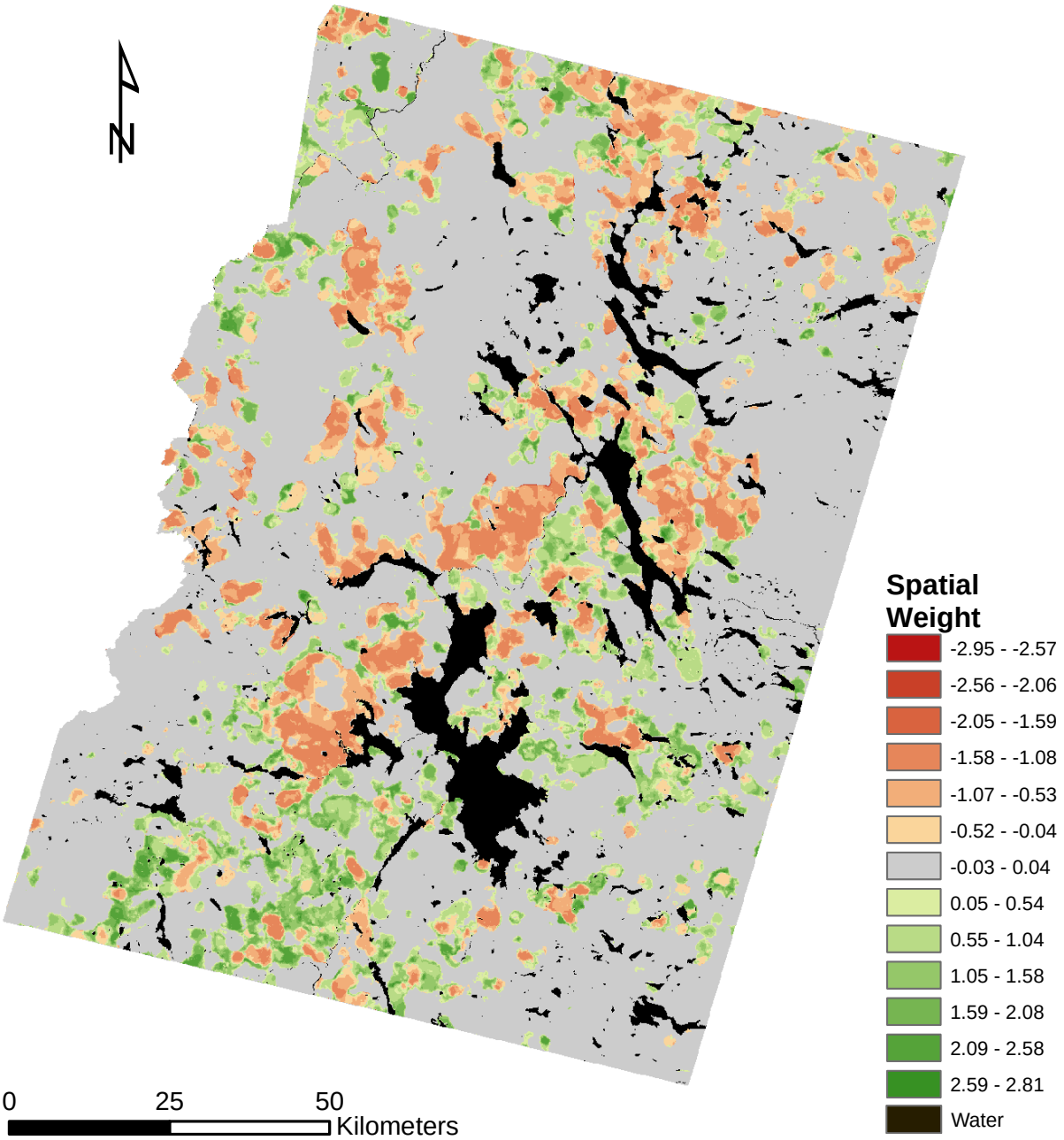

Figure 1.10. Surface describing the spatial EOF weighting associated with male temporal mode 2. In areas where the spatial weightings associated with mode 2 were negative, the decline in POC started at the beginning of the time series (1975-1988) and quickly approached 0%. In areas where the spatial weightings were positive, the POC decline was initiated after 1985 and continued to decline through the rest of the time series.

that seen in the female POC time series. Where mode 2 spatial weightings were strongly positive (value ≥1), the period of POC decline was initiated after 1985 and continued declining, followed by a slight increase in the rate of decline starting in 2001.

Additional to the effects of habitat loss and fragmentation, I estimated that 33% of the marten habitat ca. 2007 received a *light* harvest 1988-2007 (Figure 1.11). More strikingly, because of the extensive nature of the *light* harvesting, habitat within 93-94% of the potential male and female home ranges received at least one *light* harvest (Figure 1.12). The 6-7% of the potential marten home ranges that were not affected occurred primarily within Maine's largest forest reserve, Baxter State Park, and other smaller forest reserves. The percentage of habitat ca. 2007 within potential home ranges that received a *light* harvests ranged widely (1-100%); overall, 34% (median for males and females) of the habitat ca. 2007 within all potential home ranges was affected. Additionally, 20,955 ha (2.2%) of marten habitat received two or more *light* harvests 1988-2007 where timber volume was removed during more than one time series harvest interval (e.g., *light* harvest 1995-1997 and again 2001-2004). These areas likely no longer represent suitable marten habitat because of inadequate canopy closure and residual basal area of overstory trees >6 m in height.

Predicted marten density

Sufficient data was available to estimate the effects of habitat change on predicted marten density for 155 complete townships in northern and western Maine that spatially overlapped the study area by >10%. In 1975, 142 townships had estimated potential marten densities of ≥1 martens/km^2 (Figure 1.13). This density was higher than the mean marten density (0.62 martens/km^2) that was estimated to occur in Baxter State Park

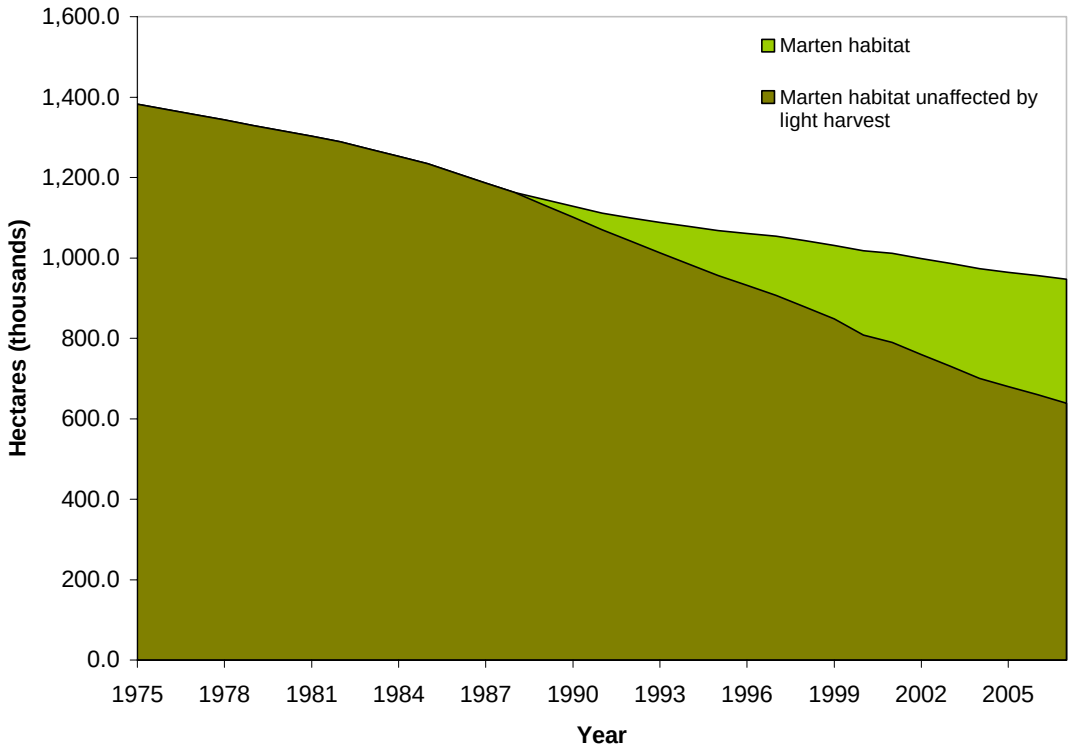

Figure 1.11. Total marten habitat amount (green) and the total amount of marten habitat unaffected by *light* harvesting 1988-2007 (brown). Areas receiving a *light* harvest may no longer represent suitable habitat for martens if they do not retain enough residual basal area and canopy closure to exceed published thresholds for marten habitat use (Payer and Harrison 2003).

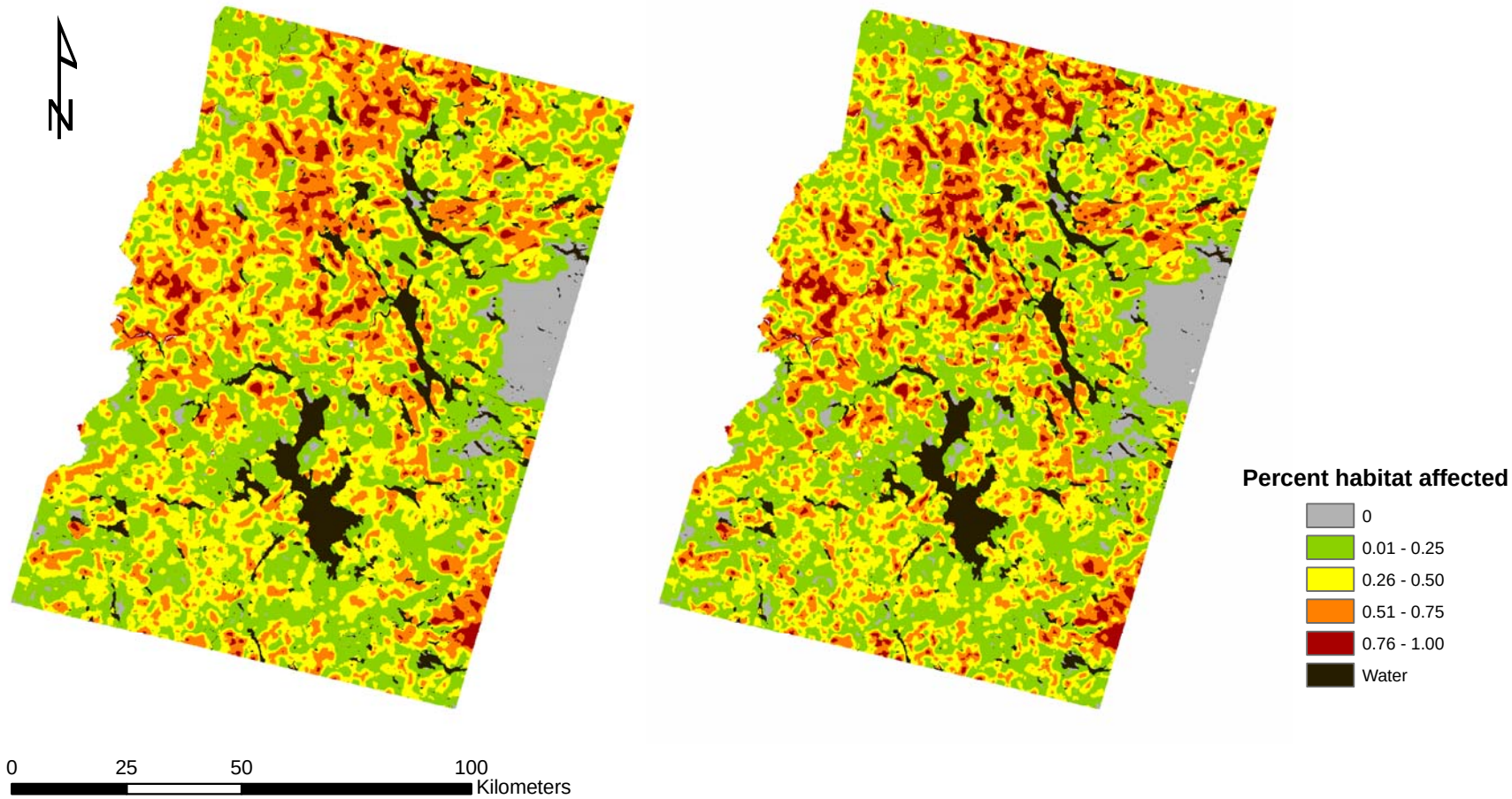

Figure 1.12. Percent of habitat within potential male (left) and female (right) home ranges ca. 2007 that received a *light* partial harvest. The 6-7% of the potential marten home ranges that have not been affected (shown in gray) occurred primarily in Maine's largest state park, Baxter State Park, and other smaller forest reserves.

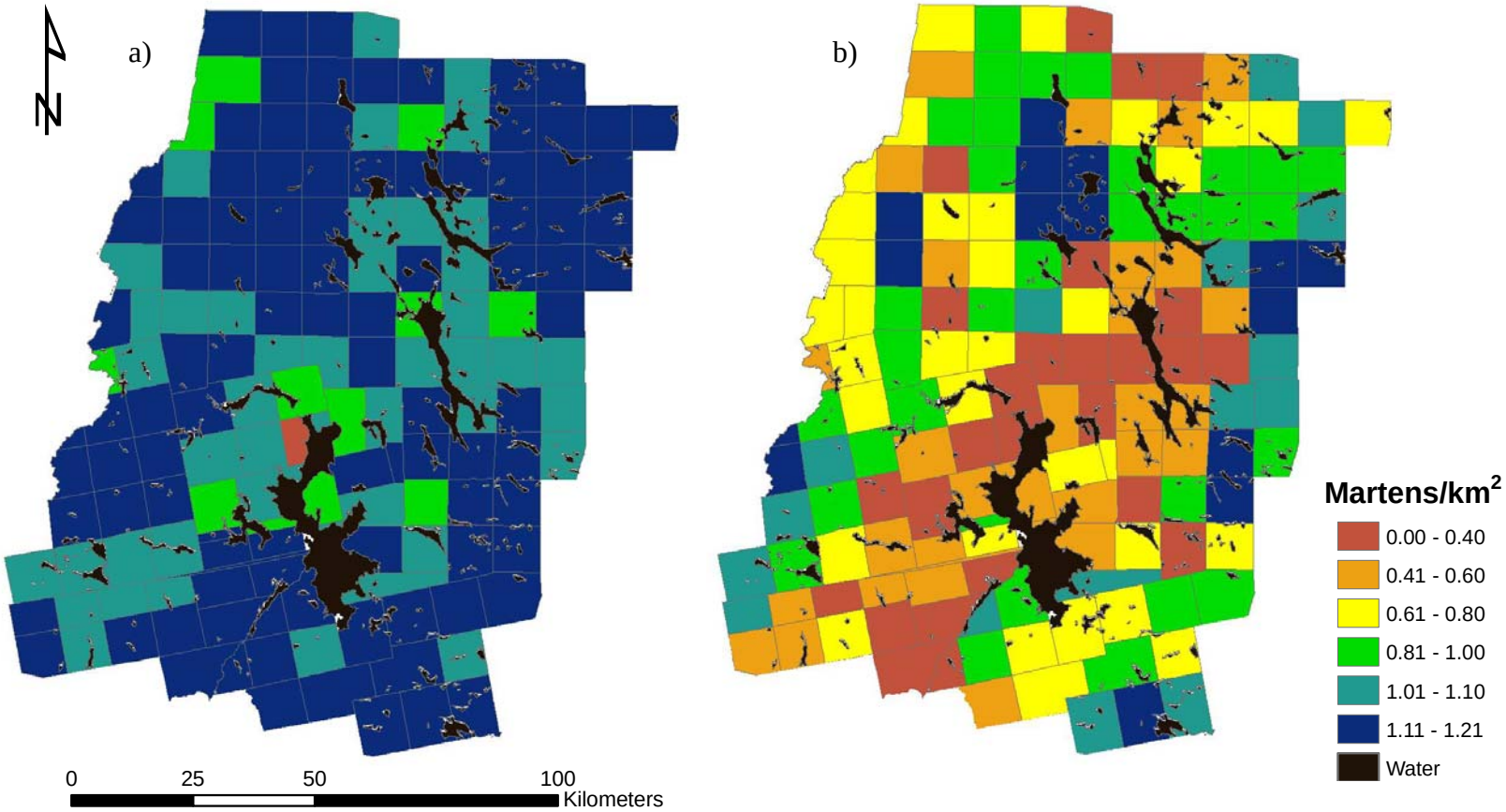

Figure 1.13. Estimated marten densities in a) 1975 and b) 2007 calculated based on the probability of marten occurrence using top-ranked models for males and females (Hepinstall et al. *In preparation*).

during a 5-year field study (1994-1998) (Payer 1999); the road-based trapping design that was used in BSP, however, may not have been adequate to capture all resident marten (Payer 1999). In 2007, the township-to township range of variability was substantially greater and only 31 townships had an estimated potential marten density of ≥1 martens/km^2 (Figure 1.13). A pairwise comparison of townships indicated that the change in potential marten density ranged from zero to a decline of >1 martens/km^2; no townships had an increase in potential marten density 1975-2007. Townships overlapping the areas of greatest POC decline experienced the most substantial declines in potential marten densities, and potential densities in 16 townships were lower than the mean density observed (Payer 1999) for an untrapped but commercially-managed township in north-central Maine (0.31 martens/km^2) that experienced ~50% habitat loss 1974-1994.

DISCUSSION

In landscapes where forest management is the dominant form of landscape disturbance, predicting the outcome of landscape change on wildlife habitat requires identification of disturbance events and the resulting changes in landscape composition and configuration to understand the species-specific effects of habitat loss and fragmentation on habitat quality and quantity. Using a habitat-based spatiotemporal approach, I have demonstrated that forest management activities since 1975 have had significant impacts on the quantity and configuration of marten habitat in northern Maine. The 1973-1985 spruce budworm outbreak initiated a period of rapid marten habitat change, resulting in the loss of >20% of marten habitat within the study area and a 5.6-fold increase in the number of habitat patches (≥2.7 ha) 1975-1991. Significant declines in probability of occurrence (POC) occurred as large blocks of mature spruce-fir forest

were salvaged and lost as marten habitat, which also set the larger landscape's trajectory towards habitat fragmentation, creating patches too small to sustain the habitat requirements of martens and shifting the configuration of marten habitat towards increasing disaggregation. Although the majority of marten habitat loss (62%) occurred during the period of preemptive and salvage logging, substantial loss of marten habitat and decline in marten POC continued 1991-2007, coinciding with changes in forest policy that contributed to an extensive increase in partial harvesting and total acreage harvested from commercial forestlands. Partial harvesting, thus, replaced clearcut harvesting in its role causing the loss and fragmentation of marten habitat. The potential for partial harvests to act additively, increasing the rates of habitat loss and fragmentation, highlights the need to future research to determine the degree to which different forms of partial harvesting can alter habitat quality for martens and other forest wildlife.

The majority (62%) of marten habitat loss occurred in the first 16 years of the time series (1975-1991), during the periods of preemptive followed by salvage logging that occurred in response to the 1973-1985 spruce budworm outbreak (Table 1.3). The highest annual rate of loss (21,941 ha/yr 1985-1988) coincided with the end of the spruce budworm post-salvage period and was consistent with the Maine Forest Service landowner annual harvest records (Maine Forest Service 1994, 1997, 2003, 2005, 2007), which showed that 1989 was the peak year 1988-2007 in terms of the annual harvested acres by clearcut harvesting across all timberlands in Maine. During the salvage period, there were no legislative definitions or standards in place to regulate the size or arrangement of clearcuts in Maine, but in 1989 the Maine Forest Practices Act (MFPA)

(12 MRSA §8867-A to §8888 & MFS Rules Chapter 20) was passed. The MFPA put forth Maine's first definition of a "clearcut" (i.e., any timber harvest greater than 5 acres in size that results in a residual basal area of trees over 4 ½ inches in diameter measured at 4 ½ feet above the ground of less than 30 ft^2/ac) and required that a landowner submit a "forest management plan" for clearcuts above certain acreage (35 acres ca. 1995) (Field 1994). The immediate effects of this legislation on forest management were that leading up to and in the first years after the MFPA was fully implemented the number of acres harvested by clearcut harvesting declined by >40%, as did the direct loss of marten habitat (Table 1.3). The rate at which marten habitat was lost due to fragmentation effects, however, increased following this period of forest policy change. The peak in fragmentation-related loss (1997-1999) occurred 10-12 years after the peak in direct habitat loss (1985-1988) (Table 1.3), which was also likely a result of the changing forest management practices that occurred after the MFPA. As the acreage harvested by clearcut declined, the average size of a clearcut also declined from >125 acres to <35 acres (Maine Forest Service 1995). Thus, individual clearcuts were on average smaller after the implementation of the MFPA; however, forest managers began to concentrate these smaller clearcuts spaced according to the 250 ft separation zones that were required by the MFPA. The "checkerboard pattern" of clearcuts that resulted created a landscape pattern that was previously not present on the landscape (Maine Forest Service 1995, Sader et al. 2003). Loss due to patch-size effects would have occurred as residual forest patches too small to contribute to marten habitat requirements (i.e., <2.7 ha; Chapin et al. 1998) were left as buffer strips in the area surrounding clearcuts. Thus, the MFPA

appears to have been responsible both for the slowdown in direct loss of marten habitat and the acceleration in loss of marten habitat via fragmentation effects in the early 1990s.

The rate at which marten habitat was fragmented into patches (2.7 - 382 ha) remained relatively constant 1975-2007 (Table 1.4) even as forest management shifted away from the use of clearcut harvests. The partial harvests that largely replaced the clearcuts in northern Maine represent a variety of silivicultural treatments, including both even-aged (e.g., shelterwood) and uneven-aged (e.g., selection) management techniques that result in a wide range of residual stand conditions (Robinson 2006). Some partial harvests leave little remaining canopy cover but sufficient live basal area post-harvest to exceed the definition of a clearcut in Maine (i.e., >30 ft^2/ac) (Robinson 2006). Because of the extent of canopy removal, many of these harvests would be categorized as *heavy* along with clearcuts based on the magnitude of NDMI change. As a category, *heavy* harvests represent not just clearcuts, but rather stand-replacing forest disturbances. Thus, these "heavy" partial harvests, like traditional clearcut harvests, will also result in loss of marten habitat because the residual forest will lack the horizontal and vertical structure marten require for protection from predators (Hargis and McCullough 1984, Hodgman et al. 1997), resting sites (Buskirk et al. 1989, Bull and Heater 2000), and access to prey (Sherburne and Bissonette 1994, Thompson and Curran 1995).

The greatest increases in the number of patches occurred in the smaller size classes (2.7 - 80 ha and 80 - 150 ha; Table 1.4), which is a concern because martens are sensitive to habitat patch size (Snyder and Bissonette 1987, Chapin et al. 1998, Hargis et al. 1999). Researchers in Maine concluded that at least half of a female marten's home range in north-central Maine was comprised of a single habitat patch; the median size of

those patches was 150 ha (Chapin et al. 1998). Thus, habitat patches in the smallest size class (2.7 - 80 ha) are likely too small to sustain the area requirements of a female marten in Maine. Patches 80 - 150 ha in size may be of intermediate value for supporting a female marten, but are too small to sustain the area requirements of a male marten (median size of largest residual patch within male marten home range = 247 ha; Chapin et al. 1998). Thus, forest management 1975-2007 created habitat patches that, although still relatively large, may only be of limited value to a marten unless they are in close proximity to other habitat patches.

The broad-scale, cumulative effects of the loss and fragmentation of marten habitat have been significant as negative shifts in the amount and configuration of habitat were observed at the home-range scale. Pairwise comparisons of PD and LSI (1975 vs. 2007) indicated that habitat present in the majority of potential home ranges has become more disaggregated and has a greater proportion of habitat edge, which is not surprising considering the increase in the number of habitat patches (Table 1.4). Concurrently, PHR declined for both sexes, with many of the female and male potential marten home ranges (29%) experiencing a reduction of only 0-10% in PHR. Because 94% of potential female and male marten home ranges in 1975 started with ≥70% PHR, the 1-10% PHR decline resulted in home ranges with 2007 PHR values of 60-99% (Figure 1.3). Although this range of percentages is still relatively high, previous research has suggested that martens are considerably less likely to occupy landscapes with less than 60-80% suitable habitat (Chapin et al. 1998, Hargis et al. 1999, Potvin et al. 2000, Fuller 2006). In a comparison of occupied and unoccupied home-range areas in north-central Maine, Fuller (2006) found that fewer than 30% of the martens occupied landscapes comprised of ≤60%

suitable habitat. Additionally, early estimates of PHR should be viewed with caution because, since no harvest information was available prior to 1970, the maps of suitable habitat likely included some degree of commission error that would contribute to an overestimation of habitat quantity. Thus, the 32% loss in marten habitat 1975-2007 likely has resulted in a >50% decline in actual marten densities given change in distribution of PHR and the non-linear habitat loss versus occupancy relationship (Fuller 2006).

The EOF analysis detailed how the processes of forest loss and fragmentation and their effects on the spatial distribution and configuration of marten habitat interacted and influenced the probability of occurrence (POC) for male and female martens 1975-2007. Two primary spatiotemporal trends emerged in the overall broad-scale decline in POC. In the majority of areas, POC decline for both male and female martens was initiated early in the time series (1978-1988), which coincided with the spruce budworm salvage period and the period of greatest direct habitat loss (Table 1.3). In many of these areas of early decline, the loss of marten habitat caused both a decrease in PHR and an increase in habitat fragmentation, leading to an increase in PD and LSI (Figure 1.4). In other areas, however, the rate and magnitude of marten habitat loss 1978-1988 were so great that PD or LSI actually decreased coincidentally with PHR as entire habitat patches were removed, further accelerating the rate of POC decline towards zero ca. 1991. So, for a species such as the marten that is affected both by habitat amount and habitat configuration steep nonlinear declines in POC should be expected in a forest managed predominantly by even-aged silvicultural techniques that does not include considerations for maintaining marten habitat. Further, the magnitude of early POC decline (1978-1988)

was more pronounced in the male POC time series. Based on PHR and LSI, areas are either associated with high probabilities or low probabilities with few intermediate values, indicating that the study area is more strongly binary for male martens. This suggests that larger area requirements may result in a greater initial impact if the average clearcut size were to increase substantially in the future.

In areas where the POC decline followed the second spatiotemporal trend, the decline was initiated at the end of the salvage period, coinciding with the passage of the MFPA and the increased reliance on partial harvests. In these areas POC declined at a relatively constant rate 1985-2007 with short-term increases in rate of decline (1997-1999 and 2001-2004). This overall pattern of decline corresponds with the substantial increase in the total acreage harvested that has occurred since the passage of the MFPA. In the 10 years following the passage of the MFPA, the total annual acreage harvested for commercial forestlands in Maine increased from ~250,000 acres to ~500,000 and the percentage of those harvests that were partial harvests increased from 60% to 94%. The total volume harvested, however, changed relatively little in the early 1990s (Maine Forest Service 1998). In Maine, as regional spruce and fir harvest declined following the spruce-budworm salvage period, there was a concurrent increase in hardwood harvest to meet continued market demand for pulpwood following the pulse of salvaged timber (Maine Forest Service 1998). Consequently, although it is often ignored as an impact of commercial forestland owners' response to natural disturbances, salvage logging and market response can result in a larger forest area being disturbed over the long term than would have been directly impacted by an insect outbreak, exacerbating any detrimental ecosystem effects (Prestemon and Holmes 2004, Foster and Orwig 2006). Despite these

predictable effects, it was recently pointed out that “remarkably little” research has been conducted on the effects of salvage operations on wildlife populations (Lindenmayer and Noss 2006), and what little research has been conducted has focused on postfire salvage logging (Lindenmayer and Noss 2006; but see Radeloff et al. 2000). This is the first study to document the immediate and the long-term effects of post-insect epidemic salvage logging on the broad-scale quantity and distribution of habitat for a forest-dependent wildlife species.

Previous research in Maine has suggested that home ranges comprised of partially-harvested forest are of lower quality for marten compared to those comprised of primarily mature, second-growth forest (Fuller and Harrison 2005). Approximately 94% of the potential marten home ranges across my study area included habitat that received a *light* harvest 1988-2007, and for 62% of the potential male home ranges (64% of the female) the amount of habitat within the home range that received a *light* harvest exceeded the median value (26.6%) Fuller and Harrison (2005) documented for martens that expanded their home ranges in the winter to include more mature, second-growth forest. Further, 6% of the male and 5% of the female potential home ranges exceeded the maximum value (73%) documented by Fuller and Harrison (2005), and if these areas effectively no longer represent suitable marten habitat because of a substantial reduction in habitat quality, then this would represent an additional loss of marten habitat ca. 2007 of ~70,907 ha. Martens, thus, may to be able to mitigate the effects of partial harvesting by expanding their home ranges in order to reduce the use of partially harvested forest at critical times of year (Fuller and Harrison 2005); however, doing so would also increase a

marten's energetic demands (Hodgman et al. 1997) and spatial requirements beyond what was modeled here.

CONSERVATION AND MANAGEMENT IMPLICATIONS

The cumulative effects of forest management have been widespread reductions in habitat supply for marten, the probability of marten occurrence, and potential marten density, which resulted both from habitat loss and fragmentation. Although the majority (62%) of marten habitat loss occurred during the period of preemptive followed by salvage logging that occurred in response to the 1973-1985 spruce budworm outbreak, habitat loss and the associated decline in POC continued after the passage of the MFPA, as partial harvesting and total acreage harvested increased. In the near future, habitat recruitment may be able to provide some positive offset to future habitat losses. It is, however, important for forest and wildlife managers to know that the legacy of past forest management will be a sustained loss of >150,000 ha of marten habitat within the study area, even based on optimistic assumptions. Further, the NDMI-based methodologies used here were not originally designed to predict residual basal area, and it is very likely that some proportion of the 307,862 ha of marten habitat that received a *light* harvest 1988-2007 (Figure 1.11) will not retain enough basal area to exceed published threshold for marten habitat use (i.e., >18 m^2/ha live basal area; Payer and Harrison 2003) even though a relatively continuous canopy may still remain. If these areas effectively no longer represent suitable habitat for martens because of a substantial reduction in habitat quality, then this would represent an additional loss of marten habitat. Thus, I recommend that additional research is needed to quantify the residual post-harvest structure (e.g., basal area and canopy closure) in forested areas that have received a *light* harvest as

classified using TM imagery. Preliminary estimates suggest that in many areas classified as *light* harvest the residual basal area was <13 m^2/ha (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*), which was the average basal area associated the partially-harvested forest occupied by martens in northern Maine (Fuller and Harrison 2005). Thus, in evaluating the effects of forest management on marten habitat loss I was conservative by focusing on *heavy* harvests, indicating that the actual loss of marten habitat 1975-2007 was between 434,978 ha (32%) and 747,480 ha (54%).

I estimated that ~35% of townships within the study area in 2007 support ½ or fewer of the adult martens that they could have potentially supported in 1975. If, however, the seasonal expansion of home ranges that previous researchers observed in north-central Maine (Fuller and Harrison 2005) were to translate into an overall increase in home range size for martens in a partially-harvested landscape then the potential density in >35% of townships has likely declined by ≥50%. Preliminary estimates suggest that township-scale marten densities would be reduced by on average 44% if median home range size were to increase uniformly by only 10%, and 10% is considerably less than the average observed increase for males and females in north-central Maine (average = 82%; Fuller and Harrison 2005). Further, although marten trapping harvest has remained relatively stable and trapper success rate has remained high in Maine since the early 1990s (Maine Department of Inland Fisheries and Wildlife *Unpublished data*), the actual number of martens harvested declined in the northern portion of my study area 1991-2006 where *light* harvesting has been extensive and increased 1991-2006 in the southern portion where the extent has been far less. Because

of the already extensive nature of partial harvesting, with ~94% of marten home ranges already affected to some degree by partial harvesting ca. 2007 and 480,000-500,000 ac of commercial forestlands being partially harvested each year, additional efforts should be directed at determining the extent that partial harvesting is affecting habitat for martens and other forest-dependent wildlife across the commercially managed forests of Maine.

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CHAPTER 2

LINKING THE EFFECTS OF FOREST MANAGEMENT TO CANADA LYNX OCCURRENCE ON COMMERCIAL FORESTLANDS IN NORTHERN MAINE

ABSTRACT

Increases in Maine's Canada lynx (*Lynx canadensis*) population in the late 1990s and early 2000s have been credited to regenerating forest conditions created by the timber harvesting patterns that resulted from salvage logging within spruce-fir forests during the 1973-1985 spruce budworm outbreak (*Choristoneura fumiferana*). Since the early 1990s, however, timber harvesting rates and patterns have changed dramatically following changes in forest policy, and current policies provide little guidance for maintaining early-successional forest habitat on privately-owned commercial forestlands. More research is needed that can help land and wildlife management agencies better understand how lynx presence is influenced by changes in forest composition and configuration. I developed a 2004 forest cover type map, based on satellite-derived forest harvest and overstory composition data, and used the map to identify regenerating forest conditions associated with high abundance of the lynx's primary prey, the snowshoe hare (*Lepus americanus*). I then derived habitat-based predictor variables to model lynx occurrence using simulated occupied and unoccupied lynx home ranges based on presence/absence data provided by snow track surveys conducted across 60 townships in northern and western Maine, 2003-2006. Candidate models were developed to evaluate the alternative hypotheses that 2nd-order habitat selection by lynx is influenced by home range composition, snowshoe hare density, and/or habitat configuration. The resulting top-ranked model included the predictor variables mean hare density, percent mature

conifer forest, and the interaction between the two main effects. The area under the receiver operating curve (AUC) based on leave-one-out cross validation indicated that there was a 69% probability that an occupied home range would have a higher mean hare density and percent of mature conifer forest than an unoccupied home range. Based on this model, I calculated the probability of occurrence for lynx across 1.62 million hectares of commercial forestlands in northern Maine and noted that 29% of the landscape had a ≥50% probability of occurrence and only 17% had a probability of occurrence ≥80%. Larger blocks of higher probability of occurrence were more spatially aggregated in the north-western and central regions of the study area where percent mature conifer forest and mean hare density were generally higher as a result of past timber harvesting patterns. Estimated potential densities for resident adult lynx were generally <3 lynx/100 km^2, but exceeded 5 lynx/100 km^2 in some townships where probability of occurrence was high. This suggests that habitat in Maine can potentially support lynx densities that are comparable to some northerly populations during the cyclic high in snowshoe hare populations. Snowshoe hare density in occupied areas (mean = 0.74 hares/ha), however, was only slightly higher than unoccupied areas (mean = 0.62 hares/ha) and probability of occurrence was sensitive to small changes in snowshoe hare density, indicating that lynx densities could decline rapidly in townships where young regenerating forest is not available to replace the advanced regenerating forest that is currently supporting high snowshoe hare densities. Further, ongoing research suggests that snowshoe hare populations in northern Maine fluctuate with a reduced-amplitude cycle and that hare densities in high-quality hare habitat have declined

in recent years, which could exacerbate any habitat-induced decline in the lynx population.

INTRODUCTION

Regional conservation planning for threatened and endangered species requires reliable information on both a species' habitat requirements and the current distribution of habitat (Osborne et al. 2001, Betts et al. 2003, Osborne and Suárez-Seone 2007, Viña et al. 2007). Resource selection functions (Manly et al. 2002) have been widely used to quantify species-habitat associations and to inform the species conservation planning process (e.g., Johnson et al. 2004, Meggs et al. 2004, Aldridge and Boyce 2007), and the availability of satellite data and remote sensing techniques have enabled predictions of species occurrence across large areas. However, spatial or temporal extrapolation of predictive models to identify areas with high habitat suitability or probability of species occurrence can be problematic if the generality or transferability of the model is restricted by model calibration or data availability (Fielding and Haworth 1995, Vaughan and Oremerod 2003, Miller et al. 2004). Species with broad geographic ranges, for example, are likely to experience spatial variation in resource availability that may be expressed as region-specific patterns of resource selection (Fortin et al. 2008). Even relatively fine-scale landscape conditions (composition and configuration) can be highly dynamic because of natural or anthropogenic disturbance process (Turner 1989); thus, dynamic landscapes limit the utility of habitat data that represents a snapshot in time. Consequently, the conservation planning process for many threatened or endangered species requires habitat studies in areas where habitat disturbances have occurred to ensure model efficacy, particularly if predictive habitat models are to be for monitoring.

The Canada lynx (*Lynx canadensis*) has a broad geographic range, extending across the boreal and sub-boreal forests of Canada and the northern United States. In 2000, the Canada lynx was designated as federally threatened under the Endangered Species Act in the contiguous United States (U. S. Department of Interior 2000) and critical habitat was recently designated in five areas currently occupied by lynx, including northern Maine, northern Minnesota, and portions of Idaho, Montana, Wyoming, and Washington (U. S. Department of Interior 2009). At the regional scale, lynx are generally thought to occur in areas with deep snowfall (Buskirk et al. 2000, Hoving et al. 2005) and across forest types that provide both denning and foraging habitat (Koehler and Aubry 1994). Although the specific forest types that provide lynx foraging habitat varies across their southern range (Koehler and Aubry 1994), the primary prey association varies far less. Lynx are specialist predators on snowshoe hares (*Lepus americanus*) across their range (Koehler and Aubry 1994, Aubry et al. 2000). In a recent analysis Roth et al. (2007) used stable isotope analysis to evaluate the degree of geographic variability in the prevalence of snowshoe hares in the lynx diet. Although they ultimately conclude that lynx are facultative rather than obligate specialists on hares, the estimated percentage of hares in the lynx diet was 45-100% for all of the states and provinces included in their analysis.

Because of the importance of snowshoe hares in the diet of lynx, the presence of snowshoe hares and their preferred habitat conditions are considered essential for lynx conservation in the U.S. (U. S. Department of Interior 2008). Lynx exhibit strong selection for habitat(s) where snowshoe hares are abundant (Parker et al. 1983, Koehler 1990, Staples 1995, Mowat and Slough 2003, Fuller et al. 2007, Vashon et al. 2008a),

and snowshoe hare abundance is closely associated with the density of vegetation cover in regenerating forest or mature forest understories (Hodges 2000). Consequently, current recommendations on federal lands occupied by lynx (US Forest Service 2000) largely emphasize limiting the stand-scale effects of timber harvesting on regenerating forest conditions, recommending, for example, precommercial thinning (PCT) be delayed in regenerating stands based the effect of PCT on snowshoe hare abundance (e.g., Sullivan and Sullivan 1988, Griffin and Mills 2007, Homyack et al. 2007). However, little research has actually evaluated the interactions between forest management, snowshoe hares, and lynx habitat selection (but see Hoving et al. 2004, Robinson 2006, Fuller et al. 2007) despite the strong influence of snowshoe hare density on lynx spatial organization and population persistence in cyclic populations (Koehler and Aubry 1994, Aubry et al. 2000, Mowat et al. 2000).

Addressing issues of land use at the landscape-scale (2nd order; *sensu* Johnson 1980) is of critical importance for territorial and wide-ranging species such as the Canada lynx because the number and distribution of home ranges that can be supported by the available habitat conditions structures the population (Fretwell and Lucas 1970). Although few studies have studied landscape-scale habitat selection by lynx (Koehler 1990, Poole et al. 1996, Hoving et al. 2004, Vashon et al. 2008a), only one has evaluated lynx habitat selection at this scale relative to both forest composition and land-use history (Hoving et al 2004). More research is needed that can provide a link between landscape change and lynx occurrence to help land and wildlife management agencies make land-use decisions that will not jeopardize the persistence of lynx in currently occupied areas.

The majority (>50%) of critical habitat for lynx was designated on federal lands managed by the federal land management agencies (U. S. Department of Interior 2009), while the overwhelming majority (>80%) of designated critical habitat in the western states (ID, MT, WA, WY) was on federal lands. In contrast, the distribution of designated critical habitat in Maine, which is occupied by the only extant population of lynx in the contiguous United States east of Minnesota (U. S. Department of Interior 2008, 2009), is comprised of predominantly (~91%) privately-owned lands (U. S. Department of Interior 2009). A total of 24,597 km^2 of northern Maine was designated as critical habitat, and these forests are principally managed for the production of wood products (U. S. Department of Interior 2009). In fact, increases in Maine's lynx population in the late 1990s and early 2000s have been credited to regenerating forest conditions created by timber harvesting patterns in the 1970s and 1980s (Hoving et al. 20004). These authors concluded that based on the distribution of forest types ca. 1993 landscape-scale occurrence of lynx was positively associated with extent of advanced regenerating forest that was created via past clearcutting. Model sensitivity was low (38%), however, and inferences about forest types selected by lynx were based on regenerating forest with undetermined stand histories (Hoving et al. 2004).

Since the early 1990s, the landscape patterns and harvest rates associated with forest practices have changed dramatically in Maine. In the 1970s and 1980s, clearcut harvesting increased as large areas of spruce-fir forest were preemptively and salvage harvested in response to the 1973-1985 spruce budworm (*Choristoneura fumiferana*) outbreak. During this period there were no legislative definitions or standards in place to regulate the size or arrangement of clearcuts (Maine Forest Service 1995), but in 1989 the

Maine Forest Practices Act (MFPA) was passed (12 MRSA §8867-A to §8888 & MFS Rules Chapter 20), which increased regulatory standards and requirements associated with clearcut harvesting. Following the implementation of the MFPA in 1991, the number of acres annually harvested by clearcut immediately declined by >40% and since year 2000, clearcuts account for only 4% of the average harvest across commercial forestlands. Forest management relies on a variety of partial harvest treatments, including both even-aged (e.g., shelterwood) and uneven-aged (e.g., selection) management techniques. Those treatments result in a wide range of residual stand conditions (Robinson 2006), which have important implications for lynx conservation in the transitional northern hardwood-boreal forest transition zone near the southeastern extent of the lynx's geographic range.

Regional habitat conditions for lynx in Maine have likely changed significantly over the last 15 years as forest managers have increased their use of partial harvesting. First and foremost, snowshoe hare densities in partially harvested forests are on average 20-90% lower than in the coniferous or mixed coniferous-deciduous advanced regenerating forest that supports the highest snowshoe hare densities in Maine (Robinson 2006). Additionally, as the total acreage harvested by clearcuts has declined since 1991, the average size of a clear-cut has also been reduced from >125 acres (Maine Forest Service 1995) to <25 acres (Maine Forest Service 2003, 2005, 2007). Although it has not yet been directly evaluated, research suggests that the spatial characteristics of regenerating forest may play a role in lynx habitat selection patterns based on studies that have shown shifts in habitat selection by lynx during changes in snowshoe hare abundance (Murray et al. 1994, Fuller 2006) and selective use of edge habitat adjacent to

regenerating forest for foraging (Staples 1995, Mowat et al. 2000). The goal of my research was to increase understanding of how forest management influences landscape-scale occurrence by lynx in the southeastern extent of the species' geographic range. The objectives of this study were to: 1) develop a satellite-based forest type map, including forest harvest history (1970-2004) and current forest composition (ca. 2004), that could also be updated in the future to facilitate lynx habitat monitoring, 2) evaluate the relative influence of home range composition, habitat patch configuration, and snowshoe hare density on landscape-scale lynx occurrence using an information-theoretic approach (Burnham and Anderson 1998), and 3) provide regional information on the status of lynx habitat in northern Maine, which has been identified as one of the primary target areas for lynx conservation and recovery.

STUDY AREA

The study area is defined by the area of overlap between the Landsat Multispectral Scanner (MSS), Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) satellite imagery (Landsat Worldwide Reference System (WRS) path 12, row 28) used to construct the harvest detection time series (see below) and the northwestern border between Maine and the province of Quebec, Canada (Figure 2.1). This area includes all or part of 174 unorganized townships that are primarily privately-owned by industrial forest products companies, family-owned corporations, and investment entities. Recent history of ownership changes within this region are broadly representative of the unorganized townships of northern Maine (Hagan et al. 2005, Jin and Sader 2006) across which 23.8 million acres (96,315 km^2) transferred ownership between 1980 and 2005. The study area includes approximately 1.62 million hectares of

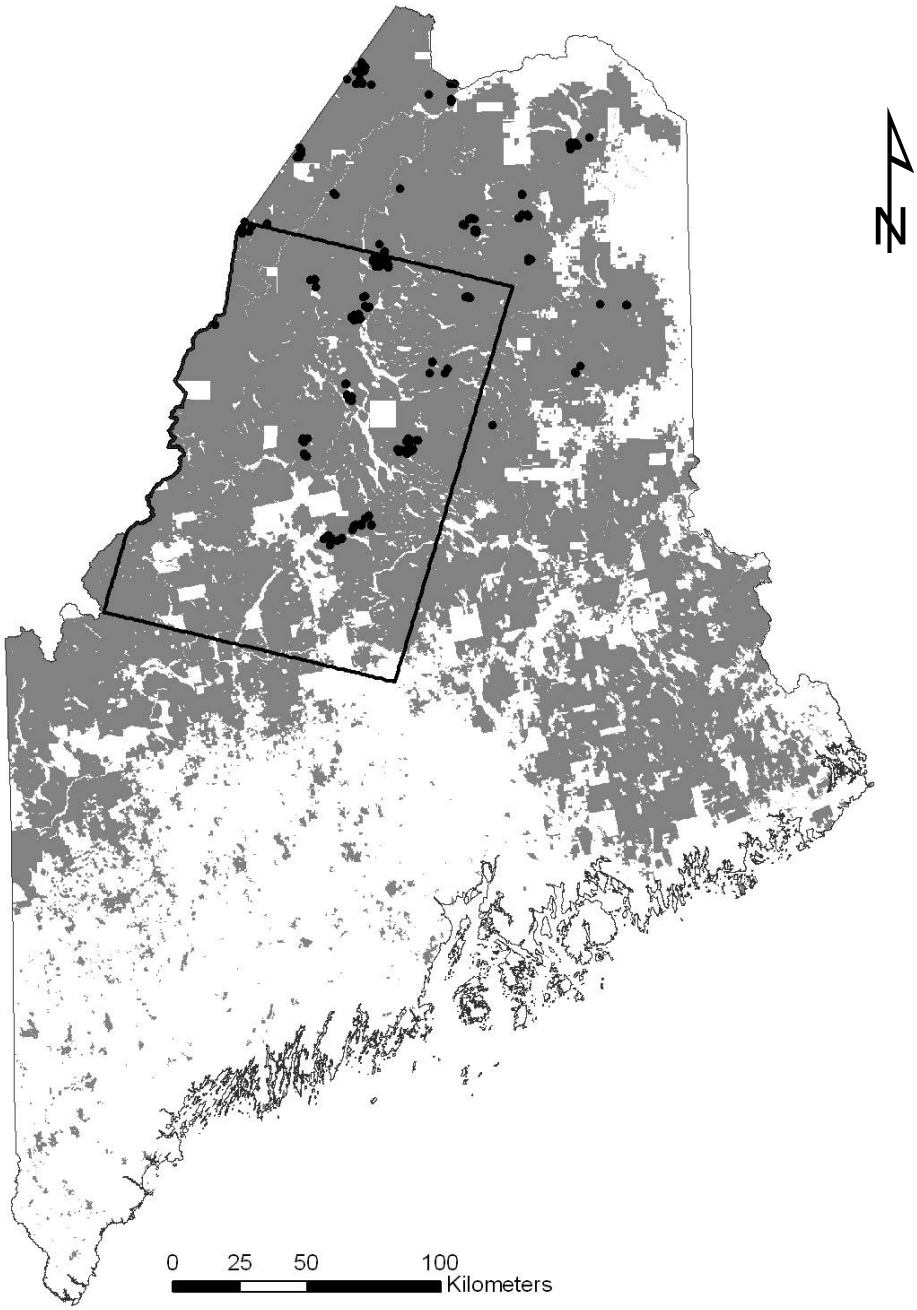


Figure 2.1. The study area (black outline) encompassed ~1.62 million hectares of commercial forestland (shown in gray), and was defined by the overlap between the Landsat satellite imagery used to construct the harvest detection time series and the Maine border. This area also overlapped with the area currently occupied by lynx, as defined by the locations of lynx (black dots) detected during snow track surveys conducted from 2003-2006.

commercial forestland within the Acadian forest ecoregion, an ecological transition zone in the northeastern U.S.A. between the southern temperate deciduous-dominated forests and the northern boreal forests (Seymour and Hunter 1992). Commonly occurring species include: balsam fir (*Abies balsamea*), white (*Picea glauca*), red (*P. rubens*), and black (*P. mariana*) spruce, white pine (*Pinus strobus*), white (*Betula papyrifera*) and yellow (*B. alleghaniensis*) birch, red (*Acer rubrum*) and sugar (*A. saccharum*) maple, and American beech (*Fagus grandifolia*). Forest harvesting is the primary form of forest disturbance (Seymour 1992, McWilliams et al. 2005) within this area and forest harvesting practices are regulated under the Maine Forest Practices Act (12 MRSA §8867-A to §8888 & MFS Rules Chapter 20). Urban and residential development is minimal (Hepinstall et al. 1999) and was concentrated in only 6% of the townships clustered in the southeastern corner of the region.

METHODS

Lynx occurrence analyses

I defined lynx occurrence and non-occurrence based on the results of snow track surveys conducted by the Maine Department of Inland Fisheries and Wildlife (MDIFW). Snow track surveys were conducted to establish the status of the lynx population in Maine (Vashon et al. 2003) and were targeted at a stratified-random sample of unorganized townships (Figure 2.2). Township-scale strata were based on the predicted probability of lynx occurrence (low, medium, high) using the model results of Hoving et al. (2004). Additionally, digital orthophotographs were used during initial township selection to increase the likelihood that ≥55km of suitable secondary roads would be accessible in the selected towns (Vashon et al. 2003). MDIFW identified 55 km as the

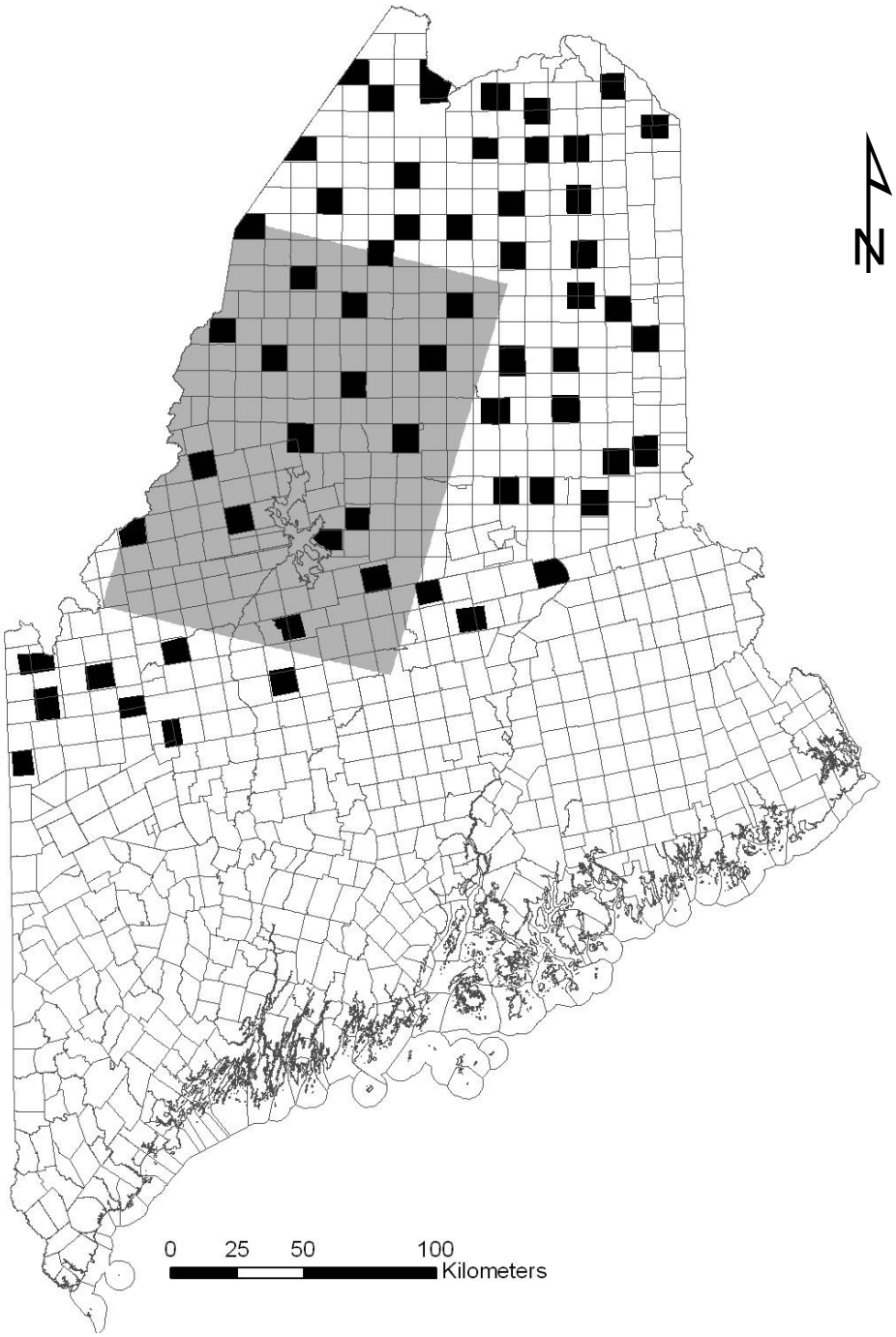


Figure 2.2. Stratified-random sample of 60 townships surveyed (shown in black) for lynx occurrence January-March, 2003-2006, with a minimum survey distance of 0.55km/km^2. Surveys were conducted by snowmobile and lynx tracks crossing survey roads were recorded with a GPS. The ~1.62 million hectare study area used for analyses is depicted in gray.

minimum distance required to detect a resident lynx within a township (MDIFW unpublished data). Unplowed logging roads within selected townships were surveyed January- March from snowmobiles 2003-2006, generally 24-72 hours after a snow event. All survey routes and the locations of lynx track crossings were recorded with a Global Positioning System (GPS). In my analysis, I only included townships where a minimum survey distance of 0.55 km/km^2 was attained.

Based on the lynx tracks recorded within my study area, I first randomly placed simulated circular lynx home ranges on the geographic center of areas of lynx activity (locations ≤5.8 km apart). The home range radius that I used to simulate the home ranges (2.9 km) was based on the 75% adaptive kernel estimates for home ranges in Maine (Vashon et al. 2008a), averaged across males and females (mean = 26.4 km^2) because it was not possible to reliably determine sex from the track measurements. Basing the analysis on the estimated area of a home range rather than, for example, a home range core, also constrained the number of home ranges that could be placed within one survey township, reducing the potential effect of pseudoreplication on error estimation (Hurlbert 1984). I then determined the minimum survey distance within these "occupied" home ranges and randomly placed "unoccupied" home ranges in surveyed areas with no lynx detections and survey effort equal to or greater than the minimum linear distance of track reconnaissance within home ranges that were simulated around lynx occurrences; this approach ensured equal survey intensity in the use and non-use datasets.

Forest cover type mapping

I developed a 2004 forest cover type map for my ~1.62 million hectare (4.0 million acre) study area based on satellite-derived forest harvest and overstory

composition data. Forest harvest data was derived from a harvest detection time series (1970-2007) assembled from five Multispectral Scanner (MSS) and nine Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) images (Legaard et al., Maine Image Analysis Laboratory, University of Maine, *In preparation*). Consecutive leaf-on (May-September) images with the lowest cloud cover and at the shortest temporal interval available were acquired to maximize the detection of harvest events based on the Normalized Difference Vegetation Index (NDVI) or Normalized Difference Moisture Index (NDMI). Extensive investigations into the use of vegetation indices to map forest change in northern Maine have indicated that NDMI-based methodology is capable of detecting partial- and clear-cut harvests with good accuracy, provided Landsat TM images are acquired 1-3 years apart (Wilson and Sader 2002, Jin and Sader 2005). After co-registration (RMS error <15 m), to improve the consistency of image interpretation during subsequent analyses, all images were transformed into a common radiometric scale using a relative radiometric normalization procedure (Legaard et al., Maine Image Analysis Laboratory, University of Maine, *In preparation*). NDMI images were calculated from the radiometrically normalized images using the TM near infrared (NIR) band 4 (0.76-0.90 μm) and mid-infrared (MIR) band 5 (1.55-1.75 μm): NDMI = (NIR - MIR) / (NIR + MIR).

A series of three-date RGB-NDMI classification sequences (Wilson and Sader 2002, Jin and Sader 2005) were performed to produce a time series of 9 harvest maps based on the TM and ETM+ imagery: 1988-1991, 1991-1993, 1993-1995, 1995-1997, 1997-1999, 1999-2000, 2000-2001, and 2001-2004. Harvests detected within each interval were classified into two intensity classes based on the magnitude of NDMI

change: heavy or light. This classification scheme was not designed to match current regulations in Maine that classify harvests based on the residual structure as “clearcut” (currently defined any timber harvest greater than 5 acres in size that results in a residual basal area of trees over 4 ½ inches in diameter measured at 4 ½ feet above the ground of less than 30 ft^2/ac; 12 MRSA §8867-A to §8888 & MFS Rules Chapter 20) or “partial harvest” (i.e., all other harvests greater than 5 acres that retain >30 ft^2/ac). The heavy harvest class represented stand-replacing or regeneration harvests targeted at initiating the next cohort of growing stock, which I expected would include both clearcut and heavy partial harvests. Light harvests represented partial harvests and tending operations targeted at the current growing stock, which I expected would retain >50% of the live basal area. A similar process was used to detect heavy harvest entries using the MSS imagery based on NDVI, expanding the time series by 5 additional intervals: 1973-1975, 1975-1978, 1978-1982, 1982-1985, and 1985-1988. NDVI, based on NIR and the red band (0.63-0.69 μm), was used in place of NDMI because Landsat MSS does not record reflected radiation in the mid-infrared range (1.55-1.75 μm). Additionally, areas disturbed ca. 1970-1973 were mapped directly from the 1973 MSS image. Light harvests were not mapped 1970-1988 because they could not be reliably classified using Landsat MSS imagery. Additional details about the image processing and timber harvest detection will be presented in Legaard et al. (Maine Image Analysis Laboratory, University of Maine, *In preparation*).

I used the timber harvest detection series to map stand-level timber harvest operations 1970-2007. Beginning with the earliest time step (1970-1973), these data were spatially combined with the subsequent time step (1973-1975) in a process to create

stand-level classes defined by their harvest history, including the time series interval during which the first timber harvest was detected, and any subsequent harvest treatments following the initial harvest entry. Prior to subsequent analysis, a minimum mapping unit of 3.5 ha (8.7 ac) was applied to the combined classes. If multiple entries into a stand were identified, the satellite images were visually interpreted to determine what harvest activities had occurred. This process was repeated with each successive time step (e.g., 1975-1978) being combined with the previously merged dataset (e.g., 1970-1975). Harvest entries classified as *heavy* in the harvest detection time series represent stand-replacing events, including commercial clear-cuts and overstory removals. Subsequent entries after an initial *heavy* harvest were assumed to represent intensive management of regenerating forest (i.e., manual or chemical thinning) if the second entry occurred ≥15 years after the initial *heavy* harvest. Harvests classified as *light* represent tending operations of the mature growing stock and so represent partial harvest treatments (e.g., selection and uneven-aged management) that retain overstory trees for future operations. Subsequent entries after an initial *light* entry were classified as partial harvest re-entries if *light* or overstory removals if *heavy*. This process resulted in the creation of 268 classes of single and multiple entry timber harvests (1970-2004), including: mature, second-growth forest, partially-harvested forest (0-16 years post-harvest), and regenerating forest (0-34 years post harvest) (Table 2.1).

The 2004 forest cover type map was developed as an update to the 1993 Maine Gap Vegetation and Land Cover map (MEGAP) following methods similar to Sader and Legaard (2008). The latter half of the harvest detection time series was first used to identify those areas where timber harvesting had occurred (1991-2004) in areas identified

Table 2.1. Generalized forest types derived from the combined harvest history dataset for forestland included in the 1.62 million hectare study area and class area.

	Forest type	**Hectares**
1	Mature forest	721,323
2	Partially harvested forest[a] - recent[b]	215,124
3	Partially harvested forest - established[b]	74,300
4	Regenerating forest[c] - 0-15 years	179,353
5	Regenerating forest - 16-34 years	270,260
6	Non-forestland[d]	193,376

[a] Partially harvested forest identified by *light* harvests in the harvest detection time series (Legaard et al., Maine Image Analysis Laboratory, University of Maine, *In preparation*).
[b] Recent and established partially harvested forest defined based on Fuller et al. (200) as *light* timber harvests 0-10 and 11-26 years post-harvest respectively.
[c] Regenerating forest identified by *heavy* harvests in the harvest detection time series (Legaard et al., Maine Image Analysis Laboratory, University of Maine, *In preparation*).
[d] Non-forestland includes water and non-forested wetland classes.

by the MEGAP as “Mature Forest.” According to the MEGAP, approximately 89% of the study area was comprised of mature forest ca. 1993 and was mapped with >94% accuracy based on interpreted aerial videography (Hepinstall et al. 1999). Mature forest pixels in the MEGAP were classified into four composition classes (Coniferous Forest, Coniferous/Deciduous Forest, Deciduous/Coniferous Forest, and Deciduous Forest; Hepinstall et al. 1999) and for the forest pixels that were unaffected by timber harvesting, the coniferous and deciduous classes were retained and the two mixed classes were combined into a single mixed class. Forest pixels that were affected by timber harvesting were replaced with composition data derived from an unsupervised classification of the same 2004 Landsat TM image used in the harvest detection time series. If pixels were not classifiable into one of the three composition classes (Coniferous, Mixed, or Deciduous Forest) resulting from recent timber harvest activity, these pixels were placed into an additional “Disturbed Forest” class.

Habitat model predictor variables

I used the combined harvest history dataset and the 2004 forest cover type map to develop a suite of habitat-based predictor variables. Variables were chosen to capture the relationship(s) between lynx occurrence and ecological factors that could be directly influenced by forest management, including elements of landscape composition and patch configuration. I calculated three measures of composition at the home-range scale that reflected observed relationships between lynx habitat use and forest structure. Lynx use of conifer-dominated regenerating forest (approximately 15-35 years old) that supports high hare densities has been documented in both the boreal (Mowat and Slough 2003) and the sub-boreal forest (Parker et al. 1983, Koehler 1990a, 1990b, Hoving et al.

2004, Robinson 2006, Fuller et al. 2007, Vashon et al. 2008a). To identify high-quality hare habitat that would provide lynx foraging areas ca. 2004 in the Acadian Forest, I first used the combined harvest history dataset to identify areas of advanced regenerating forest >15 years post-harvest (maximum 34 yrs from harvests that occurred 1970-1971). I then used the 2004 forest composition map to identify areas of conifer or mixed forest, and combined the two datasets to create a binary map of (1) conifer or mixed, advanced regenerating forest and (0) all other forest types. I created two additional binary maps, the first for mature conifer (i.e., uncut since 1970) because of the important role that this forest type appears to play in supporting lynx populations in some areas of the boreal forest (e.g., Murray et al. 1994, Poole et al. 1996). Finally, landscape-scale lynx occurrence in Maine was previously found to be negatively associated with partially-harvested forest (Hoving et al. 2004). Recently, however, 3rd-order habitat selection by lynx was found to be positively associated with "established" partially-harvested forest in northern Maine (11-26 years post-harvest; Fuller et al. 2007). Consequently, it seemed important to reevaluate the relationship between lynx occurrence and partially-harvested forest in the contemporary landscape; so, I created a binary map representing (1) established, partially harvested forest and (0) all other forest types. I calculated the percent of the available forestland area within the occupied and unoccupied home ranges that was comprised of high-quality hare habitat (R), mature conifer (C), and established, partially-harvested forest (PH).

I calculated six landscape configuration metrics that were ecologically relevant (Li and Wu 2004) and that quantified different measures of habitat patch area and configuration which I hypothesized may influence lynx habitat selection. All metrics

chosen used contiguous patches of high-quality hare habitat to define patches. No previous study had directly investigated the response of lynx to habitat configuration, but previous studies conducted at the 3rd order (Murray et al. 1994) and 4th order (sensu Johnson 1980) (Staples 1995, Mowat et al. 2000, Fuller 2006) suggest that habitat selection by lynx may be influenced by the spatial characteristics of habitat patches. When selecting the candidate metrics, I also referenced Neel et al. (2004) to ensure that the selected metrics, as calculated by FRAGSTATS version 3.3 (McGarigal et al. 2002), were likely to respond monotonically to the amount and/or aggregation of high-quality hare habitat. The metric influenced primarily by the amount of high-quality hare habitat was area-weighted mean patch size (AWMPS). AWMPS equals the sum across all habitat patches of the mean patch size multiplied by the proportional abundance of each patch, which adjusts the estimate of the mean such that larger patches have greater weight than smaller patches. Metrics influenced by the configuration of habitat included: patch density (PD) and percent like adjacencies (PLADJ). PD is an area-based measure of the number of patches and PLADJ provides a measure of the contagion or aggregation of habitat patches and is insensitive to class area.

Finally, I included mean landscape-scale hare density (HARES) as an additional predictor variable to evaluate the cumulative effect of home-range composition on prey density and, ultimately, on lynx occurrence. Mean hare density values for occupied and unoccupied home ranges were calculated using a map of 2004 forest cover types and their associated stand-scale hare densities (Table 2.2). For the majority of types I was able to use density estimates provided by research in Maine (Litvaitis et al. 1985, Lachowski 1997, Fuller and Harrison 2005, Robinson 2006, Homyack et al. 2007) or Quebec (de

Table 2.2. Stand-scale snowshoe hare density estimates for forest types associated with harvest history (1970-2004) and 2004 overstory composition.

Stand type	Years post-harvest	hares/ha
Mature forest[a]		0.25
Partially-harvested forest[b]		0.80
Conifer or mixed regenerating forest (unthinned[c])		
	0 - 9[d]	0
	10 - 17[e]	0.2 - 1.6
	≥18[f]	1.8
Deciduous regenerating forest[d]		0.4

[a] Mature forest includes all overstory composition classes, including mature conifer. Hare density estimate based on Lachowski (1997) and Fuller and Harrison (2005).
[b] Partially-harvested forest includes all overstory composition classes. Hare density estimates based on Robinson (2006).
[c] Hare density estimates for thinned regenerating forest reduced by 50% based on the results of Homyack et al. (2007).
[d] Hare density estimate based on de Bellefeuille et al. (2001).
[e] Assumed a linear relationship between stand age and hare density 10-18 years post-harvest, resulting in an estimated increase of 0.2 hares/ha/year.
[f] Hare density for regenerating forest ≥18 years post-harvest based on three years of data collected for seven conifer-dominated, advanced regenerating stands (≥18 years post-harvest) in north-central Maine for which researchers documented high hare densities 2002, 2003, and 2005 (Robinson 2006, Homyack et al. 2007). This period may represent a temporal high point for those stands (Scott *In preparation*).
[g] "Deciduous regenerating forest" includes all ages classes of regenerating forest (0-34 years post-harvest). Hare density estimate based on Litvaitis et al. (1985).

Bellefeuille et al. 2001). I estimated the average leaf-off hare density for high-quality hare habitat (i.e., 1.8 hares/ha; Table 2.2) based on three years of data collected for seven conifer-dominated, advanced regenerating stands (≥18 years post-harvest) in north-central Maine for which researchers documented relatively high hare densities 2002, 2003, and 2005 (Robinson 2006, Homyack et al. 2007). Although southern populations (<49º N) of snowshoe hares are generally not expected to be strongly cyclic (Hodges 2000), ongoing research has recently suggested that the years used to derive the average hare density for high-quality hare habitat may represent a temporal high point for those stands (Scott *In preparation*). Thus, results should be viewed with some caution as potentially being representative of 2nd-oder habitat selection by lynx during a period of relative high for snowshoe hare densities in northern Maine. I assumed that young regenerating forest <10 years post-harvest would support 0.0 hares/ha (de Bellefeuille et al. 2001), and assumed a linear relationship between stand age (10-18 years post-harvest) and hare density (0.0-1.8 hares/ha), which resulted in an annual estimated increase of 0.2 hares/ha/yr. Hare density estimates for conifer or mixed, advanced regenerating stands affected by precommerical or commercial thinning were reduced by 50% based on research in Maine that compared hare density estimates of thinned vs. unthinned regenerating stands of the same age (Homyack et al. 2007). In addition to mean hare density, I included a variable that measured the habitat interspersion (IJI) between low (0.25 - 0.8 hares/ha), medium (0.8 - 1.4 hares/ha) and high (1.4 - 1.8 hares/ha) hare density forest types, because habitat edges may provide valuable foraging habitat for lynx (Staples 1995, Mowat et al. 2000).

Model development and validation

I built *a priori* candidate models and used the corrected Akaike's Information Criterion (AIC_c; Burnham and Anderson 1998) to rank the candidate models to obtain a resource selection probability function (RSPF; Manly et al. 2002). I used binary logistic regression (Systat version 12) to estimate the RSPF coefficients included in the *a priori* models. Prior to subsequent analyses, I used Hosmer and Lemeshow (2000) goodness-of-fit test statistic to assess model fit. Candidate models (Table 2.3) were chosen to evaluate the alternative hypotheses that 2nd-order habitat selection by lynx is based on: 1) home range composition (models 1-3); 2) hare density (model 4); 3) landscape-scale hare density and home range composition (models 5 and 6); 4) landscape-scale hare density and habitat configuration (models 7 - 12); or 5) habitat configuration (model 13). Prior to coefficient estimation, I assessed each variable for outliers and influential cases (Cook's D >1) (Hosmer and Lemeshow 2000). Coefficients for the top-ranked RSPF model are presented as unstandardized estimates and standard errors.

The predictive accuracy of logistic regression models are typically evaluated by classifying observations (in-sample or out-of-sample) as used or unused based on a threshold value or a range of threshold values (Fielding and Bell 1997, Pearce and Ferrier 2000). An evaluation conducted over a range of threshold values can be used to generate a receiver operating characteristic (ROC) curve and the area under the ROC curve (AUC) provides an index of a model's ability to discriminate between positive and negative observations that is independent of species prevalence (Hanley and McNeil 1982). Because of the relatively small sample size, I was unable to partition the data into split-sample training and testing datasets for validation. Instead I used leave-one-out cross-

Table 2.3. *A priori* set of candidate models chosen to evaluate the influence of: home range composition (models 1-3); landscape-scale hare density (model 4); landscape-scale hare density and home range composition (models 5 and 6); landscape-scale hare density and habitat configuration (models 7 - 12); and habitat configuration (model 13) on 2nd-order habitat selection by lynx in northern and western Maine.

Model no.	Model variables	K
1	R[a]	2
2	C[b]	2
3	R + PH[c]	3
4	HARES[d]	2
5	HARES + C	3
6	HARES + C + HARES*C	4
7	HARES + AWMPS[e]	3
8	HARES + PD[f]	3
9	HARES + PLADJ[g]	3
10	HARES + AWMPS + PLADJ	4
11	HARES + IJI[h]	3
12	AWMPS + PLADJ + PD + IJI	5

[a] R = percent of available forestland within simulated home range comprised by high-quality hare habitat (i.e., conifer or mixed, advanced regenerating forest >15 years old).
[b] C = percent of available forestland within simulated home range comprised by mature conifer forest (i.e., uncut since 1970).
[c] PH = percent of available forestland within simulated home range comprised by established, partially-harvested forest (i.e., 11-26 years post-harvest).
[d] HARES = mean snowshoe hare density (hares/ha) within simulated home range.
[e] AWMPS = area-weighted mean patch (ha) size for high-quality hare habitat.
[f] PD = patch density (no. patches/home range area) for high-quality hare habitat.
[g] PLADJ = percent like adjacencies between pixels of high-quality hare habitat.
[h] IJI = interspersion and juxtaposition index describing the interspersion between low (0.25 - 0.8 hares/ha), medium (0.8 - 1.4 hares/ha) and high (1.4 - 1.8 hares/ha) hare density forest types (see Table 2.2).

validation to calculate AUC values to quantify the ability of the candidate models to discriminate between occupied and unoccupied home ranges. Additionally, for the top-ranked model I also used a *k*-fold cross-validation procedure recently proposed by Boyce et al. (2002). This latter method is used for evaluating RSPFs and is based on presence-only data. Based on this method, the model in question is used to classify the study area, which is then used to bin the per-cell predictions into a number of arbitrary categories (or RSPF scores). For each category *i*, the predicted frequency (P_i) is calculated as:

$$P_i = p_i / \sum_j p_j$$

where p_i is the number of presence observations predicted to fall in each category and $\sum_j p_j$ is the total number of presence observations. P_i is then adjusted for area (P_i/E_i) using the expected frequency (E_i), which is given by the relative proportion of the study area in each category:

$$E_i = a_i / \sum_j a_j$$

where a_i is the area (or number of cells) covered by a category *i* and $\sum_j a_j$ is the overall area (or total number of cells) in the study area. The area-adjusted frequencies (P_i/E_i) should be positively correlated with the probability category, and Boyce et al. (2002) recommends evaluation using the Spearman-rank correlation.

Habitat assessment

Predictions from the top-ranked candidate model were used to derive a map of lynx probability of occurrence for the study area. This continuous surface was calculated using a circular moving-window function to provide a value for each cell (30m) within the study area based on the characteristics of the neighboring area. I selected 2.9 km as the neighborhood radius to match the scale of the simulated home ranges used in the

development of the predictive model. I quantified the results by calculating the area of forestland within 10% probability bins and by estimating lynx density for the study area ca. 2004. Ideally, abundance data would be available when estimating density based on habitat suitability (Van Horne 1983); however, abundance data is often unavailable, making it necessary to index or estimate abundance directly from the predictions of occurrence models (Johnson and Seip 2008). Boyce and McDonald (1999) recommended an estimation method based on resource selection function that has since been used to estimate densities for grizzly bear (*Ursus* arctos; Boyce and Waller 2003), black bear (*Ursus americanus*; Gaines et al. 2005), and mountain caribou (*Rangifer tarandux caribou;* Seip et al. 2007). This method requires the availability of reference abundance data across all habitat types, which were not readily available for lynx in northern Maine.

Alternatively, I estimated density using a fixed grid and matched the grid size to the exclusive area occupied by an individual resident lynx so that I could simply sum the mean grid probability values (Manly et al. 2002). The mean probability value (x_{ij}) for grid cell *i* can be thought of as the likelihood (0.01 - 1.0) of an individual lynx occupying *i* at time *j*. Because it was not possible to identify the sex of the individual lynx detected during the snow track surveys, it was necessary that I estimate a single value to represent the average (intra-sexual) exclusive home-range area used by a resident adult lynx in northern Maine. I determined the appropriate grid size by referencing recent research conducted in northern Maine (Vashon et al. 2008a) to provide an estimate of the average spatial overlap between neighboring adult lynx (male:male, female:female, male:female). Using this research I determined that the weighted-average spatial overlap between adult lynx was 20.3% (Vashon et al. 2008a), and estimated the exclusive home-range area

(21.0 km^2) used by a resident adult based on the average intra-sexual home range size (26.4 km^2). This estimated exclusive area corresponded to a grid cell side length of 4,095 m. I aligned the fixed grid with the south-west/north-east orientation of my study area (Figure 2.1) to retain all available surface data and intersected it with a GIS layer of township boundaries (http://megis.maine.gov). I then calculated the mean probability of lynx occurrence for each intersected grid cell (x_{ij}). To estimate township-scale lynx densities I summed grid cell values by township ($\Sigma\, x_{ij}$) and then divided by the forestland area (A) within each township, such that: lynx density = $\Sigma\, x_{ij}/A$.

RESULTS

Lynx occurrence analyses

Eighteen of the 70 townships that were surveyed by MDIFW 2003-2006 overlapped with my study area and had a survey distance of ≥0.55 km/km^2 (Figure 2.2). The snow track surveys recorded 124 lynx track crossings in 12 of the 18 townships, which I used to simulate 18 occupied home ranges using a radius of 2.9 km (26.4 km^2) (Figure 2.3). The average survey intensity within the occupied home ranges was 19 km surveyed per 26.4 km^2 home range or 0.72 km/km^2 (range = 0.24 - 1.40 km/km^2). I simulated 25 non-occupied home ranges in areas with a minimum survey intensity of 0.24 km/km^2 and a maximum overlap of 4%, which resulted in an average survey intensity within non-occupied home ranges of 0.72 km/km^2 (range = 0.51 - 1.15 km/km^2). The range in the number of simulated home ranges (occupied or unoccupied) per township was 1-3 (Figure 2.3).

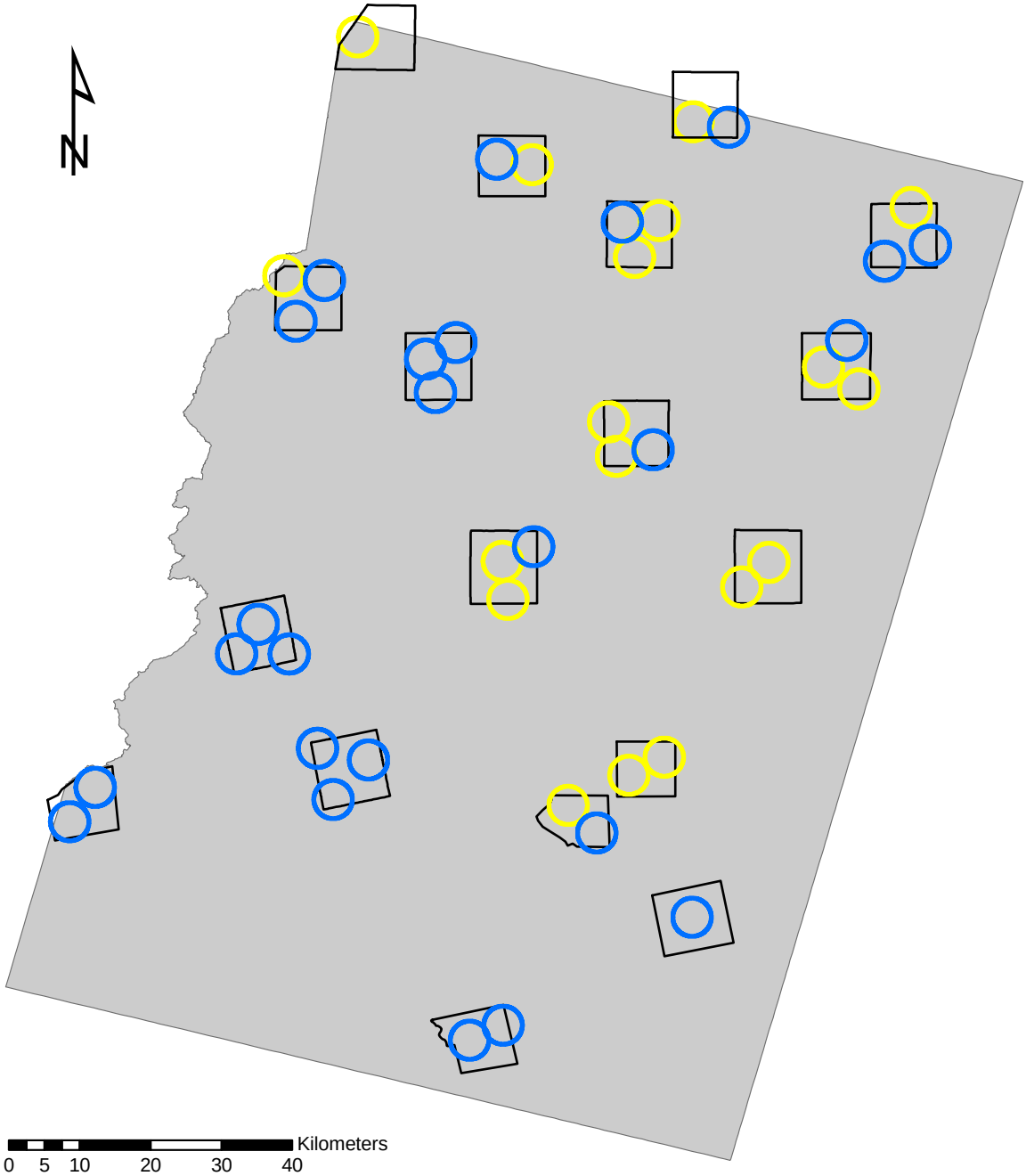


Figure 2.3. Simulated occupied (yellow line) and unoccupied (blue line) lynx home ranges located in surveyed townships (black line) overlapping the study area (gray).

Model development and validation

The top-ranked *a priori* model describing 2nd-order habitat selection by lynx in northern Maine (Table 2.4) included the predictor variables: mean hare density (HARES), percent of mature conifer (C), and the interaction between the two (HARES*C). Hosmer-Lemeshow statistic values for this model (0.888) and the global model (0.918), and McFadden's rho-squared for the top model (0.272) suggested that the data fit the logistic regression model and that the variables included in the top model explain a high proportion of the variability in the data. One unoccupied home range was removed on the basis of high influence (Cook's D >1). Correlation between HARES and C was low ($r < |0.1|$) (Table 2.5) and the 95% confidence interval for the odds ratio for both C and the HARES*C interaction did not include 1. This model (HARES + C + HARES*C; Table 2.4) received 59% of the weight of evidence ($w_i = 0.59$) and no candidate model had a $\Delta AIC_c \leq 2$ relative to the top model. Only one candidate model (HARES + C) had a $\Delta AIC_c \leq 4$ and the three single variable models (HARES, R, C) performed similarly with a $\Delta AIC_c = 4 - 6$. The HARES + AWMPS model performed the best among those including landscape-scale hare density and habitat configuration ($\Delta AIC_c = 6.33$). Results for the R + PH model that was included to further evaluate the relationship between lynx habitat selection and established, partially-harvested forest agreed with previous research in Maine (Hoving et al. 2005) that found a positive association with advanced regenerating forest ($\beta_R = 4.837$) and a negative association with partially harvested forest ($\beta_{PH} = -3.865$). The configuration-only model (AWMPS + PLADJ + PD + IJI) was the only model with $\Delta AIC_c > 10$.

Table 2.4. Akaike's Information Criterion corrected for small sample size (AIC_c) for the *a priori* set of candidate models for predicting presence and absence of lynx at the scale of the 75% adaptive kernel area in northern Maine, USA.

Rank	Model	K[a]	AIC_c	ΔAIC_c	w_i[b]	AUC[c]	Sensitivity	Specificity
1	HARES + C + HARES*C	4	50.82	0	0.59	0.692	0.667	0.875
2	HARES + C	3	52.90	2.08	0.21	0.650	0.667	0.833
3	C	2	55.77	4.95	0.05	0.692	0.556	0.875
4	R	2	56.52	5.70	0.03	0.650	0.500	0.792
5	HARES	2	56.76	5.93	0.03	0.662	0.444	0.792
6	HARES + AWMPS	3	57.16	6.33	0.03	0.660	0.611	0.833
7	R + PH	3	58.51	7.69	0.01	0.597	0.500	0.750
8	HARES + IJI	3	58.55	7.73	0.01	0.650	0.389	0.792
9	HARES + AWMPS+ PLADJ	4	58.62	7.80	0.01	0.688	0.667	0.750
10	HARES + PLADJ	3	58.82	8.00	0.01	0.631	0.556	0.792
11	HARES + PD	3	59.07	8.25	0.01	0.648	0.444	0.792
12	AWMPS + PLADJ + PD + IJI	5	65.03	14.20	0	0.627	0.556	0.750

[a] K = number of estimable parameters.
[b] w_i = Akaike's weight.
[c] AUC = Area under the ROC curve as determined from leave-one-out cross-validation.

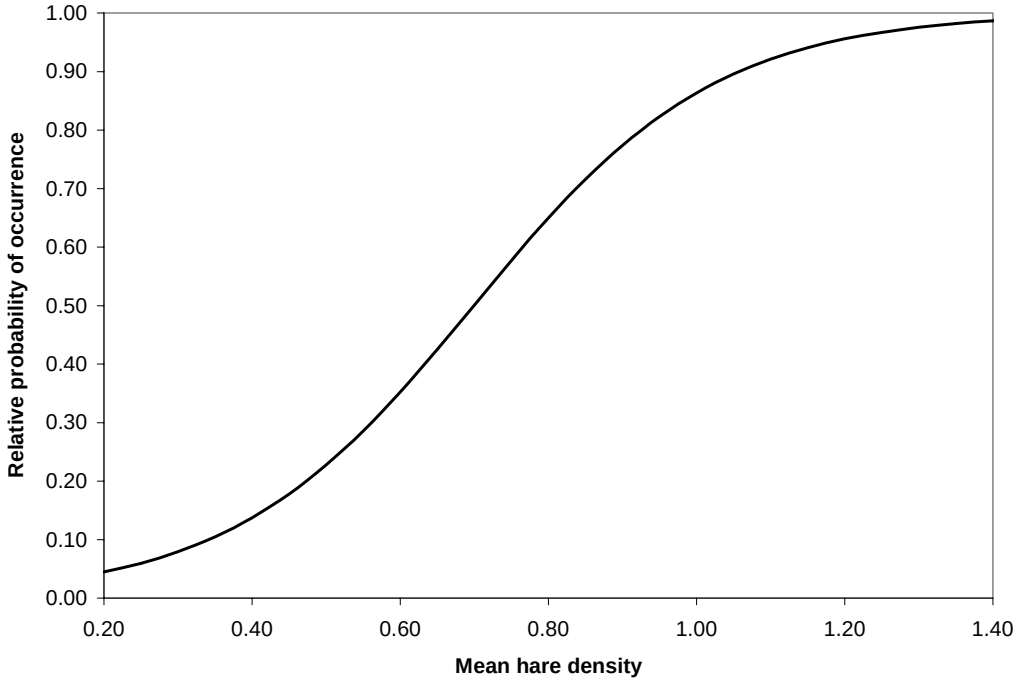
Table 2.5. Pearson correlation coefficients among the eight variables considered for inclusion in *a priori* candidate models for predicting presence and absence of lynx at the scale of the 75% adaptive kernel area in northern Maine, USA.

	HARES	**R**	**PH**	**C**	**IJI**	**PD**	**AWMPS**	**PLADJ**
HARES[a]	1.000							
R[b]	0.967	1.000						
PH[c]	-0.223	-0.323	1.000					
C[d]	0.009	0.055	-0.175	1.000				
IJI[e]	-0.078	-0.111	0.128	0.179	1.000			
PD[f]	0.174	0.149	-0.063	-0.197	0.290	1.000		
AWMPS[g]	0.846	0.874	-0.311	0.023	-0.156	-0.148	1.000	
PLADJ[h]	0.694	0.794	-0.225	0.311	-0.020	-0.085	0.694	1.000

[a] HARES = mean snowshoe hare density (hares/ha) within simulated home range.
[b] R = percent of available forestland within simulated home range comprised by high-quality hare habitat (i.e., conifer or mixed, advanced regenerating forest >15 years old).
[c] PH = percent of available forestland within simulated home range comprised by established, partially-harvested forest (i.e., 11-26 years post-harvest).
[d] C = percent of available forestland within simulated home range comprised by mature conifer forest (i.e., uncut since 1970).
[e] IJI = interspersion and juxtaposition index describing the interspersion between low (0.25 - 0.8 hares/ha), medium (0.8 - 1.4 hares/ha) and high (1.4 - 1.8 hares/ha) hare density forest types (see Table 2.2).
[f] PD = patch density (no. patches/home range area) for high-quality hare habitat.
[g] AWMPS = area-weighted mean patch (ha) size for high-quality hare habitat.
[h] PLADJ = percent like adjacencies between pixels of high-quality hare habitat.

The AUC for the top-ranked model (HARES + C + HARES*C) based on the leave-one-out cross-validation method was 0.69 (Table 2.4). This measure of model performance suggests that there is a 69% probability that an occupied home range will have a higher mean hare density and percentage of mature conifer than an unoccupied home range. AUC values were generally >65% for all the candidate models. The inclusion of the percent of mature conifer (C) appears to be particularly important for improving model sensitivity, and was less influential on model specificity, as the sensitivity of the C only model (rank 3; sensitivity = 56%) was quite a bit higher than the sensitivity of the HARES only model (rank 5; sensitivity = 44%). Area- adjusted frequencies calculated using the "Boyce index" displayed significant positive ranking against RSPF bins (r_s = 0.736; P <0.01).

Although the relationship was moderated by the main effects coefficients, the probability of lynx occurrence showed a strong positive association to both mean hare density and percent of mature conifer forest (Figure 2.4), as expressed via the interaction term. When percent mature conifer was held constant at the average value for occupied home ranges (10%), the probability of lynx occurrence increased at the greatest rate when landscape-scale hare densities increased from 0.65 hares/ha to 0.70 hares/ha (Figure 2.4). Combined across the range of data included in the occurrence dataset, when mean hare density was near zero the percent of mature conifer alone provided little increase in the predicted probability of lynx occurrence. When the mean hare density was ≥0.5 hares/ha, the probability of lynx occurrence was >50% regardless of the percent of mature conifer. As the percent mature conifer forest approached approximately 20% and mean hare density was ≥0.5 hares/ha, the probability of lynx occurrence increased rapidly to 90-



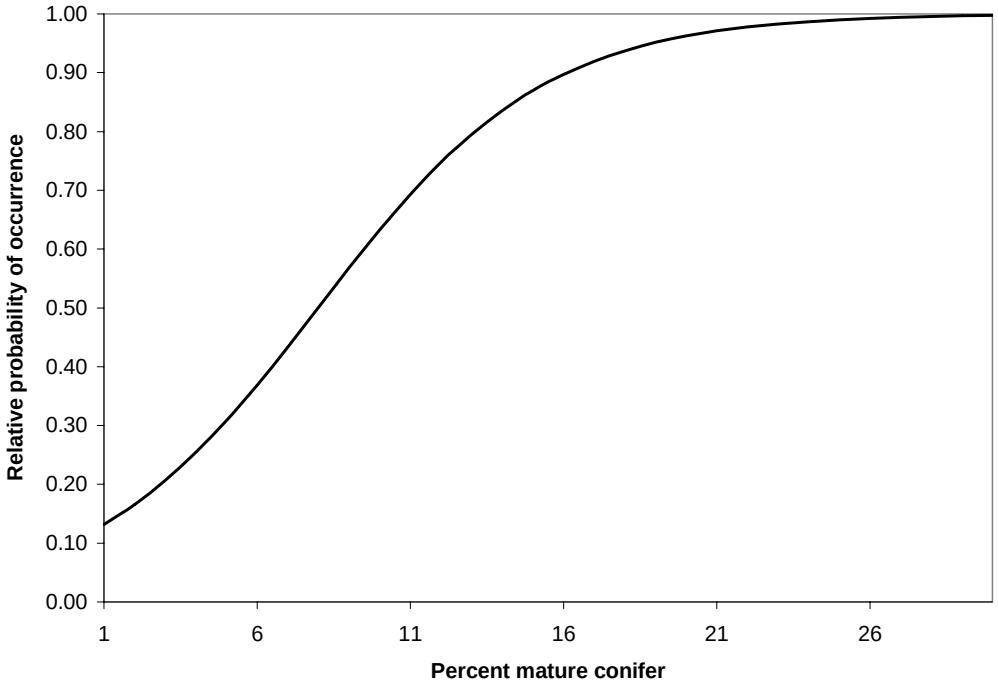


Figure 2.4. The relative probability of occurrence for lynx in northern Maine as a function of landscape-scale hare density (mean = 0.74 hares/ha) and percent mature conifer (mean = 8%), while holding the other variable constant at the respective overall mean.

100%. These strong associations were apparent in the modeling results despite relatively small differences in mean values between occupied and unoccupied home ranges for these variables (Table 2.6). Mean hare density in occupied ranges was 0.74 hares/ha (range = 0.47 - 1.21) and percent mature conifer forest was 10.1% (range = 3.48 - 19.85), compared to 0.62 hares/ha (range = 0.38 - 0.98) and 6.1% (range = 1.34 - 27.10) (Table 2.6) in unoccupied areas.

Habitat assessment

I applied the complete top-ranked model, which took the form

$$(\pi / 1 - \pi) = -1.268 - 1.271(\text{HARES}) - 0.378(\text{C}) + 0.926(\text{HARES*C}), \qquad \text{Eqn. 1}$$

to the ca. 2004 surfaces of percent mature conifer (Figure 2.5) and mean hare density (Figure 2.6) to create a 2004 probability of lynx occurrence for the study area (Figure 2.7). When I mapped the probability of lynx habitat into 10% probability bins I found that 29% of the landscape (436,851 ha) had a ≥50% probability of lynx occurrence and 17% (257,050 ha) had a probability of occurrence ≥80%. Areas with probability ≥50% were smaller and more interspersed throughout the southern portion of study area (Figure 2.7) relative to the north, and coincided with localized areas of higher percent mature conifer (Figure 2.5) and hare density (Figure 2.6). Large blocks of higher lynx probability of occurrence were more spatially aggregated in the north-western and central regions of the study area where percent mature conifer and mean hare density were generally higher relative to the south. A qualitative comparison of occupied and unoccupied home ranges in the northern half of the study area showed that occupied home ranges included a higher density of edge habitat between the mature and high quality hare habitat. To evaluate this association I performed a *post hoc* comparison of the edge density between

Table 2.6. Average (SE) values for predictor variables estimated for simulated occupied (n=18) and unoccupied (n=24) lynx home ranges. Variables were used in candidate models to evaluate 2nd-order lynx habitat selection in northern Maine.

Predictor variable		**Occupied**	**Unoccupied**
HARES	Mean hare density (hares/ha)	0.74 (0.04)	0.62 (0.04)
R	Percent high-quality hare habitat (%)	26.6 (3.3)	16.8 (3.8)
PH	Percent established partially-harvested forest (%)	4.9 (0.8)	7.1 (1.4)
C	Percent mature conifer (%)	10.1 (1.2)	6.1 (1.1)
IJI	Interspersion and Juxtaposition Index[a]	58.95 (2.66)	57.21 (2.64)
PD	Patch density[b] (no. patches/lynx home range area)	3.16 (0.23)	2.98 (0.30)
AWMPS	Area-weighted mean patch size[c] (ha)	198.39 (48.47)	130.13 (37.37)
PLADJ	Percent like adjacencies[d] (%)	80.7 (1.7)	76.2 (1.6)

[a] Interspersion and Juxtatposition Index provides a measure of the degree to which patch types are interspersed that is insensitive to the number, size contiguity, or dispersion of habitat patches.
[b] Patch density (PD) is an area-based measure of the number of patches.
[c] Area-weighted mean patch size (AWMPS) equals the sum across all habitat patches of the mean patch size multiplied by the proportional abundance of each patch.
[d] Percent like adjacencies (PLADJ) provides a measure of the contagion or aggregation of habitat patches that is insensitive to class area.

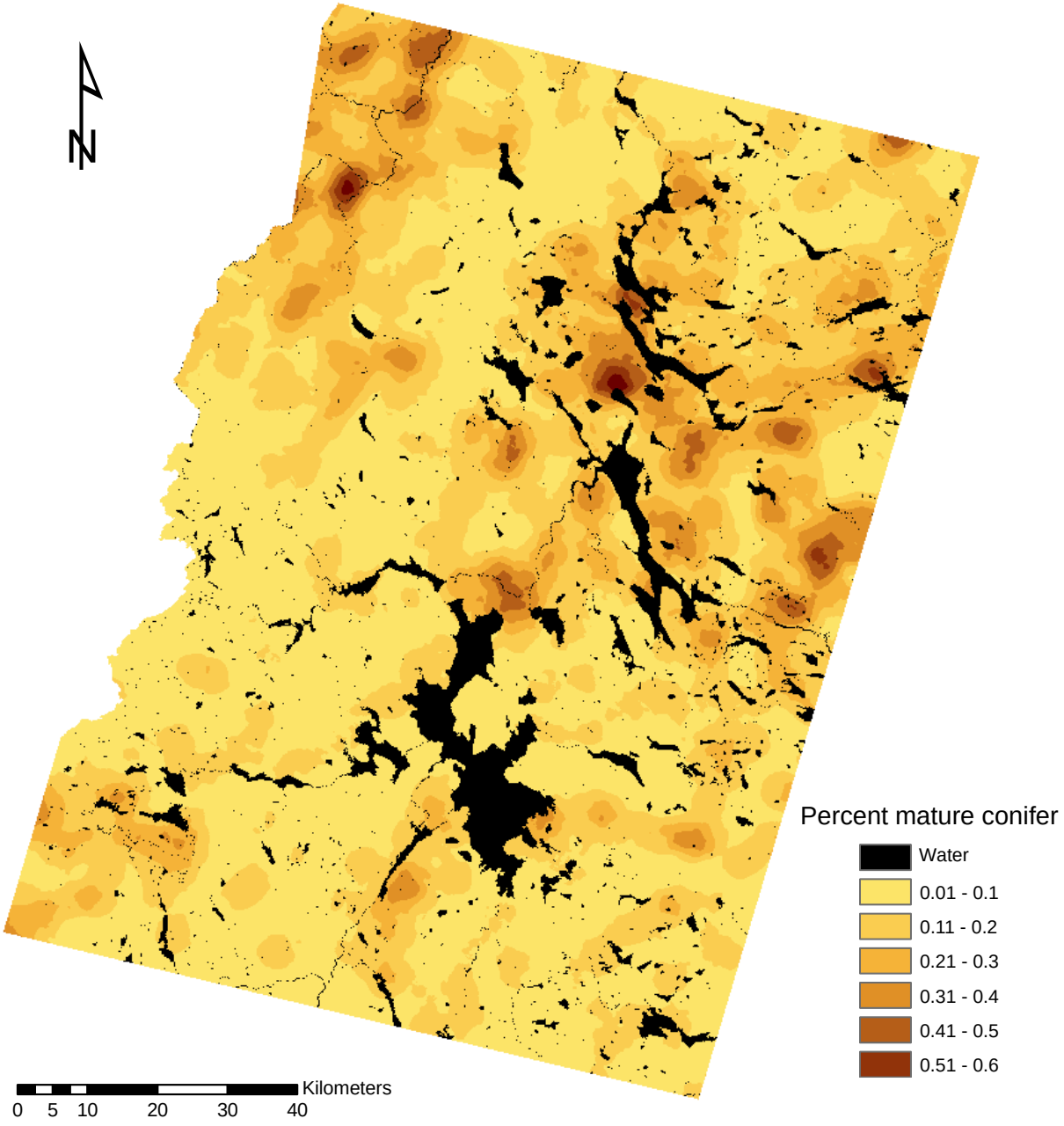


Figure 2.5. Percent mature conifer at the lynx home-range scale across a 1.62 million hectare study areas in northern Maine, 2004. Darker colors indicate higher percentages.

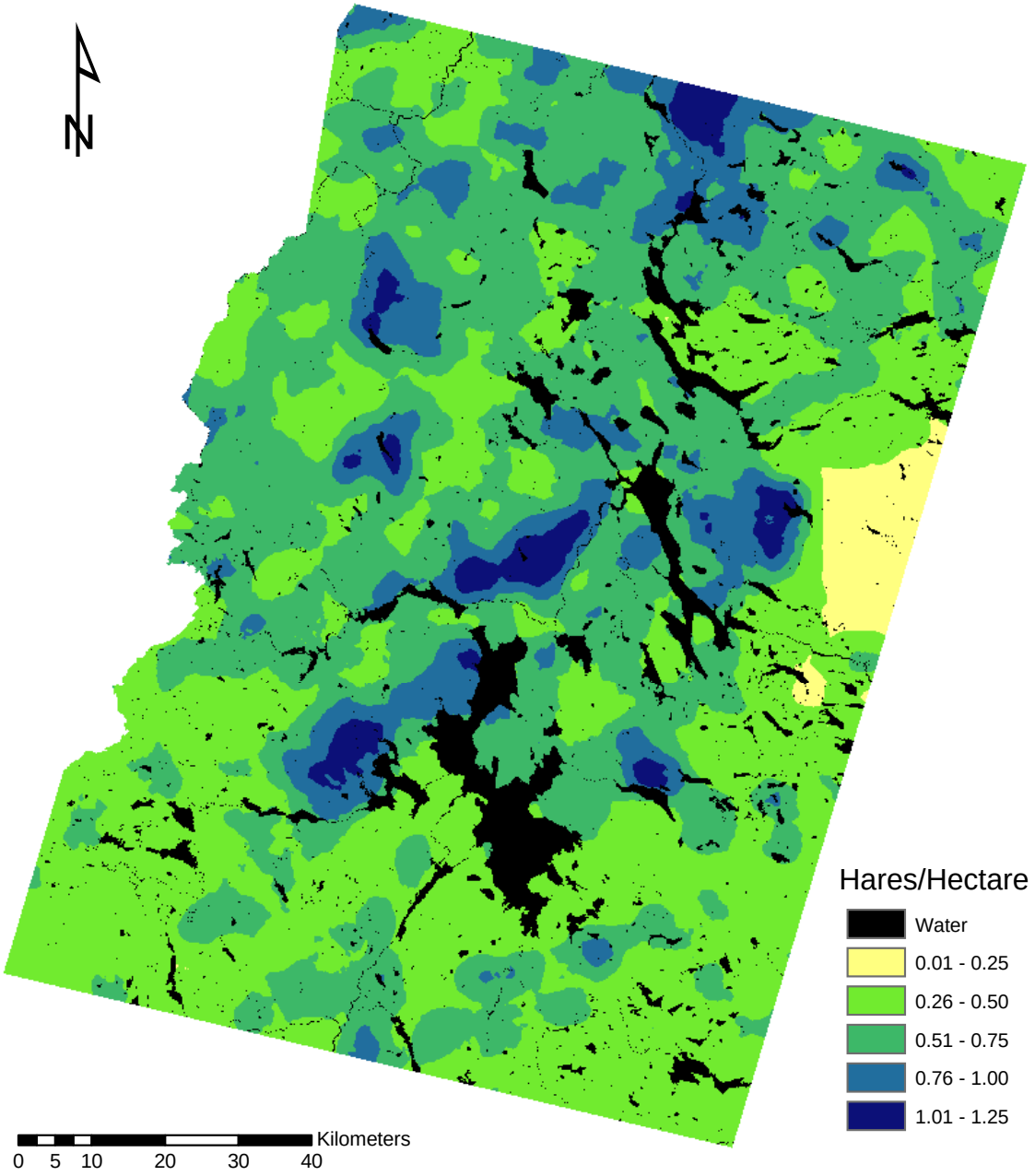


Figure 2.6. Mean hare density at the lynx home-range scale across a 1.62 million hectare study areas in northern Maine, 2004. Darker colors indicate higher hare densities.

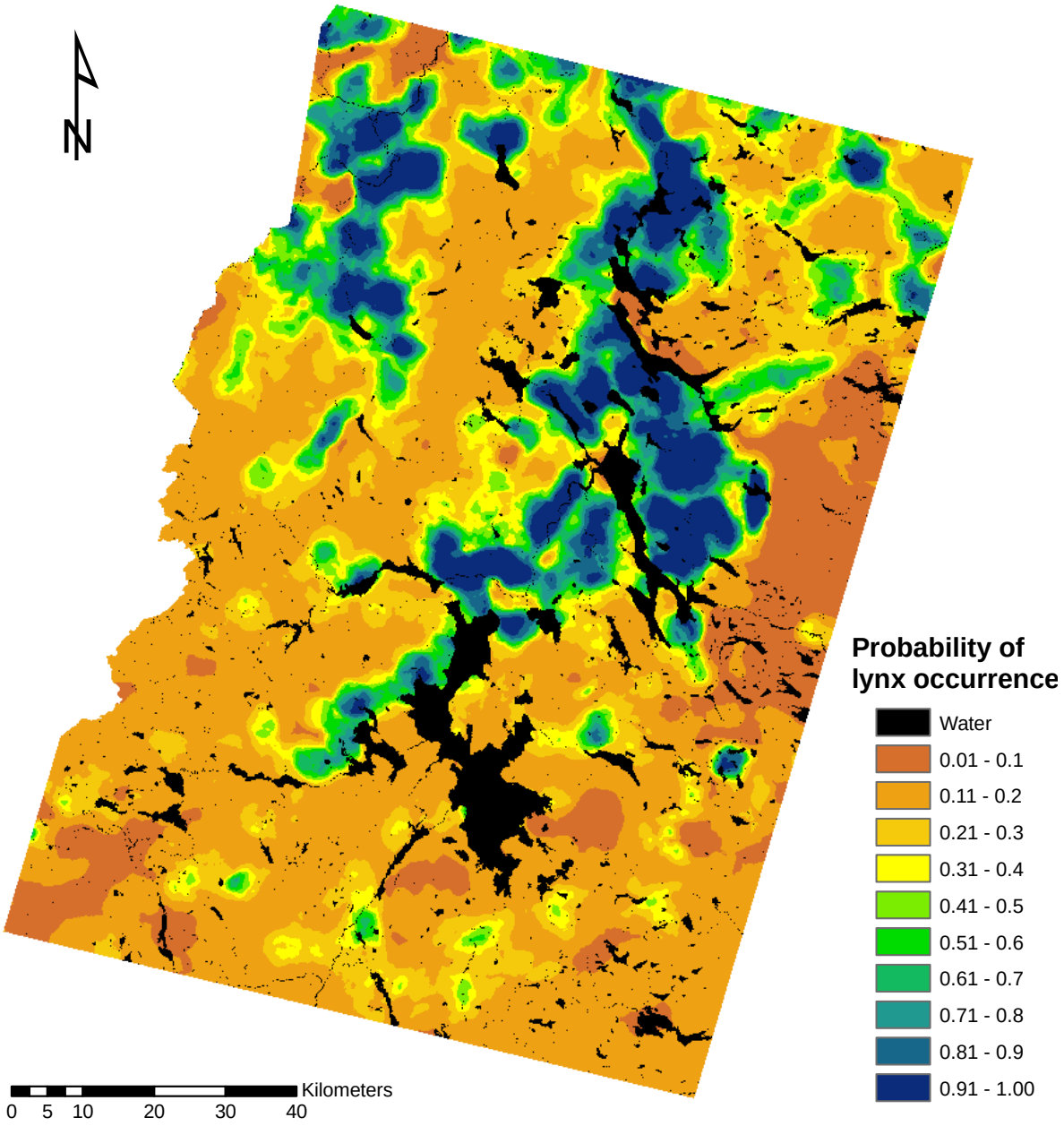


Figure 2.7. Probability of landscape-scale lynx occurrence across a 1.62 million hectare study areas in northern Maine, 2004. Results derived from the mature conifer surface (Figure 2.5) and mean hare density surface (Figure 2.6) based on the top-ranked candidate model (HARES + C + HARES*C).

those two types in occupied and unoccupied ranges (t = -2.94; p-value = 0.003) and found that occupied ranges (mean = 7.69 meters/ha; SD = 4.21) had almost 2x greater the average edge density compared to unoccupied ranges (mean = 4.0 meter/ha; SD = 3.88).

I estimated lynx density (lynx/100km^2) for the 160 unorganized townships in northern and western Maine that overlapped the study area by ≥70% (Figure 2.8). Density estimates ranged widely between 0.4 – 6.0 lynx/100 km^2 and there was a relativelyhigh degree of variability between adjacent townships. The majority of the townships (61%; 98 out of 160) had an estimated lynx density of 0.4 – 2.0 lynx/100 km^2 and townships with an estimated lynx density >3.0 lynx/100 km^2 occurred almost exclusively in the northern half of the study area.

DISCUSSION

In general, my 2nd-order modeling results agree with recent 3rd-order studies (Fuller et al. 2007, Vashon et al. 2008a) that have both reinforced the importance of dense regenerating forest as essential lynx foraging habitat, and suggested that other forest types likely also influence lynx habitat selection in the southeastern region of the lynx range. Additionally, this study supports previous landscape modeling studies (Hoving et al. 2004), which indicated that 2nd-order habitat selection by lynx in northern Maine is negatively influenced by the amount of partially-harvested forest present in an area. Although established partial harvests appear to provide a preferred foraging habitat within the home ranges of resident lynx in northern Maine (Fuller et al. 2007), my results, in conjunction with those of Hoving et al. (2004), indicate that the forest conditions created by partial harvests do not, in general, replace even-aged regenerating clearcuts in their ability to foster broad-scale lynx presence in the Acadian Forest.

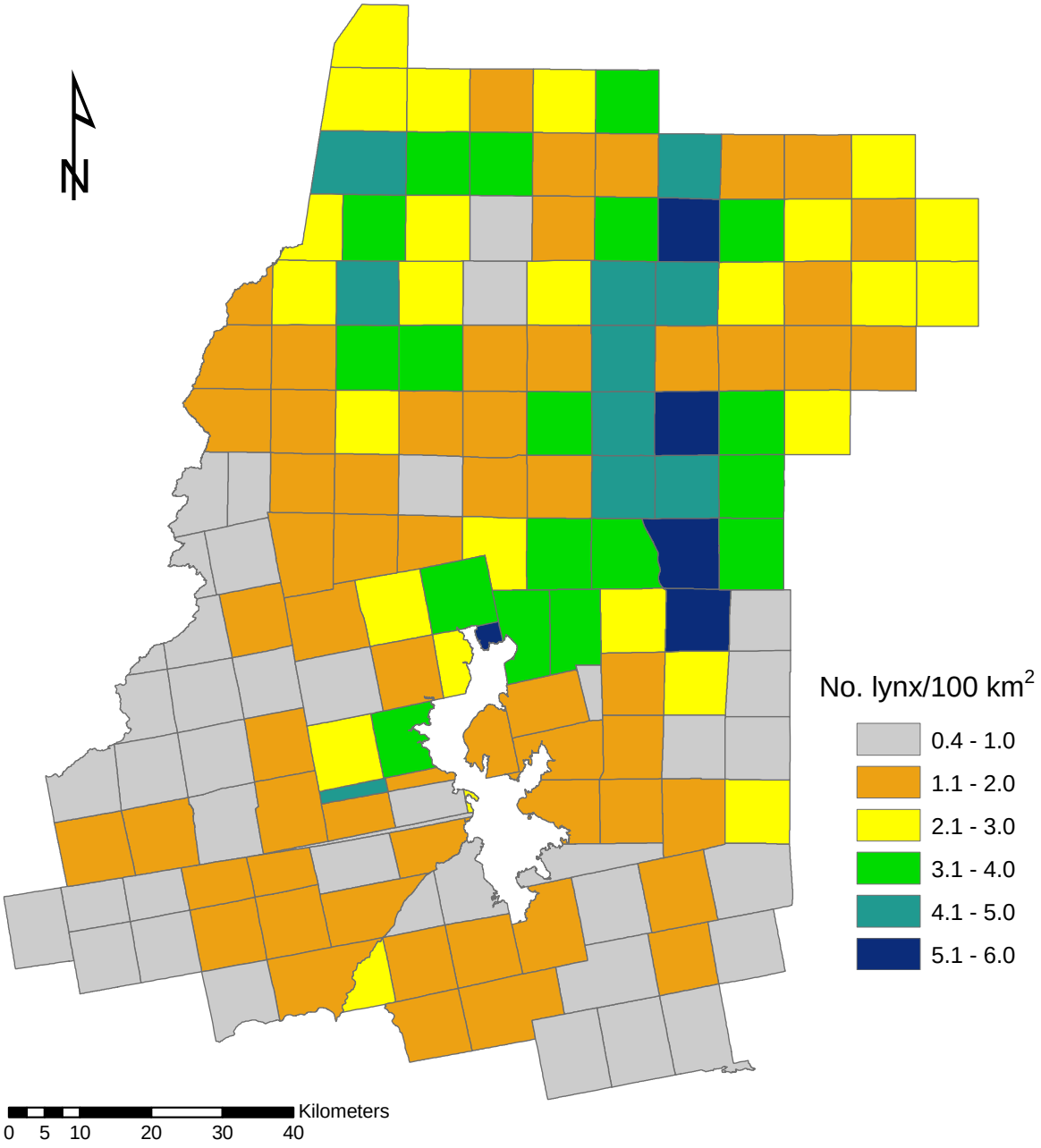


Figure 2.8**.** Potential density of adult resident lynx that could be supported at the township-scale (number of lynx/100km^2) across 160 townships in northern Maine ca. 2004. Densities calculated based on the summed probability of lynx occurrence using a fixed grid representing exclusive home range area.

This is the first study to address the cumulative effects of forest composition and configuration on landscape-scale snowshoe hare density and lynx habitat selection. Probability of occurrence by lynx was positively influenced by mean snowshoe hare density and percent mature conifer forest in the landscape. The positive association with snowshoe hare density was not surprising because snowshoe hares constitute ≥50% of the lynx diet throughout its range (Roth et al. 2004). However, until the present study, associations between 2nd-order habitat selection by lynx and snowshoe hare density have evaluated selection for forest types and made indirect inferences based on stand-scale (i.e., 3rd order) hare densities (Koehler 1990, Vashon et al. 2008a). Snowshoe hare density was highly dependent on the amount of high-quality hare habitat where snowshoe hare abundance is highest (Robinson 2006, Homyack et al. 2007); however, hare density performed better than the amount of high-quality hare habitat as a predictor variable when coupled with mature conifer. This finding suggests that other forest types likely influence lynx occurrence through their mediating effect on landscape-scale hare density. Thus, lynx likely place their home ranges in areas with the lowest foraging costs, allowing them to maximize optimal foraging habitat, while avoiding large areas of unsuitable habitat patches supporting few hares (Palomares 2001).

The probability of lynx occurrence was strongly influenced by the percent mature conifer, even though the difference between the average percent mature conifer in occupied areas (10%) and unoccupied areas (6%) was not very great. Second-order selection by lynx for mature conifer forest has been previously noted by other researchers when mature conifer forest was associated with high hare densities (Poole et al. 1996), but this is the first study to demonstrate 2nd-order selection for mature conifer when

snowshoe hare density in this forest type is low (mean = 0.24; Fuller and Harrison 2005). Third-order selection by lynx for mature conifer has also been previously noted (Koehler 1990, Squires et al. 2008), as a forest type that provides the horizontal cover and abundant coarse woody debris associated with lynx den sites. In the Acadian forest, however, lynx den in a variety of forest types, including sapling stands, pole-sized stands, and mature forest stands (Organ et al. 2008). Many of the occupied home ranges occurred in the northern half of the study area where mature conifer forest is generally more available (Figure 2.5), and a *post hoc* comparison indicated that the mean edge density between mature conifer and high-quality hare habitat in occupied areas (mean = 7.69 meters/ha; SD = 4.21) was almost 2x the average edge density in unoccupied areas (mean = 4.0 meter/ha; SD = 3.88). Edge habitat between mature conifer and advanced regenerating forest where hare abundance is high (Robinson 2006, Homyack et al. 2007) likely provides valuable foraging habitat (Staples 1995, Mowat et al. 2000), and also potential travel corridors (Parker et al. 1983, Vashon et al. 2008a). Thus, as a predictor variable in this study, percent mature conifer likely captured both the regional availability of mature conifer forest in the broader landscape context and its juxtaposition with high-quality hare habitat at the home-range scale.

Overall, the top candidate model performed reasonably well (AUC=0.69) and provided additional insights and enhanced accuracy over earlier work. Previous modeling work has focused primarily on the influence of forest composition on landscape-scale lynx occurrence with little to no knowledge of forest history or age structure (Koehler 1990, Poole et al. 1996, Hoving et al. 2004). Model specificity (88%) was comparable to the top model developed by Hoving et al. (2004) for lynx in northern Maine (91%),

which included limited harvest information based on the Maine GAP Vegetation and Land Cover map (Hepinstall et al. 1999). Model sensitivity (67%), however, was significantly improved by my top model relative to that previously published model (38%), indicating that the current model's ability to accurately predict occurrence was greatly improved. Because model specificity (88%) was higher than the sensitivity (67%), there was still a tendency for the model to underestimate probability in some areas occupied by lynx. A qualitative assessment indicated that underestimation was particularly likely when percent mature conifer forest was <10%. Although I attempted to limit the potential for including a false absence in the training dataset by only simulating non-occurrence home ranges with adequate survey intensity, it was also possible that model sensitivity was reduced (and model specificity increased) due to non-detection. It was not possible to calculate the detection probability (MacKenizie et al. 2002) associated with the survey design because the snow-track surveys were only conducted once in each area. Based on a similar protocol, Squires et al. (2004) estimated that the probability of detecting lynx tracks during a single visit ranged from 23-78% depending on the number of days after snowfall the survey was conducted. Because it is highly likely that the detection probability in the surveyed townships included in this analysis is less than one, additional days of survey would have helped to further increase model sensitivity.

No occupied home ranges occurred in areas where landscape-scale hare densities were less than 0.5 hares/ha. Where landscape-scale hare densities were >0.5 hares/ha, the probability of lynx occurrence increased rapidly in a threshold fashion (Huggett 2005) as percent mature conifer forest increased. For example, the probability of lynx occurrence

was predicted to be >50% in areas with mean hare density ≥1 hares/ha when the percent mature conifer exceeded just 4%. Previous researchers have suggested that 0.5 hares/ha may be a minimum hare density required to maintain a lynx population (Ruggerio et al. 2000); however, greater than 1.5 hares/ha has been postulated as the minimum density of hares that may be required to sustain a southern (<49º N) lynx population (Steury and Murray 2004). These estimates have, however, been based on stand-scale estimates in presumably optimal habitat; previous work has not addressed the overall density of hare required to support lynx at the scale of a home range, which is the parameter most important for lynx recovery. Stand-scale hare densities often exceed 1.5 hares/ha in conifer-dominated regenerating forest in northern Maine (Robinson 2006, Homyack et al. 2007), but the maximum landscape-scale hare density estimated ca. 2004 within my study areas was 1.25 hare/ha (Figure 2.6). Further, the mean hare density in occupied lynx ranges was only 0.74 hares/ha (range = 0.47 – 1.2 hares/ha), suggesting that *landscape-scale* hare densities do not need to be as high as 1.5 hares/ha to ensure the occurrence of a southern lynx population.

The probability of lynx occurrence showed a strongly positive response as mean hare density increased from 0.5 hares/ha to 0.95 hare/ha (Figure 2.4). This is important to note because of the narrow difference between the mean hare density in occupied (0.74 hares/ha) and unoccupied (0.61 hares/ha) home ranges, which may suggest that recently occupied landscapes could quickly become less suitable if hare densities decline in high-quality hare habitat as a result of succession-induced reductions in cover and/or forage (Fuller et al. 2007). Further, the stand-scale estimates for hare densities in regenerating conifer and mixed forest were based on what may have been a relative high for those

stands that were measured (1.8 hares/ha; Homyack et al. 2007). Ongoing research suggests that snowshoe hare populations in northern Maine fluctuate with a reduced-amplitude cycle and recent estimates showed that in 2007 hare densities had declined by ~30% in those same stands (Scott *In preparation)*. Southern populations (<49º N) of snowshoe hares are generally not expected to be strongly cyclic (Hodges 2000); nonetheless, even a reduced-amplitude cycle in Maine could result in changes in landscape-scale hare densities that may be significant enough to negatively influence lynx occurrence.

Larger and more contiguous areas with associated probability of lynx occurrence exceeding 50% were spatially aggregated in the northern and central regions of the study area where both mean hare densities and percent mature conifer were generally higher. Smaller, more localized areas of predicted lynx occurrence were interspersed throughout the southern portion of the study area (Figure 2.7). Approximately 29% of the study area had a probability of lynx occurrence ≥50% and only 17% had a probability ≥80%. Predicted lynx densities in townships overlapping with these higher probability areas were commonly >3 lynx/100km^2 and exceeded 5 lynx/100km^2 in a few areas. These estimated township-scale densities agree with Vashon et al. (2008b), who estimated that the adult resident density in what is expected to be an optimal area for lynx in northern Maine at 4.8 adults/100 km^2. Total lynx density within their ~300 km^2 study area was estimated to be 9.6 - 13.3 lynx/100 km^2 (Vashon et al. 2008b), which suggests that habitat in Maine can support lynx densities that are comparable to some more northerly populations during the cyclic high in hare populations (Brand et al. 1976, Parker et al. 1983, O'Donoghue et al. 1997). Maine also appears to be unique among southern

populations with respect to the higher hare densities that are supported in regenerating stand types associated with lynx foraging habitat (mean = 1.8 hares/ha; Homyack et al. 2007) compared to other southern areas (mean = 1.09 hares/ha; Murray 2000). From 2001-2006 (Robinson 2006, Homyack et al 2007) hare densities in these stands were higher than has been observed in similar stands during the low hare phase in more northerly cyclic populations (Murray 2000, Steury and Murray 2004). Thus, if the lynx population in Maine is essentially non-cyclic, as has been suggested for southern populations (Hodges 2000, Roth et al. 2007), intermediate and more stable hare densities may support a more robust and stable lynx population.

Conservation and Management Implications

Advanced, coniferous or mixed coniferous-deciduous regenerating forest provides the most highly preferred lynx habitat in the Acadian Forest at both the 2nd- and 3rd-orders of selection. Based on the methods used here to identify regenerating forest and to map high-quality hare habitat, I predict that this habitat type will decline in extent during the next 20-30 years because the amount young regenerating forest (179,353 ha 0-16 years post-harvest; Table 2.1) within the study area is far less than the amount of advanced regenerating forest (270,260 ha 16+ years post-harvest; Table 2.1), which will soon start to transition out of lynx habitat. It is also important to note that although the NDMI-based methodology has been shown to be 87-91% accurate for mapping clearcut vs. partial cuts in the Acadian Forest (Sader et al. 2003), it is likely that a small proportion of harvests classified as *light* (1991-2004) may have adequate conifer stem densities to support high (>1 hare/ha) hare densities. For example, if the understory conifer stem density prior to harvest is high (>7,000 stems/ha; Robinson 2006), a

moderate overstory removal could result in regenerating forest conditions that may also support high snowshoe hare densities in the future (Fuller et al. 2007). Additional to this potential omission error, the harvest detection time series provides no information about harvest history prior to 1970; so, regenerating forest created by clearcuts in the 1960s, for example, would not be identified. This potential error is likely a minor consequence because regenerating forest that originated prior to 1970 would have been 34+ years old ca. 2004 and hare densities are expected to decline after 35 years (Fuller et al. 2007). More research is needed to better understand the typical post-harvest structures associated with *heavy* and *light* harvests and to improve habitat classification; nonetheless, maintaining high-quality hare habitat at current levels within the study area will require proactive management.

Lynx occurrence appears to be sensitive to relatively small increases in high-quality hare habitat and snowshoe hare density. Occupied lynx home ranges were comprised on average of 27% high-quality hare habitat and had a mean landscape-scale hare density of 0.74 hares/ha. In unoccupied home ranges the percent high-quality hare habitat was 37% less (mean = 17%), but the mean hare density was only 18% lower (mean = 0.61 hares/ha), and was caused by the relatively higher percent partial harvest in unoccupied home ranges (70% vs. 50% in occupied). These results suggest that lynx densities in northern Maine could decline rapidly in townships where young regenerating forest is not available to replace advanced regenerating forest once hare densities begin to decline in these stands, and where partial harvesting has replaced clearcutting as the predominant management practice. I recommend maintaining a minimum of 27% high-quality hare habitat in townships where lynx conservation is a priority. Configuration of

the high-quality hare habitat appeared to have little relative effect on lynx occurrence; however, the area-weighted mean patch size of high-quality hare habitat in occupied home ranges (198 ha) was substantially larger than in unoccupied areas (130 ha), which contributed to the higher landscape-scale hare densities in occupied ranges. Thus, the size of clearcuts should be increased in areas targeted for lynx habitat planning. The probability of lynx occurrence in townships with sufficient high-quality hare habitat can be increased further by also maintaining at least 8-10% mature conifer and promoting adjacency between these two forest types. In deciding which townships should be targeted for lynx conservation, it is important to consider the location of the township relative to the current distribution of lynx densities. Adjacent townships can have very different disturbance histories and targeting isolated townships may be of lesser conservation value than townships adjacent to or near townships with higher (i.e., >3 lynx/100 km^2) estimated lynx densities.

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CHAPTER 3

SPATIOTEMPORAL PATTERNS OF HABITAT CHANGE FOR CANADA LYNX IN MAINE 1970-2007 AND THE IMPLICATIONS FOR FUTURE HABITAT SUSTAINABILITY

ABSTRACT

Canada lynx (*Lynx canadensis*) are a specialist predator and often exhibit habitat selection for regenerating conifer forests where snowshoe hares (*Lepus americanus*) are abundant. The quantity and spatial distribution of high-quality hare habitats are strongly influenced by forest disturbance and succession; however, little is known about cumulative effects of timber harvesting on the spatiotemporal dynamics of lynx and hare habitat (but see Robinson 2006). I developed a forest cover time series derived from Landsat satellite imagery to study the interactions among forest management, snowshoe hare density, and predicted lynx occurrence and to evaluate trends in habitat supply for lynx within an extensively managed landscape 1970-2007. I also estimated the future supply of high-quality hare habitat 2007-2022 based on timber harvesting patterns in the 1990s and 2000s. Timber harvesting was widespread with 55% of the commercial forestlands receiving a timber harvest 1970-2007. Rates and patterns of harvesting during the 1970s and 1980s were strongly influenced by salvage logging within spruce-fir forests during the 1973-1985 spruce budworm (*Choristoneura fumiferana*) outbreak, which resulted in the removal of >30% of the mature conifer forest 1975-1988. There was a broad-scale and rapid increase in high-quality hare habitat as regenerating forest created via salvage harvesting began to reach 16 years post-harvest starting in 1986, resulting in a median change in hare density within potential lynx home ranges of +0.32

hares/ha (range = -0.02 - 1.34 hare/ha) 1988-2007. That increase in landscape-scale hare density resulted in broad-scale changes in probability of lynx occurrence, and between 1991 and 2007 potential lynx density increased on average by 1.23 lynx/100 km^2 (range = -1.19 - 4.19 lynx/100 km^2). These results suggest that the increase in the actual lynx population that occurred in northern Maine beginning in the mid-1990s (Hoving et al. 2004) resulted from human-induced habitat changes. Quantity of high-quality hare habitat will remain relatively stable 2007-2022; however, the location and configuration will shift substantially as a result of timber harvesting patterns in the 1990s and 2000s. A greater proportion of habitat will occur in areas of low estimated lynx density ca. 2007 and where future lynx occurrence may be constrained by additional extrinsic factors (e.g., competition and climate change), suggesting that habitat management to maintain Maine's lynx population should be targeted at providing future habitat in areas that currently provide favorable habitat conditions.

INTRODUCTION

Habitat management to conserve wide-ranging wildlife species requires methods that link landscape change and species occurrence patterns. Studies targeted at understanding the effects of landscape change on species presence or habitat selection are often mensurative, taking advantage of the available spatial variation in natural or anthropogenic disturbance processes to evaluate, for example, the effects of fragmentation on species diversity (McGarigal and Cushman 2002 and citations therein). However, little attention is generally directed at documenting or quantifying underlying processes that contribute to current habitat distribution or the associated species-habitat relationships (Knick and Rotenberry 2000). Forest management, for example, creates

landscape patterns that can differ significantly from those that develop under natural disturbance regimes (Franklin and Forman 1987, Li et al. 1993, Mladenoff et al. 1993, Wallin et al. 1994, James et al. 2007). Although numerous studies have evaluated species distributions and abundance in landscapes degraded or fragmented by timber harvesting (e.g., McGarigal and McComb 1995, Cushman and McGarigal 2003, Betts et al. 2006), few attempt to understand the spatial and temporal structure of the habitat changes that have previously occurred. Further, models to predict the effects of habitat change on species distributions have generally focused on direct effects (e.g., habitat loss) and typically have overlooked potential indirect effects (e.g., interspecific interactions) that may also threaten long-term species persistence (Ryall and Fahrig 2006). Species-level response to habitat disturbance can be complex and can take time to emerge (Ewers and Didham 2006); therefore, understanding the spatial and temporal dynamics of disturbance processes that influence species occurrence can enhance land-use decision making.

Data provided by satellite sensors (e.g., Landsat Thematic Mapper (TM)) are increasingly being used to monitor the broad-scale effects of land use and landscape change. Using a time series approach, image data from consecutive satellite images can be compared to identify changes in land cover composition and configuration (e.g., Turner et al. 1996), or to map forest disturbance directly (Sader et al. 2003, Jin and Sader 2006, Kuemmerle et al. 2007). Satellite-derived data has also provided new opportunities for mapping habitat attributes that are often incorporated into habitat models (e.g., Osborne et al. 2001, Betts et al. 2003, Aldridge and Boyce 2007). These types of data have been particularly valuable for studying habitat use and availability of wide-ranging species such as medium- or large-sized mammalian carnivores (e.g., Mladenoff et al.

1995, Mace et al. 1999, Hoving et al. 2004), which are often expected to be sensitive to habitat disturbance, but for which it is generally difficult to assess population status. Only recently, however, has satellite imagery has been used to map or model broad-scale variability in habitat conditions for wildlife using a time series approach similar to that which has been applied to monitor landscape change (Osborne and Suárez-Seone 2007, Viña et al. 2007, Mueller et al. 2008), despite the widespread availability of satellite data and methodologies. Methods that can integrate predictive habitat modeling and time series analysis are needed to better understand how landscape change influences habitat supply and to predict the effects of future habitat change on species occurrence patterns, particularly for wide-ranging species.

The Canada lynx (*Lynx canadensis*) is a U.S. federally threatened species (U.S. Department of Interior 2000) that occupies the boreal and sub-boreal forests of Canada and the northern United States. Lynx are specialist predators on snowshoe hares (*Lepus americanus*) (Koehler and Aubry 1994, Aubry et al. 2000), which is apparent in the high proportion of hares in the diet of lynx throughout their geographic range (45-100%; Roth et al. 2007), and via relationships between hare density and lynx survival and productivity (Brand and Keith 1979, Parker et al. 1983, Koehler 1990, Poole 1994, Slough and Mowat 1996, O'Donoghue et al. 1997). Further, prey abundance is a critical characteristic of habitat quality for carnivores (Carbone and Gittleman 2002) and research has suggested that forest management can strongly influence lynx habitat use through its effects on snowshoe hare density (Hoving et al. 2004, Robinson 2006, Fuller et al. 2007, Vashon et al. 2008a, Chapter 2). Snowshoe hare density is closely associated with the density of vegetation cover in regenerating forest or mature forest understories

(Hodges 2000), and because the quantity and spatial distribution of regenerating forest conditions are strongly influenced by forest disturbance and succession dynamics (Agee 2000), this creates a pathway by which lynx may be indirectly affected by human land-uses. Theoretical models that have evaluated the potential for indirect effects of landscape change on specialist predators such as lynx have indicated that a predator population can be driven towards extinction even without direct effects, if the landscape change causes a significant loss of prey habitat (Nakagiri et al. 2001). Increased understanding of the factors that influence the spatiotemporal variability of habitat supply and species occurrence patterns in managed landscapes will be essential for making informed land-use decisions and for developing effective strategies for habitat monitoring.

Despite expressed concerns about the potential for forest management to have negative effects on the persistence of lynx populations in the contiguous U.S. (U.S. Department of Interior 2000), little research has been conducted that has evaluated the interactions among timber harvesting, snowshoe hare density, and lynx occurrence or habitat selection (but see Hoving et al. 2004, Fuller et al. 2007). Estimates of the minimum hare density required to support a lynx population range from 0.5 hares/ha (Ward and Krebs 1985, Brocke et al. 1992) to as high as 1.5 hares/ha (Steury and Murray 2004); however, these estimates provide no information about the relationship between lynx occurrence and snowshoe hare density at the landscape (or home-range) scale. Further, nothing is currently known about the cumulative effects of broad-scale landscape change on the spatial and temporal dynamics of hare densities or predicted lynx occurrence. The main goal of my research was to develop a time series based on Landsat

satellite imagery that would allow me to evaluate the direct and indirect effects of forest management on the spatiotemporal patterns of habitat supply for lynx across ~1.62 million hectares (4 million acres) of commercial forestlands in northern Maine. I used a predictive model of lynx occurrence based on extensive, systematic field surveys that was developed using remotely-identified timber harvesting patterns in northern Maine (Chapter 2) to: 1) document the effects of broad-scale harvest patterns on forest conditions associated with lynx occurrence 1970-2007; 2) evaluate the influence of landscape change 1988-2007 on the spatiotemporal patterns of forest conditions and probability of lynx occurrence at the scale of lynx home range; 3) evaluate the potential effects of forest changes on lynx density between 1988 and 2007; and 4) estimate the future quantity and spatial distribution of lynx foraging habitat (2007-2022) based on timber harvesting spatial patterns. A key strength of this approach is that the data structure underlying both the predictive habitat model (Chapter 2) and the time series (this study) is the same, which enhances the model's capacity to accurately predict changes in the probability of lynx occurrence in response to habitat changes (Strauss and Biederman 2007).

STUDY AREA

The study area was defined by the area of overlap between the Landsat Multispectral Scanner (MSS), Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) satellite imagery (Landsat Worldwide Reference System path 12, row 28) used to construct the harvest detection time series (see below) and by the northwestern political boundary between Maine and the province of Quebec, Canada (Figure 3.1). This area included all or part of 174 unorganized townships that were primarily privately-

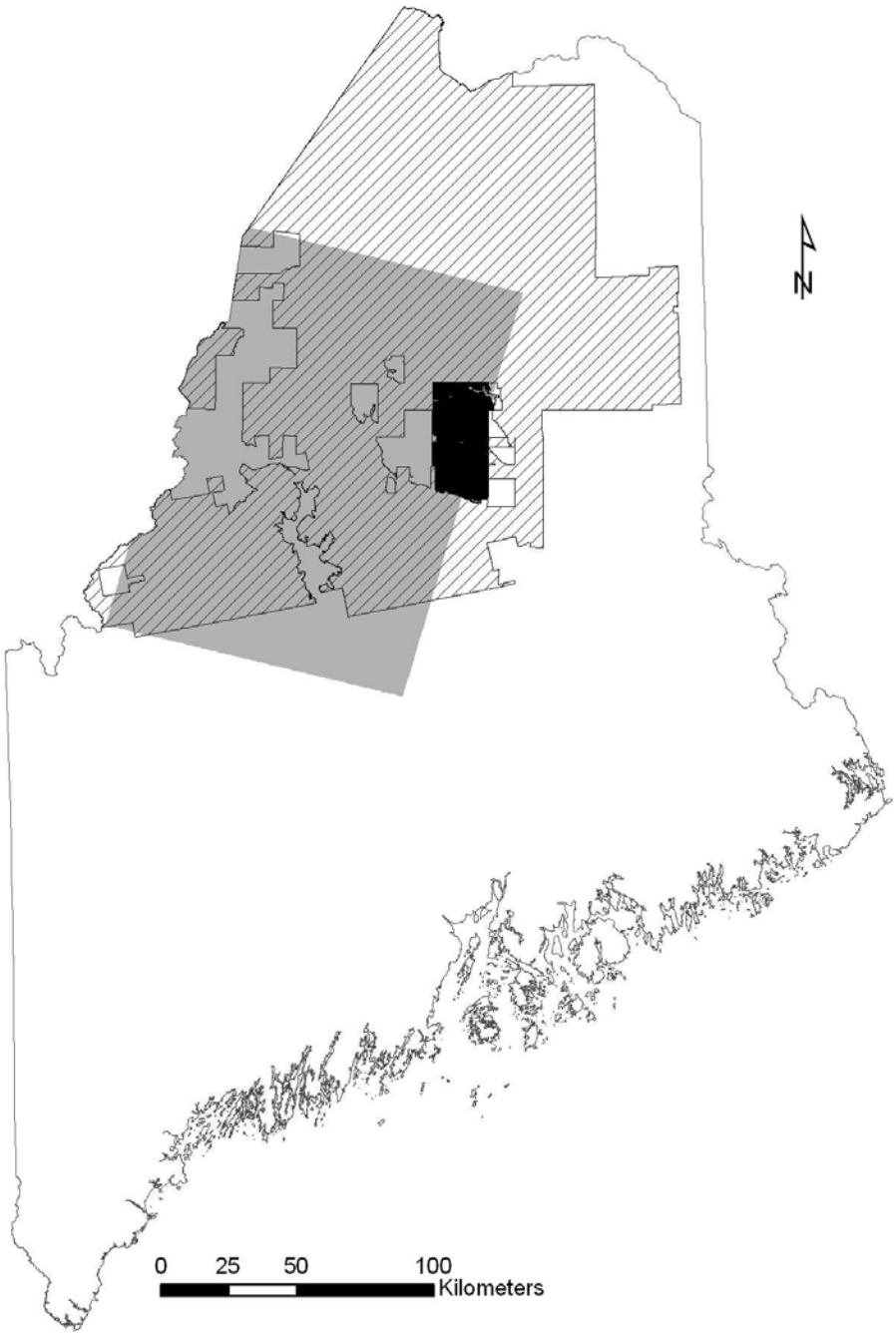

Figure 3.1. The location of the study area (shown in gray) was defined by the overlap between the Landsat satellite imagery used to construct the harvest detection time series and the western border of Maine, USA. This area overlapped with the area designated as critical habitat for lynx (shown in hatched area), which was considered occupied at the time of listing (U.S. Department of Interior 2000, 2008, 2009), and Baxter State Park (shown in black).

owned and forest ownership types (e.g., industrial forest products companies, family-owned corporations, investment entities) within this region were broadly representative of the unorganized townships of northern Maine (Hagan et al. 2005, Jin and Sader 2006). Interspersed among these townships were some state-owned parcels managed by the Maine Bureau of Parks and Lands, including some reserve areas the largest of which, Baxter State Park, was located along the eastern edge of the study area (Figure 3.1).

The study area included approximately 1.62 million hectares of commercial forestland within the Acadian forest ecoregion, an ecological transition zone in the northeastern U.S.A. between the southern temperate deciduous-dominated forests and the northern boreal forests (Seymour and Hunter 1992). Commonly occurring tree species included: balsam fir (*Abies balsamea*), white (*Picea glauca*), red (*P. rubens*), and black (*P. mariana*) spruce, white pine (*Pinus strobus*), white (*Betula papyrifera*) and yellow (*B. alleghaniensis*) birch, red (*Acer rubrum*) and sugar (*A. saccharum*) maple, and American beech (*Fagus grandifolia*). Forest harvesting was the primary form of forest disturbance within this area (Seymour 1992, McWilliams et al. 2005) and forest harvesting practices were regulated under the Maine Forest Practices Act (12 MRSA §8867-A to §8888 & MFS Rules Chapter 20). Urban and residential development was minimal (Hepinstall et al. 1999) and was present in only 6% of the townships clustered in the southeastern corner of the area. The study area also overlapped with the majority of the 24,597 km^2 (9,497 mi^2) of critical habitat that was designated for lynx in northern Maine (Figure 3.1) (U.S. Department of Interior 2009), which represents the area occupied by lynx at the time of listing (U.S. Department of Interior 2000, 2008, 2009). Previous research has suggested that lynx occurrence within this region of Maine is positively associated with

both annual snowfall depth (Hoving et al. 2005) and the quantity of advanced, conifer-regenerating forest (Hoving et al. 2004, Vashon et al. 2008a). Within home ranges in northern Maine, lynx habitat selection (3rd order; Johnson 1980) is influenced by snowshoe hare density and forest understory density (Fuller et al. 2007, Vashon et al. 2008a). Researchers have recommended that in areas where lynx conservation is a priority, conifer-regenerating forest with intermediate stem density (7,000-11,000 stems/ha) and overstory canopy closure <60% should be maintained (Fuller et al. 2007).

METHODS

Timber harvest time series

I developed the forest cover time series for the 1.62 million hectare (4.0 million acre) study area to depict the cumulative effects of forest harvesting on forest stand age and composition. I then applied the successive cover maps to the predictive habitat models developed previously (Chapter 2) to evaluate the effects of forest management on the spatiotemporal patterns of lynx habitat supply in northern Maine, 1970-2007. The timber harvest detection time series (1970-2007) was assembled from five Multispectral Scanner (MSS) and ten Thematic Mapper (TM) and Enhanced Thematic Mapper Plus (ETM+) images (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*). As described in Chapter 2, the harvest detection time series was produced using a series of three-date classification sequences (Wilson and Sader, 2002, Jin and Sader, 2005) based on the Normalized Difference Moisture Index (NDMI; 1988-2007) and the Normalized Difference Vegetation Index (NDVI; 1973-1988). Previous investigations into the use of vegetation indices to map forest change in northern Maine have indicated that NDMI-based methodology is capable of detecting partial- and clear-

cut harvests with good accuracy, provided Landsat TM images are acquired with a separation interval of 1-3 years (Wilson and Sader, 2002, Jin and Sader, 2005). Harvests detected within each interval were classified into two intensity classes based on the magnitude of NDMI change: heavy or light. This classification scheme was not designed to match current regulations in Maine that classify harvests based on the residual structure as "clearcut" (currently defined any timber harvest greater than 5 acres in size that results in a residual basal area of trees over 4 ½ inches in diameter measured at 4 ½ feet above the ground of less than 30 ft^2/ac; 12 MRSA §8867-A to §8888 & MFS Rules Chapter 20) or "partial harvest" (i.e., all other harvests greater than 5 acres that retain >30 ft^2/ac). The heavy harvest class represented stand-replacing or regeneration harvests targeted at initiating the next cohort of growing stock, which I expected would include both clearcut and heavy partial harvests. Light harvests represented partial harvests and tending operations targeted at the current growing stock, which I expected would retain >50% of the live basal area. A similar process was used to detect heavy harvest entries using the MSS imagery based on NDVI, expanding the time series by 5 additional intervals: 1973-1975, 1975-1978, 1978-1982, 1982-1985, and 1985-1988. NDVI, based on NIR and the red band (0.63-0.69 μm), was used in place of NDMI because Landsat MSS does not record reflected radiation in the mid-infrared range (1.55-1.75 μm). Additionally, areas disturbed ca. 1970-1973 were mapped directly from the 1973 MSS image. Light harvests were not mapped 1970-1988 because they could not be reliably classified using Landsat MSS imagery. Additional details about the image processing, timber harvest detection methods, and accuracy assessment will be presented in Legaard et al. (Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*).

Habitat selection study (Chapter 2)

During a companion study, information provided by the harvest detection time series was used to develop a spatially-explicit habitat model for predicting lynx occurrences based on observed patterns of 2nd-order habitat selection by lynx in northern and western Maine (Chapter 2). Timber harvest data were combined to map stand-level harvest operations 1970-2004, resulting in a classification scheme that included a range of regenerating forest (0-34 years post-harvest) and partially harvested forest (0-16 years post harvest) conditions ca. 2004. These data were then combined with a 2004 forest composition map (Legaard, Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*), which was developed as an update to the 1993 Maine GAP Vegetation and Land Cover map (MEGAP; Hepinstall et al. 1999). The resulting 2004 forest cover type map depicts harvest history, age structure, and current composition (i.e., coniferous, mixed, deciduous). A suite of predictor variables were developed from the 2004 forest cover type map reflecting current knowledge of lynx habitat associations in the Acadian Forest (Parker et al. 1983, Hoving et al. 2004, Fuller et al. 2007, Vashon et al. 2008a) and elsewhere (Koehler 1990, Staples 1995, Poole et al. 1996, Mowat and Slough 2003), and *a priori* candidate models were constructed to evaluate alternative hypotheses about the relationship(s) between landscape-scale occurrence of lynx and habitat amount, hare density, and habitat configuration (Chapter 2). Candidate models were parameterized using simulated occupied/unoccupied home ranges based on systematic snow track surveys conducted by the Maine Department of Inland Fisheries and Wildlife 2003-2006 (Chapter 2) and compared using an Information Theoretic approach (Burnham and Anderson 1998).

The top-ranked candidate model (w_i = 0.59) for predicting lynx occurrence and non-occurrence included the predictor variables: mean hare density (HARES), percent mature conifer (C), and the interaction term (HARES*C) (Chapter 2). This model took the form,

$$(\pi / 1 - \pi) = -1.268 - 1.271(\text{HARES}) - 0.378(\text{C}) + 0.926(\text{HARES*C}). \qquad \text{Eqn. 1}$$

Hosmer-Lemeshow statistic values for this model (0.89) and the global model (0.92), and McFadden's rho-squared for the top model (0.27) suggested that the data fit the logistic regression model and that the variables included in the top model explained a high proportion of the variability in the data. Correlation between HARES and C was low ($r < |0.1|$) and no candidate model had a ΔAIC ≤ 2 relative to the top model. The predictive accuracy was evaluated using leave-one-out cross-validation and based on the area under the receiver operating curve (AUC), and the AUC for the top-ranked model was 0.69, indicating that the top model provided good overall reliability at predicting areas occupied versus unoccupied by lynx.

Habitat time series

I used the harvest detection time series and forest composition information to track and map changes affecting the ecological factors that drive landscape-scale occurrence of lynx (Chapter 2) in northern Maine (i.e., HARES and C). The information provided by the harvest detection time series allowed me to track both *heavy* (i.e., stand-replacing or regeneration) and *light* (i.e., partial or tending) harvests and, consequently, to map the spatial distribution of regenerating forest, partially-harvested forest, and second-growth mature forest for each harvest interval. I then determined the spatial distribution of mature conifer forest 1975-2007 using a modified version of the MEGAP.

Regenerating forest classes resulting from 1975-1993 timber harvests were replaced with the ca. 1975 mature forest composition class derived from an unsupervised classification of the 1975 MSS image, which used the 1991 TM image included in the original MEGAP development as a reference dataset for classification (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*). I then used the harvest detection time series to create a mature conifer map for each harvest interval, removing areas of mature conifer from the resulting time series when either a *heavy* or *light* harvest had occurred.

Additional to facilitating delineation of regenerating forest at the end of each interval, the harvest detection time series also enabled mapping of subsequent treatments after an initial *heavy* harvest. Subsequent entries (*heavy* or *light*) after an initial *heavy* harvest were assumed to be intensive management or stand thinning. Thinning is a silvicultural technique that decreases stem density in regenerating stands, which also has been shown to reduce snowshoe hare densities (Sullivan and Sullivan 1988, Griffin and Mills 2007, Homyack et al. 2007). I then combined each of the resulting regenerating forest maps with the 2004 forest composition map to generate maps of snowshoe hare density for each interval. Maps of hare density were refined to reflect the classification scheme used in development of the predictive model (Chapter 2) by adjusting the density values associated with the regenerating forest conditions based on: stand age, the presence and type of intensive stand management, and regenerating forest composition (Table 3.1). I estimated the average leaf-off hare density for high-quality hare habitat (i.e., 1.8 hares/ha; Table 2.2) based on three years of data collected for seven conifer-dominated, advanced regenerating stands (≥18 years post-harvest) in north-central Maine

Table 3.1. Stand-scale snowshoe hare density estimates for forest types associated with harvest history (1970-2004) and 2004 overstory composition.

Stand type	Years post-harvest	hares/ha
Mature forest[a]		0.25
Partially-harvested forest[b]		0.80
Conifer or mixed regenerating forest (unthinned[c])		
	0 - 9[d]	0
	10 - 17[e]	0.2 - 1.6
	≥18[f]	1.8
Deciduous regenerating forest[d]		0.4

[a] "Mature forest" includes all overstory composition classes, including mature conifer. Hare density estimate based on Lachowski (1997) and Fuller and Harrison (2005).
[b] Partially-harvested forest includes all overstory composition classes. Hare density estimates based on Robinson (2006).
[c] Hare density estimates for thinned regenerating forest reduced by 50% based on the results of Homyack et al. (2007).
[d] Hare density estimate based on de Bellefeuille et al. (2001).
[e] Assumed a linear relationship between stand age and hare density 10-17 years post-harvest, resulting in an estimated increase of 0.2 hares/ha/yr.
[f] Hare density for regenerating forest ≥18 years post-harvest based on three years of data collected for seven conifer-dominated, advanced regenerating stands (≥18 years post-harvest) in north-central Maine for which researchers documented high hare densities 2002, 2003, and 2005 (Robinson 2006, Homyack et al. 2007). This period may represent a temporal high point for those stands (Scott *In preparation*).
[g] "Deciduous regenerating forest" includes all ages classes of regenerating forest (0-34 years post-harvest). Hare density estimate based on Litvaitis et al. (1985).

for which researchers documented relatively high hare densities 2002, 2003, and 2005 (Robinson 2006, Homyack et al. 2007). As described in Chapter 2, although southern populations (<49º N) of snowshoe hares are generally not expected to be strongly cyclic (Hodges 2000), ongoing research has recently suggested that the years used to derive the average hare density for high-quality hare habitat may represent a temporal high point for those stands (Scott *In preparation*). I assumed that young regenerating forest <10 years post-harvest would support 0.0 hares/ha (de Bellefeuille et al. 2001), and assumed a linear relationship between stand age (10-18 years post-harvest) and hare density (0.0-1.8 hares/ha), which resulted in an annual estimated increase of 0.2 hares/ha/yr. Hare density estimates for conifer or mixed, advanced regenerating stands affected by precommerical or commercial thinning were reduced by 50% based on research in Maine that compared hare density estimates of thinned vs. unthinned regenerating stands of the same age (Homyack et al. 2007).

Spatiotemporal analyses

To better understand the broad-scale spatiotemporal patterns associated with hare density and mature conifer, I first summarized harvesting trends directly from the harvest detection time series. I calculated the area affected by *heavy* harvest and the area of regenerating forest treated with herbicide or thinning 1970-2007. After 1988, I also calculated the area affected by *light* harvest based on the TM-derived portion of the harvest data. I quantified the direct effects of the harvesting patterns on mature conifer and high-quality hare habitat (HQHH) by calculating the amount of each habitat type 1988-2007. HQHH was previously defined as conifer or mixed regenerating forest ≥16 years post-harvest in the habitat selection study (Chapter 2) based on the relationship

between stand age and hare density (Homyack et al. 2007). Consequently, I used 1988 as the starting point for subsequent analyses because it was during the 1985-1988 harvest interval that regenerating forest ≥16 years post-harvest first became available within the study area (i.e., regeneration of 1970-1973 *heavy* harvests into HQHH).

I also generated a time series depicting temporal changes in percent mature conifer and mean snowshoe hare density at the lynx home-range scale. Each continuous surface was calculated using a circular moving-widow function to provide a value for each cell within the study area based on the characteristics of the neighboring area. I selected 2.9 km as the neighborhood radius to match the scale of the simulated home ranges used in the development of the predictive model (Chapter 2) and the 75% adaptive kernel home-range area for lynx documented during concurrent telemetry studies on my study area (Vashon et al. 2008b). I quantified the spatiotemporal variability in the resulting hare density series by first categorizing the estimated mean hare densities into five bins: 0.0 - 0.25 hares/ha, 0.26 - 0.50 hares/ha, 0.51 - 0.75 hares/ha, 0.76 - 1.0 hares/ha, and 1.01 - 1.25 hares/ha. I then calculated the percentage of the landscape in each category. I performed a similar temporal analysis for the percent of mature conifer forest using a 2.9 km neighborhood radius and 10% bins.

Finally, I generated a time series of lynx probability of occurrence (1988-2007) based on the top-ranked model (see above; Chapter 2). I assumed that the resource selection probability function (Eqn. 1) was representative and could be spatially extrapolated to the entire study area because the lynx data used in model development was collected using a stratified-random sampling scheme and selected townships were well distributed within my study area (see Figure 2.2: Chapter 2), which captured a broad

range of habitat conditions. Additionally, I assumed that temporal extrapolation based on the habitat time series was appropriate because lynx habitat use patterns associated with hare abundance are consistent across their range (Parker et al. 1983, Koehler et al. 1990, Murray et al. 1994, Staples 1995, Mowat and Slough 2003, Fuller et al. 2007, Vashon et al. 2008a) and during all phases of the hare cycle in northerly populations (Murray et al. 1994, Mowat and Slough 2003). I quantified spatiotemporal trends in the probability time series by calculating the area of forestland with ≥50% and ≥80% probability of lynx occurrence for each interval 1988-2007, and by estimating lynx density based on the 1991 and 2007 probability of occurrence surfaces following the methods outlined in Chapter 2 (see *Habitat assessment*).

Broad-scale future habitat trends

The combined harvest dataset allowed me to quantify and depict the broad-scale development and current status of lynx habitat conditions ca. 2007 and also provided information needed to assess future quantity and spatial distribution of HQHH in northwestern Maine over the next 15 years (2007-2022). The map of HQHH map represented habitat conditions ca. 2007 and was based on the spatial distribution of conifer or mixed regenerating forest 16-36 years post-harvest. Additionally, I mapped the spatial distribution of young regenerating forest (0-15 yrs) originating from *heavy* harvests 1991-2007 and combined the results with the modified MEGAP (*Habitat time series*) to determine the overstory composition of those areas prior to *heavy* harvest (i.e., coniferous, mixed, deciduous). I assumed that young regenerating stands in areas that were coniferous or mixed coniferous-deciduous composition in 1991 would eventually regenerate as coniferous or mixed forest after a *heavy* harvest and so retained those areas

as future HQHH. I did not include young regenerating forest in areas that were previously mature deciduous forest as these areas would likely require intensive management (e.g., herbicide application or precommerical thinning) to increase the proportional representation of conifer in the future stand. Finally, I determined the year in which each cohort of young regenerating forest would reach 16 years post-harvest and estimated the quantity of HQHH 2007-2022. I assumed that regenerating forest >35 years post-harvest would no longer function as HQHH based on research in Maine that has suggested that hare densities on average will start to decrease when the maximum stand age exceeds 35 years post-harvest (Fuller et al. 2007).

To evaluate the future effects of the changing spatial distribution of HQHH, I mapped the 2007 and 2022 probability of lynx occurrence using a single-variable model based on the proportion of HQHH within the occupied and unoccupied lynx home ranges (R). This model was included in the set of *a priori* candidate models (model rank #4 from Table 2.4; Chapter 2) and took the form:

$$(\pi / 1 - \pi) = -1.423 + 5.312(R), \qquad \text{Eqn. 2}$$

where R ranged from 0-1.0. Ranked candidate models 1-3 were not used for this application because they included other predictor variables. Hosmer-Lemeshow statistic value (0.349) and McFadden's rho-squared (0.09) indicated that the data fit the logistic regression model reasonably well and the variable explained a limited proportion of the variability in the data. The AUC for this model (0.65) was slightly lower than the top model (0.69), as were the sensitivity (0.50 vs. 0.67) and specificity (0.79 vs. 0.88). Although this model represented an *a priori* hypothesis (i.e., lynx occurrence determined only by the amount of HQHH) that was not strongly supported by the data compared to

the top model (Chapter 2), the model does capture an ecological factor that contributes heavily to lynx habitat supply in Maine through its strongly positive correlation to mean hare density (r = 0.97). Further, it is a factor that can be manipulated by forest management operations to benefit lynx habitat in the near-term by providing future HQHH. Thus, this single-variable model provides a useful comparison for considering the potential for areas to support lynx in the future.

RESULTS

Spatiotemporal analyses

Based on the satellite-derived time series, 55% of the 1.62 million hectares of forestland within my study area was classified as receiving a timber harvest 1970-2007. The majority (94%) of timber harvests represented single-entry harvest operations (*heavy* or *light*). Area affected by *heavy* harvests increased during each interval 1970-1988 (Figure 3.2), reflecting the transition from preemptive to salvage logging operations that occurred in response to the 1973-1985 spruce budworm (*Choristoneura fumiferana*) outbreak. The annual rate of *heavy* harvests more than doubled during this period, from approximately 11,568 ha/year just before the outbreak (1970-1973) to 25,723 ha/yr at the peak of salvage operations (1985-1988). The rate of *heavy* harvest began to decline after 1988 and by 1993 was exceeded by the rate of *light* harvests (Figure 3.2). From 1993-2007 the annual rate of *light* partial harvests remained relatively stable at an average of approximately 19,400 ha/yr (range = 17,591 - 21,775 ha/yr). The rate of thinning operations in salvage origin stands (1973-1985) appeared to increase sharply 2004-2007; however, omission error rates were likely high when identifying thinning events, particularly in high density stands where PCT primarily affected the stand composition

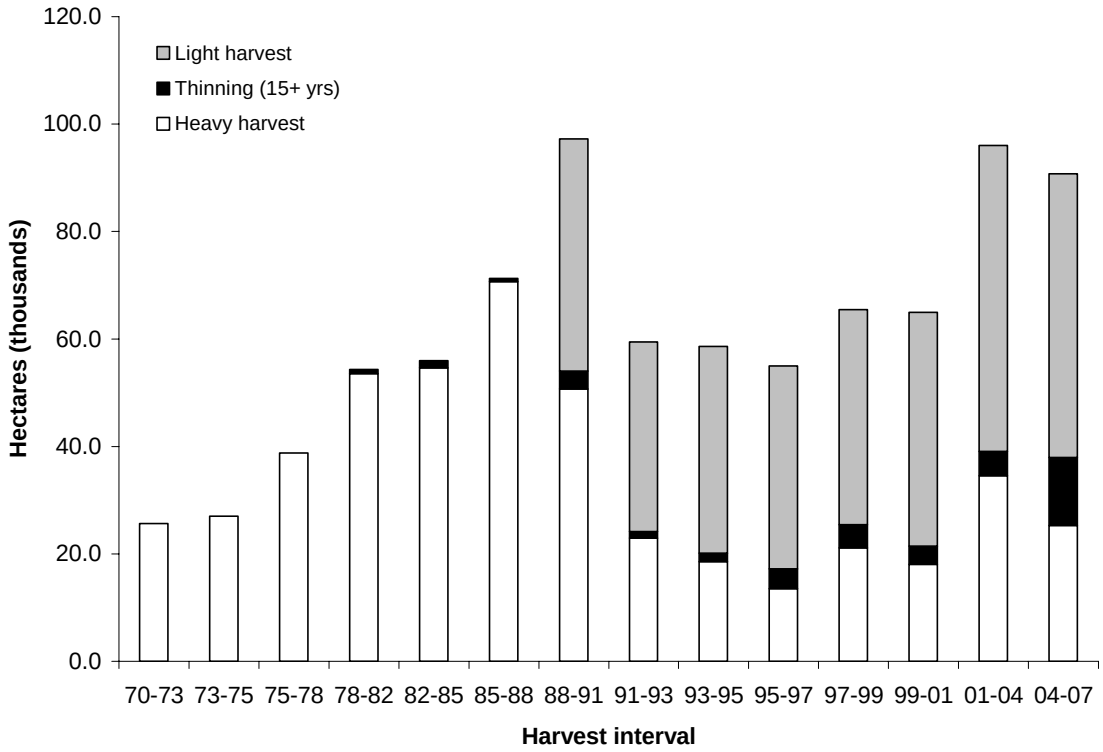

Figure 3.2. Broad-scale temporal harvesting trends, showing the area affected in hectares for each of the harvest intervals, as classified by the harvest detection time series (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*). Single-entry *heavy* (white bar) and *light* (gray bar) harvests and stand thinning in regenerating stands (black bar) are depicted. Note that *light* harvests were not mapped 1970-1988 because they could not be reliably classified using Landsat MSS imagery.

(i.e., hardwood saplings were removed) and the relative loss of canopy cover was minor. A preliminary estimate of accuracy rates associated with this class was performed using an ancillary dataset (Homyack et al. 2007) and results suggested that commission accuracy was 42% and omission accuracy was 100%; these results should be viewed with caution, however, because estimates were based on a small sample size of ground locations of known stand history (n = 26).

Starting in 1986, there was a broad-scale and rapid increase in high-quality hare habitat (HQHH) as the cohort of regenerating forest that was created via preemptive salvage harvesting began to reach 15-18 years old. There was a gain of 18,605 ha of conifer or mixed advanced regenerating forest 1985-1988 (Figure 3.3), which represented 1.3% of the available forestland area ca. 1988; area in HQHH accrued at an annual rate of ~6,200 ha/yr. The HQHH accumulated during the 1991-1993, 1995-1997, and 1997-1999 periods at an increasing rate as a consequence of elevated harvest rates 1975-1985 (Figure 3.3). There was a net decline in HQHH 1993-1995 and 1997-1999 resulting from a combination of a temporal lag in additional conifer or mixed regenerating ingrowth and precommerical thinning in existing HQHH. Overall, there was a total of 63,140 ha of conifer or mixed regenerating forest ingrowth and 6,249 ha of thinning, resulting in a net gain of 56,891 ha of HQHH 1991-1999. There was a steady gain (16,660-17,540 ha/yr) in HQHH 1999-2004, which resulted from stands harvested during the peak *heavy* harvest period (1985-1988, Figure 3.2). In 2004 HQHH accounted for 179,518 ha (11.8% of the forestland). Area in HQHH peaked at 188,879 ha in 2007 after accumulating at a slower rate 2004-2007 because of the decrease in *heavy* harvests beginning in 1988 (Figure 3.2) and an increase in thinning operations in salvage origin stands (Figure 3.2). In total, 8.4%

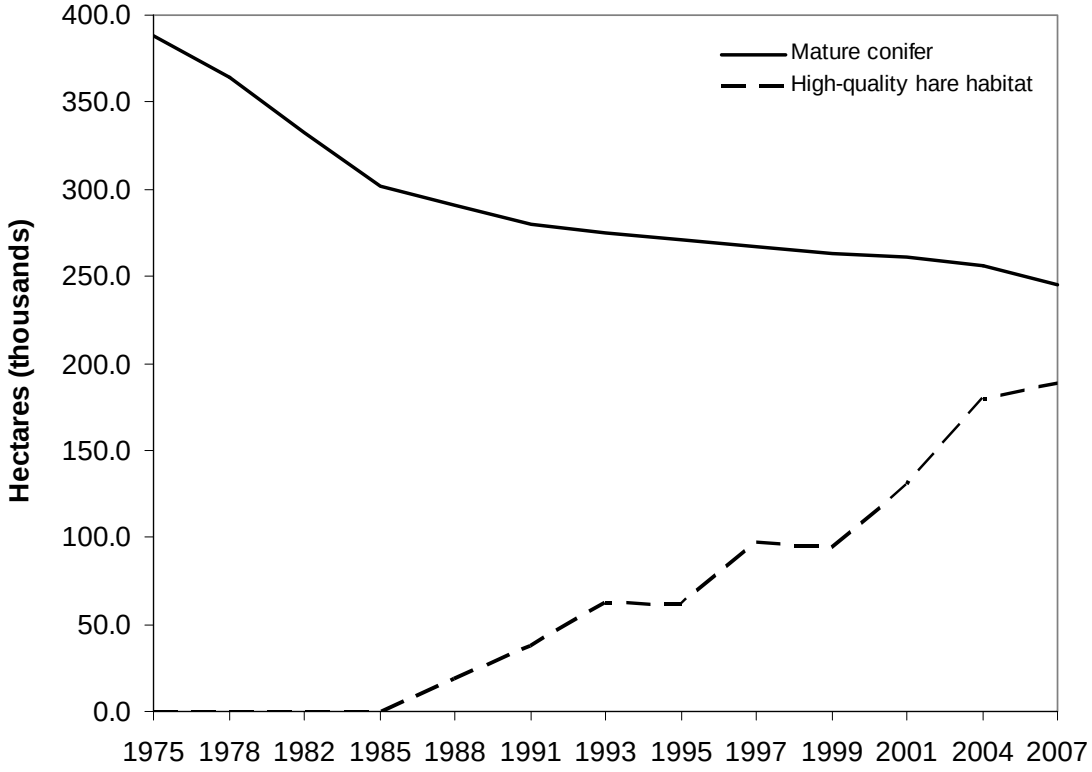

Figure 3.3. Cumulative trends in the quantity of mature conifer (black line) and high-quality hare habitat (dashed line) 1975-2007. High-quality hare habitat begins to accumulate during the 1985-1988 interval as regenerating forest created early in the time series (i.e., 1970-1973) begins to reach ≥16 years post-harvest.

of the conifer or mixed, advanced regenerating forest ca. 2007 was classified by the time series as having received a chemical or manual thinning treatment >15 years post-harvest 1988-2007. As previously mentioned, however, omission rates associated with thinning were likely high, suggesting that a greater percentage of regenerating stands were likely thinned than the methods here would indicate, which could have resulted in modest overestimates of the area in HQHH.

The quantity and spatial distribution of mature conifer forest was also largely a product of harvest rates and patterns during the spruce budworm salvage period. Harvest operations during this period targeted mature spruce-fir stands, leading to the removal of 31% of the mature conifer forest in the study area by heavy harvests 1975-1988. The average annual rate of harvest during this period was ~3%. The 1988 distribution of the remaining mature conifer (Figure 3.4) was the result of the pre-existing prevalence of mature conifer in the northern half of the study area and harvesting patterns. At the scale of a lynx home range (26.4 km^2) 34% of the forestland area was comprised of <10% mature conifer forest, 83% had <30% mature conifer forest, and 98% had <50% mature conifer forest. During the 1990s, the annual rate of harvest of mature conifer tapered off towards ~1% (Figure 3.3) and by 1997 64% of potential lynx ranges were comprised of <10% mature conifer forest (Figure 3.4). This general rate of harvesting continued through most of the 2000s, with a slight increase 2004-2007 (Figure 3.3). By 2007, 50% of the mature conifer forest present ca. 1975 remained and the percentage of the potential home ranges with <10% mature conifer was 49%, and 1% were comprised of 40-60% mature conifer forest.

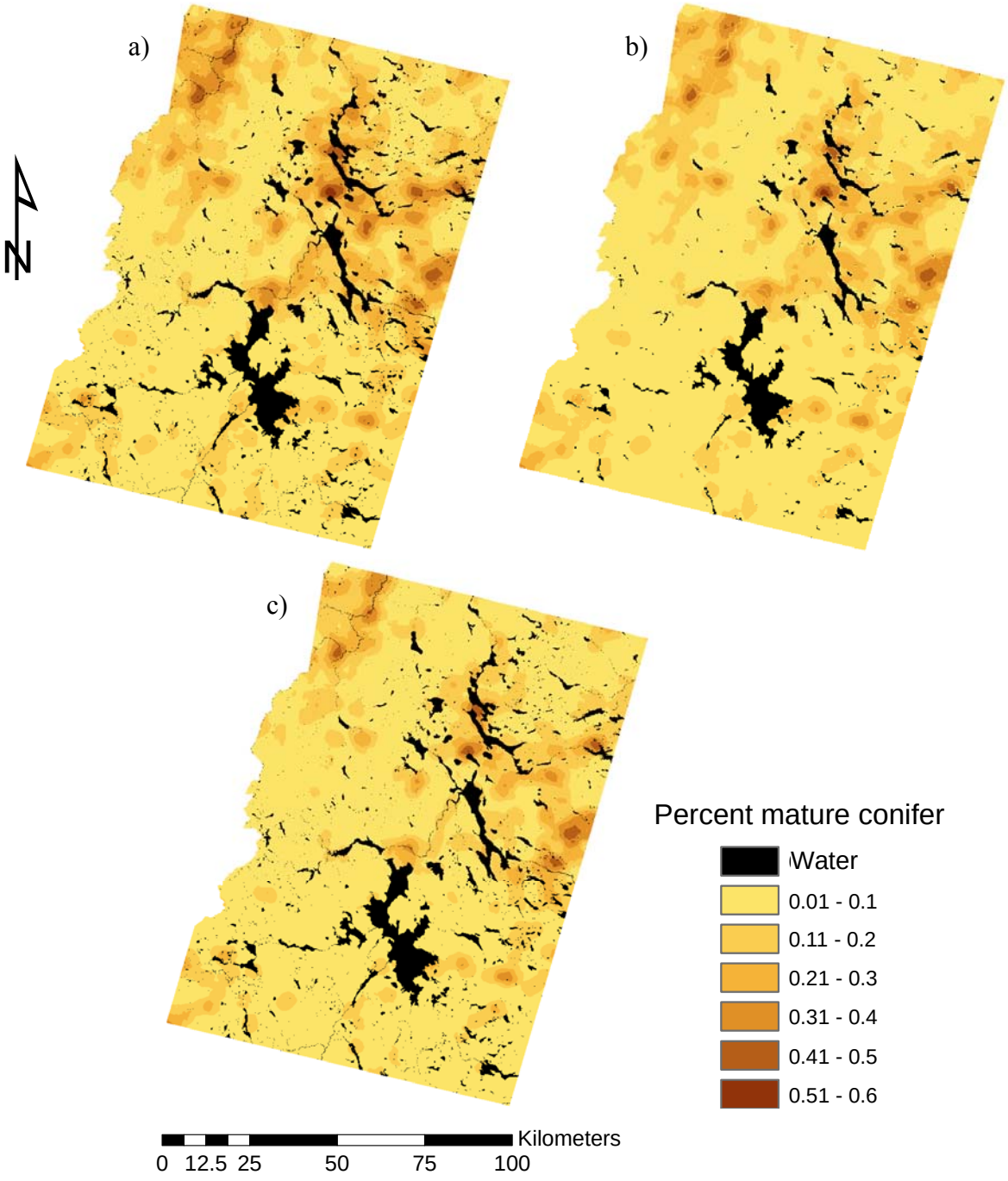

Figure 3.4. Spatial distribution of mature conifer forest at the scale of potential lynx home ranges (26.4 km^2) in a) 1988, b) 1997, and c) 2007 across my 1.62 million hectare study area in northern Maine, USA. Areas with >20% mature conifer (identified by the darker color) occur primarily in the east-central and north-western regions of the study area.

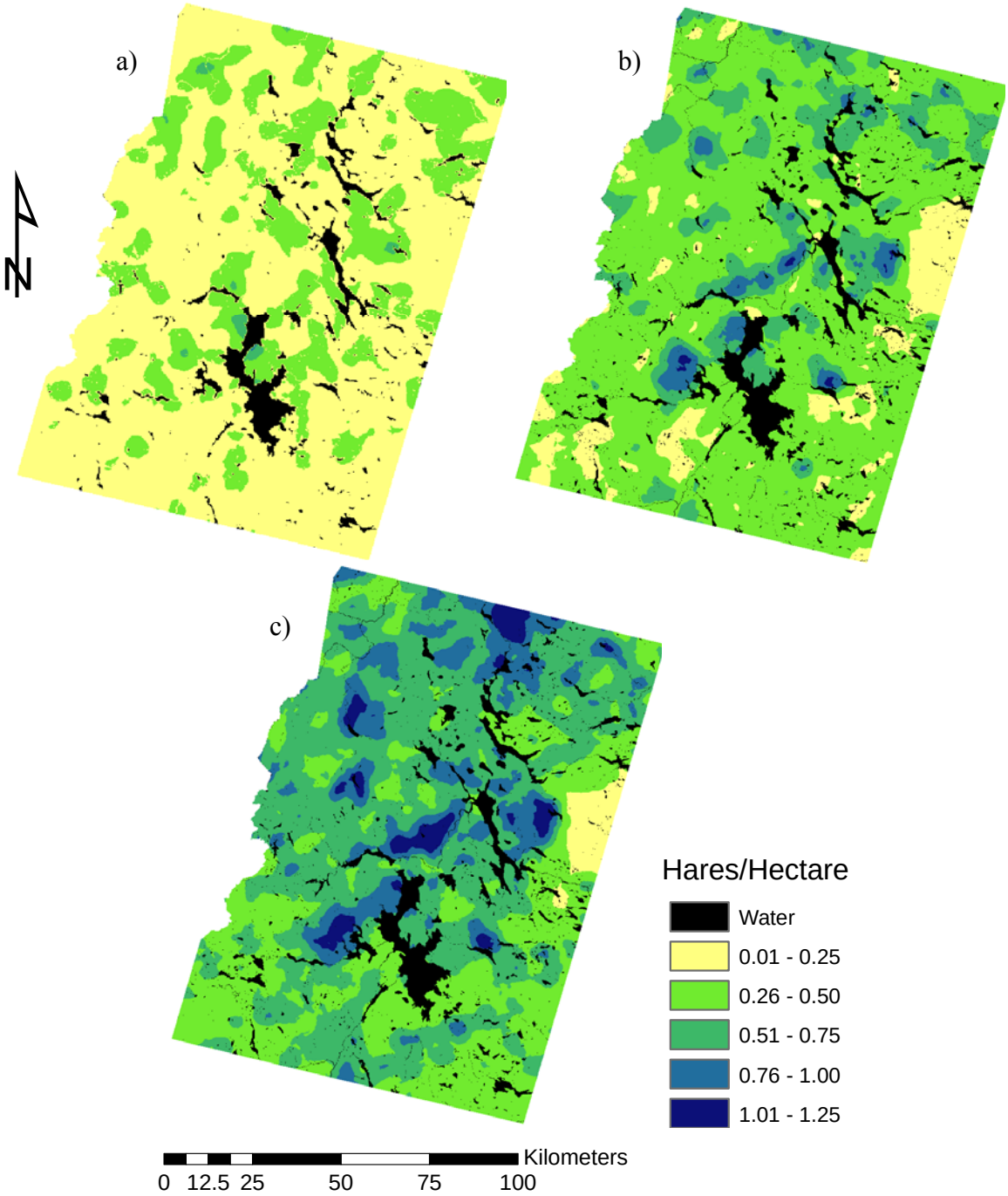

Figure 3.5. Spatial distribution of mean hare density at the scale of potential lynx home ranges (26.4 km^2) in a) 1988, b) 1997, and c) 2007 across my 1.62 million hectare study area in northern Maine, USA. Areas identified as having ≤0.25 hares/ha in 2007 (yellow) occur in Maine's largest state forest reserve, Baxter State Park.

The cumulative increases in HQHH contributed substantially to increases in landscape-scale hare densities 1985-2007. In 1988, 99% of the forestland area had a predicted mean hare density of 0.0 - 0.5 hare/ha at the lynx home-range scale (Figure 3.5), and only 1% had an estimated landscape-scale hare density greater than the inferred threshold to support a lynx population (0.5 hares/ha; Ward and Krebs 1985, Brocke et al. 1992). In 1997, the accumulation of 96,811 ha of HQHH had a broad-scale effect on landscape-scale hare densities, and coincided with a decreasing percentage of total forestland with mean hare densities 0.0 - 0.25 hare/ha (10%) and an increasing percentage of forestland with ≥0.5 hares/ha (21%). Ten years later, only 2% of potential home ranges had a mean hare density of 0.0 - 0.25 hare/ha, and these area occurred almost exclusively in Maine's largest forest reserve, Baxter State Park (Figure 3.5). In fact, the majority (65%) of potential home ranges had a mean hare density ≥0.5 hares/ha in 2007. Approximately 16% of the forestland (246,374.8 ha) had estimated hare densities that exceeded the mean hare density observed within simulated home ranges around positive lynx occurrences (i.e., 0.74 hares/ha; Chapter 2), and all potential lynx home ranges in these areas had 20-70% HQHH (median = 28%). Based on a pairwise comparison, the median change in landscape-scale hare density within potential lynx home ranges was +0.32 hares/ha (range = -0.02, +1.34) 1988-2007.

The top model for predicting hare densities (Chapter 2) showed a positive association to both mean snowshoe hare density (H), which was increasing during the period 1988 to 2004, and the percent forestland in mature conifer forest (C), which was declining during that interval, and via a strong interaction between H and C (Table 3.2). Overall, increased landscape-scale hare density was the dominant variable influencing

Table 3.2. Parameter estimates and associated odds ratios for the top-ranking model for predicting lynx occurrence and non-occurrence in northern Maine, USA (Chapter 2). This model included the predictor variables[a]: mean snowshoe hare density[b] at the lynx home-range scale (HARES), the percent of mature conifer[b] at the lynx home-range scale (C), and the interaction between those two variables (HARES*C).

Parameter	**Estimate**	**95% Lower**	**95% Upper**	**Odds Ratio**
Constant	-1.268	-5.545	3.010	
HARES	-1.271	-7.880	5.337	0.280
C	-0.378	-0.930	0.173	0.685
HARES*C	0.926	-0.025	1.877	2.525

[a] Candidate predictor variables were derived from a combination of timber harvest data used to map stand-level harvest operations 1970-2004 (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*) and a 2004 forest cover type map (Chapter 2).
[b] Mean snowshoe hare density was included as a candidate variable to evaluate the cumulative effect of home-range composition on prey density and lynx occurrence. Values for occupied and unoccupied home ranges were calculated by applying stand-scale hare densities (Table 3.1) to forest types identified by harvest history and 2004 composition.
[b] Percent mature conifer was included as a candidate variable because of the important role that this forest type appears to play in supporting lynx populations in some areas of the boreal forest (e.g., Murray et al. 1994, Poole et al. 1996). Variable was defined as "mature" based on the timber harvest data (i.e., uncut since 1970).

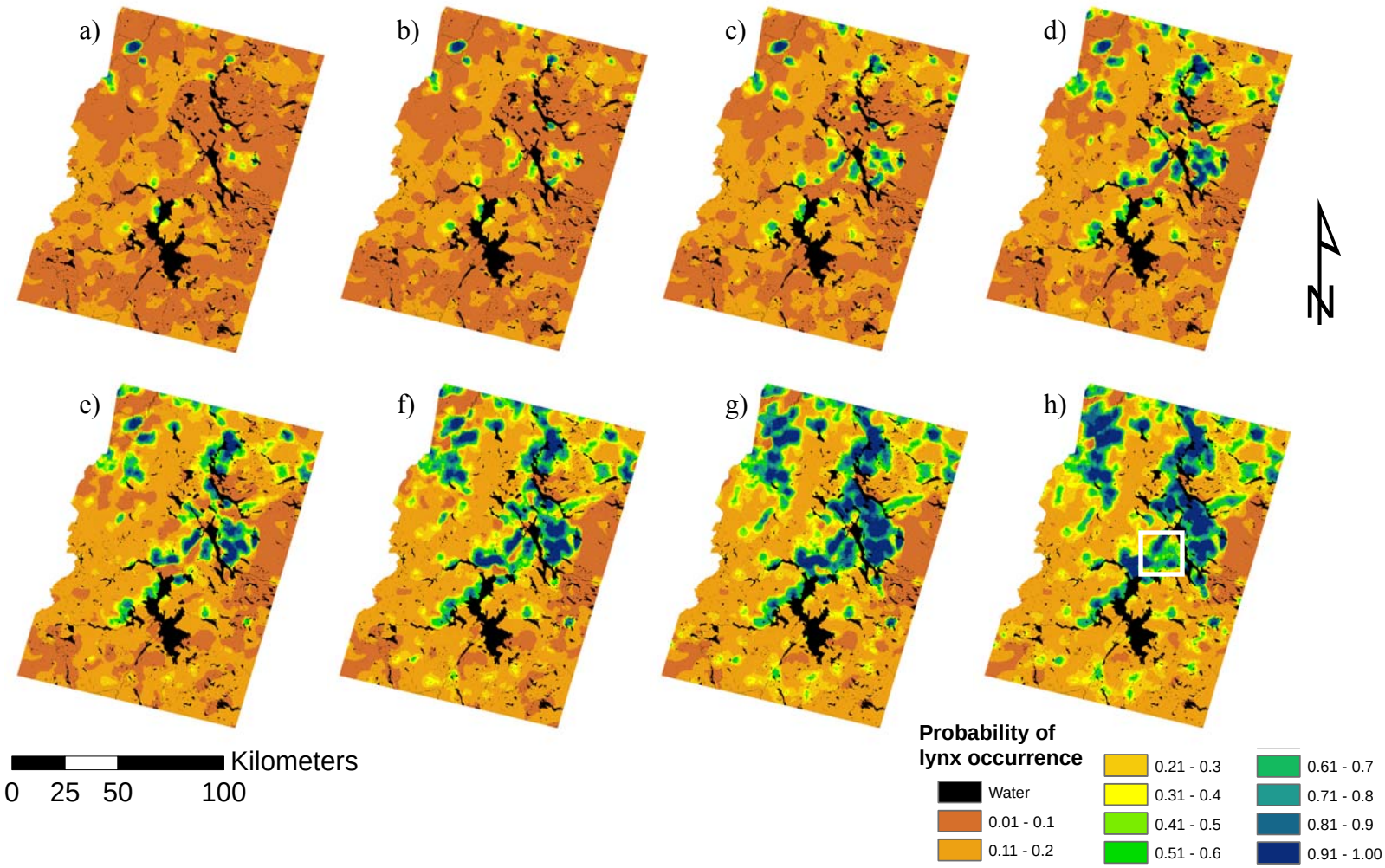

Figure 3.6. Probability of lynx occurrence across my 1.62 million hectare study area, 1991-2007, based on the top-ranked model developed for northern Maine, USA (Chapter 2). Years shown are a) 1991, b) 1993, c) 1995, d) 1997, e) 1999, f) 2001, g) 2004, and h) 2007. The first area of decline in probability of occurrence is outlined in 2007.

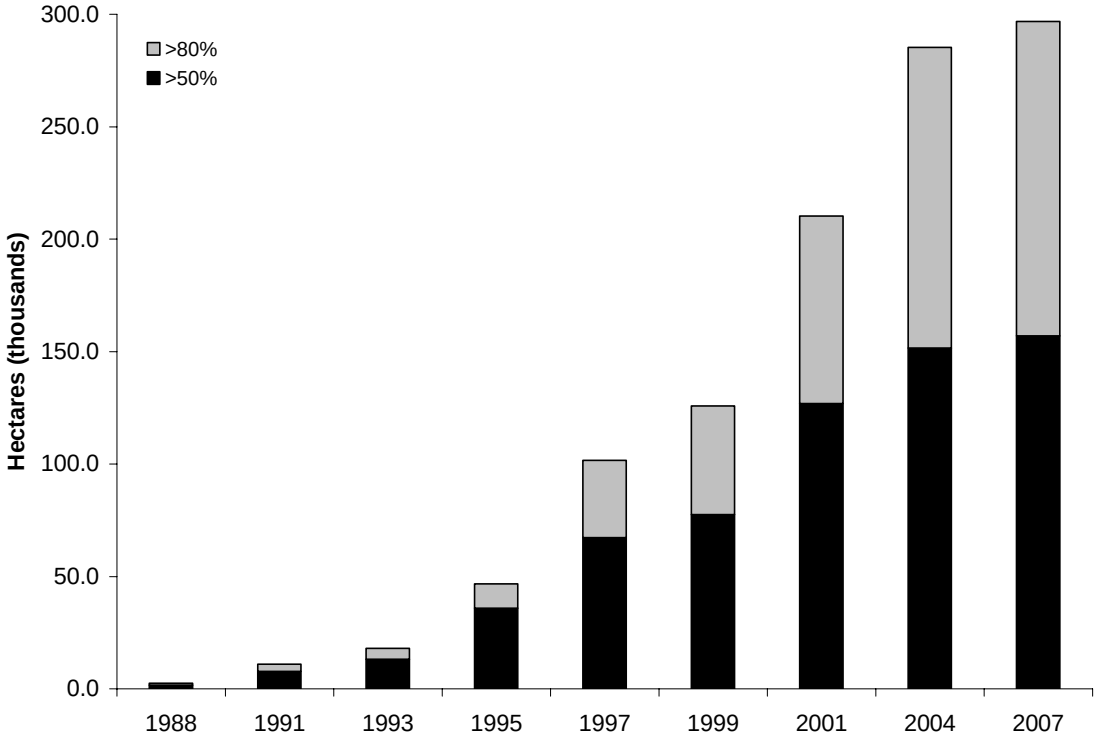

Figure 3.7. Cumulative area (hectares) of forestland at the scale of a lynx home range (26.4 km^2) with predicted probability of lynx occurrence >50% (black bar) and >80% (gray bar).

changes in the probability of lynx occurrence (POC) 1988-2004 because that variable experienced a greater magnitude of change. The first areas of ≥50% POC occurrence emerged (Figure 3.6) in areas where HQHH increased 1985-1991 (Figure 3.3). In 1991, 10,961 ha of forestland (1%) had a POC ≥50% and only 3,273 ha (<1%) had a probability of lynx occurrence ≥80% (Figure 3.7). During the 1990s, new areas of high POC continued to emerge in the northern and central regions of the study area and many expanded over time as adjacent regenerating forest stands were recruited into HQHH (Figure 3.6). As HQHH steadily accumulated 1999-2004 (Figure 3.3), the area of forestland with ≥50% POC increased even more rapidly (Figure 3.7). Between 1999 and 2004, the area of forestland with ≥50% POC more than doubled and the area with ≥80% POC increased by almost 3-fold. After 2004, however, a different pattern started to emerge in the lynx time series. There was only a small increase in area with lynx probability ≥50% 2004-2007 (Figure 3.7) and this was accompanied by the emergence of the first areas of localized decline in lynx POC (Figure 3.6). Areas of localized POC decline occurred where little regenerating forest was being recruited and where the mature conifer forest also declined.

I estimated lynx density for the 160 unorganized townships in northern and western Maine that overlapped the study area by ≥70% (Figure 3.8) using the 1991 and 2007 POC maps (Figure 3.6). The majority of the townships in 1991 (78%; n=160) had an estimated potential lynx density of 0 - 1.0 lynx/100 km^2. Townships with habitat potential to support ≥1.0 lynx/100 km^2 occurred in areas where landscape-scale hare densities were increasing (Figure 3.5) and mature conifer was present ca. 1991 (Figure 3.4). Between 1991 and 2007, potential lynx density increased on average

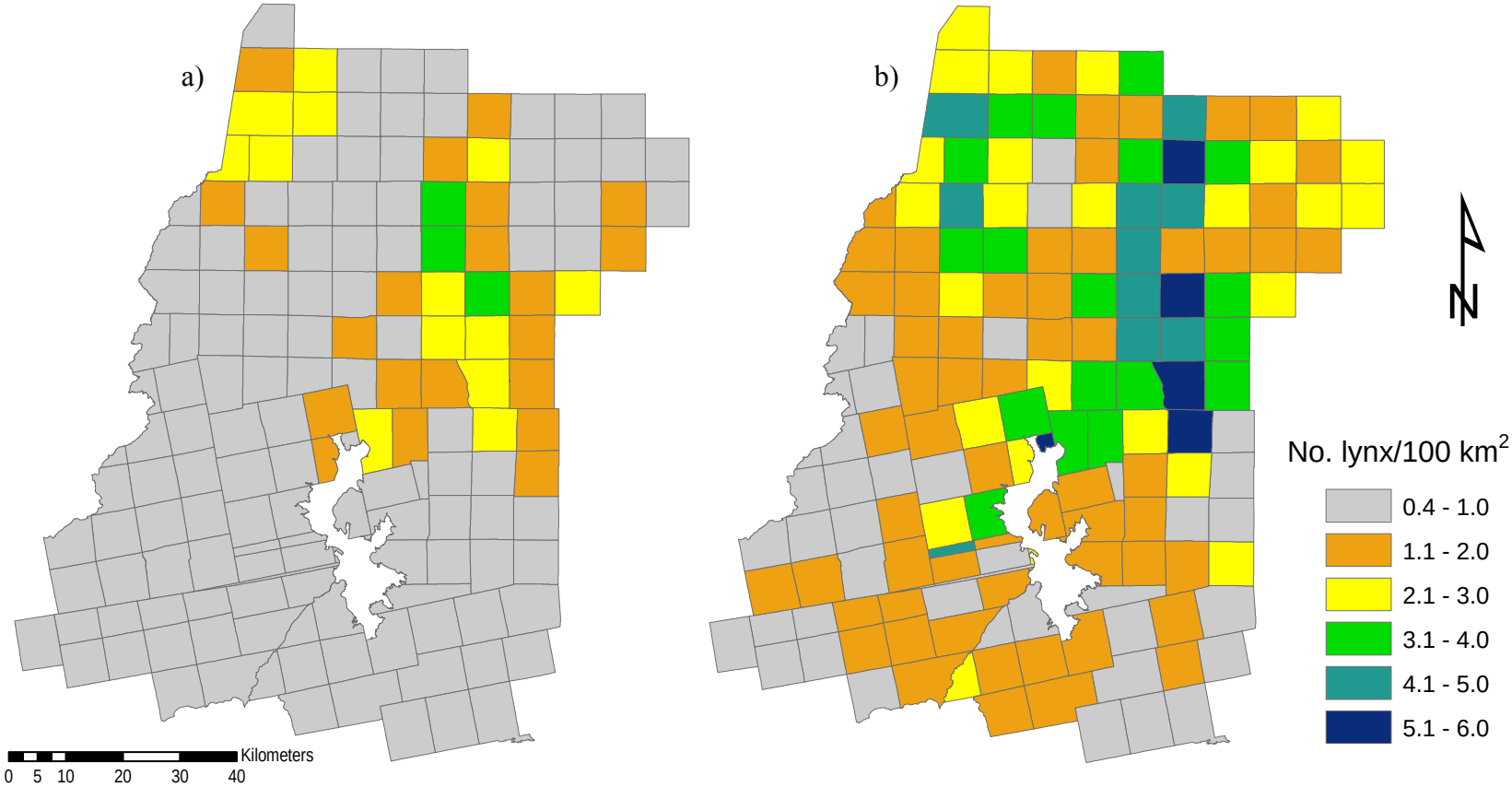

Figure 3.8. Potential density of adult resident lynx that could be supported at the township-scale (number of lynx/100km^2) in a) 1988 and b) 2007 across 155 townships in northern Maine, USA. Densities calculated based on the summed probability of lynx occurrence using a fixed grid representing potential home ranges that would be exclusive of other lynx of the same sex (Vashon et al. 2008b, Chapter 2).

1.23 lynx/100 km^2 (SD = 0.89; range = -1.19 - 4.19 lynx/100 km^2) across those townships and in 2007, 75% had a potential density of ≥1.0 lynx/100 km^2 (Figure 3.8). Twenty-one percent of the townships had potential density of ≥3.0 lynx/100 km^2, occurring in the central and north-western regions of the study area where increases in hare density (Figure 3.5) and lynx POC (Figure 3.6) were greatest.

Broad-scale future habitat trends

Between 2007 and 2022, quantity of HQHH is projected to remain relatively stable at approximately 200,000 ha (Figure 3.9). The location and configuration of HQHH, however, will shift substantially (Figure 3.10). By 2022, HQHH will be more uniformly distributed throughout the study area, with substantial increases in the southern portion (Figure 3.10). The aggregation of this habitat type in 2022 will be lower in many areas compared to 2007, resulting in fewer potential lynx home ranges with >30% HQHH. The shift in the spatial distribution of HQHH 2007-2022 (Figure 3.10) will have two primary effects on lynx POC. First, areas with POC ≥50% will likely expand in the southern region of the study area, and will coincide with a decrease in POC ≥50% the central and northern regions (Figure 3.11). This would result in an estimated 51% decline of the landscape with ≥50% POC (Equation 2) from 170,283 ha to 83,439 ha. Additionally, the successive disaggregation of habitat suggests an outcome where none of the landscape will support ≥80% lynx POC by 2022 (Figure 3.11).

DISCUSSION

The research presented here evaluates interactions between timber harvesting, snowshoe hare density, and lynx habitat supply during the period 1970-2007. By integrating the spatially- and temporally-explicit information in the habitat time series

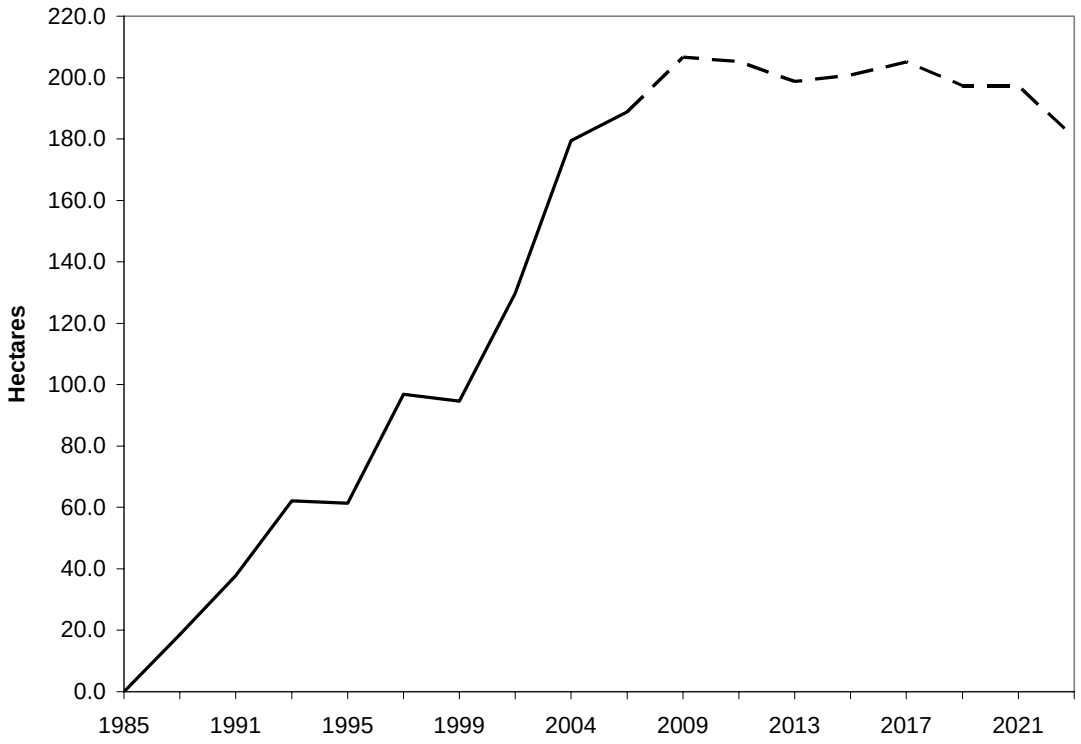

Figure 3.9. Aspatial trend in cumulative area (hectares) of high-quality hare habitat (HQHH) 1985-2022. The trend (black line) for 1985-2007 was based on accumulation of HQHH, as documented via the satellite-derived time series. The trend for 2007-2022 (dashed line) was estimated based on the accumulation of regenerating forest ingrowth from *heavy* harvests beginning with the 1991-1993 harvest interval. Prior forest composition was assumed to predict future composition. Estimations do not account for habitat loss resulting from stand thinning after 2007.

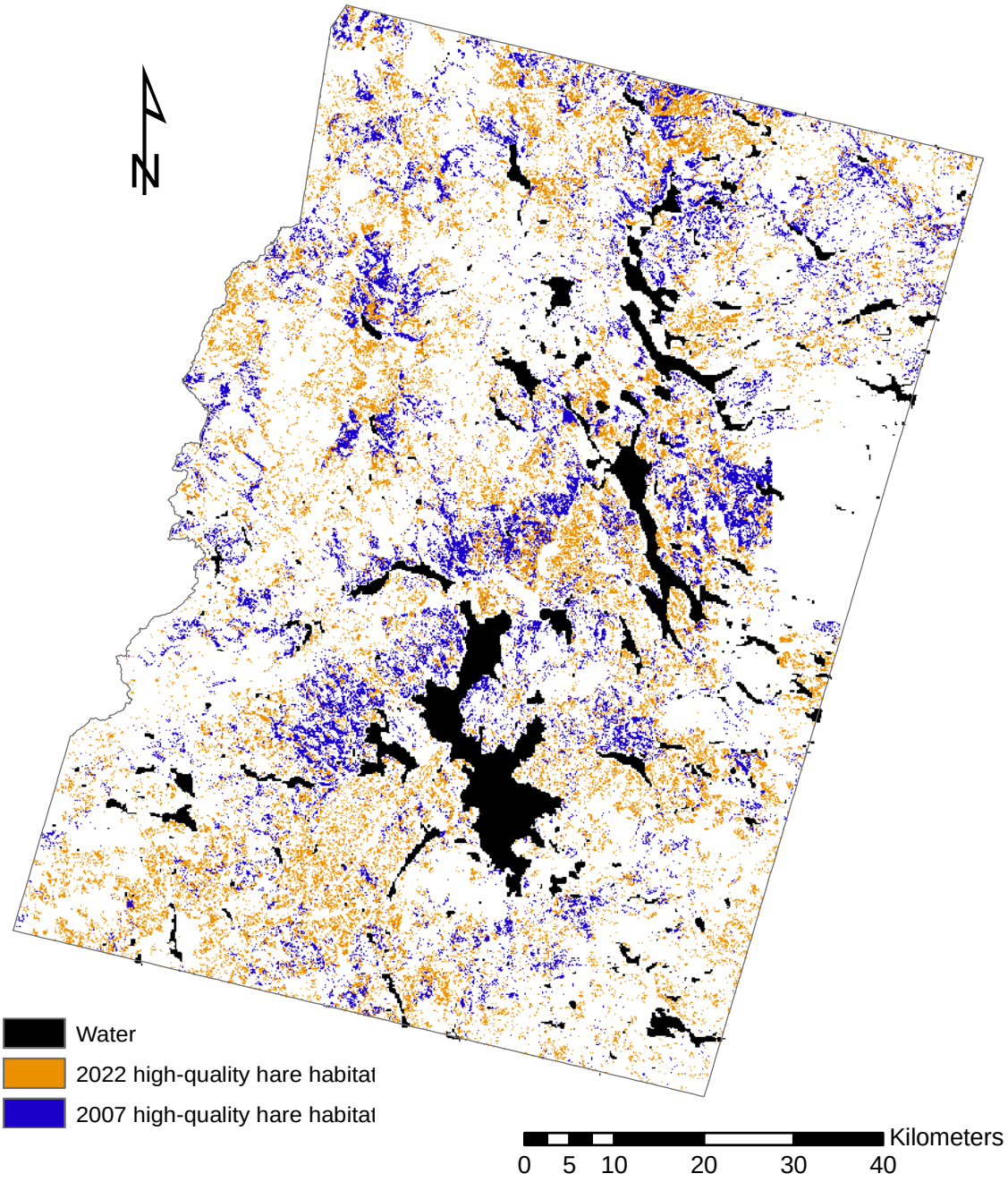

Figure 3.10. Current (blue) and future (orange) ca. 2022 spatial distribution of high-quality hare habitat across my 1.62 million hectare study area in northern Maine, USA. Spatial projections for 2022 were based on the growth of regenerating forest resulting from 1991-2007 *heavy* harvests in previously conifer or mixed, mature forest. Estimations do not account for habitat loss resulting from stand thinning after 2007.

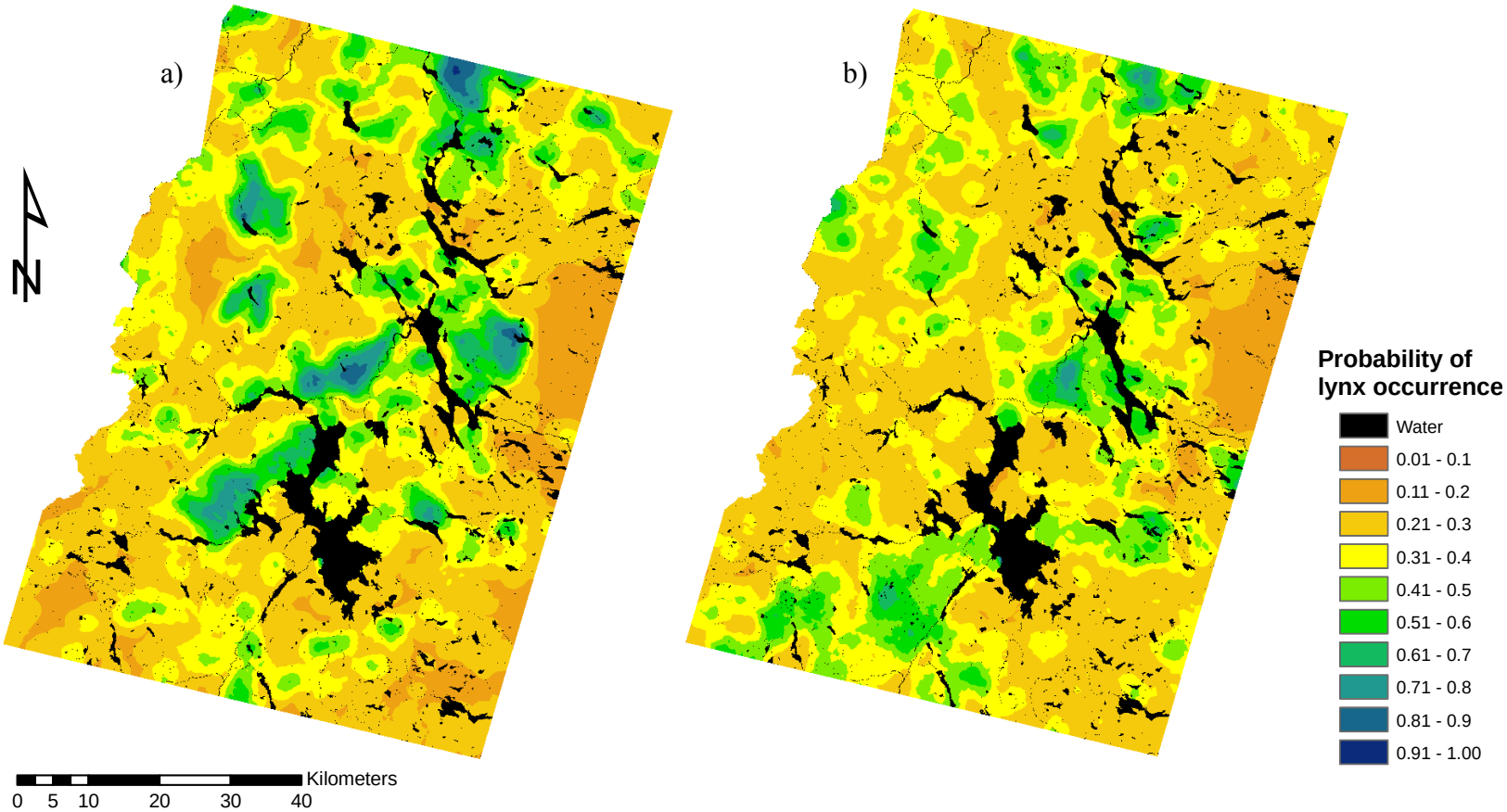

Figure 3.11. Probability of lynx occurrence surfaces for a) 2007 and b) 2022 based solely on percent of high-quality hare habitat across my 1.62 million hectare study area in northern Maine, USA. Cooler colors are associated with higher probabilities of occurrence.

with the predictive landscape-scale habitat model (Chapter 2), I have demonstrated that forest management activities since 1970 have resulted in broad-scale changes in quantity and distribution of mature and regenerating forest, and dramatic changes in both the spatial and temporal habitat supply for lynx. During the 1973-1985 spruce budworm outbreak, harvest rates in mature conifer increased as infested spruce-fir forest stands were salvage logged, which created large areas of what would become high-quality hare habitat (HQHH) that would support significant increases in landscape-scale hare densities beginning in the 1990s. The previously small lynx population in northern Maine is also thought to have increased in the mid- to late-1990s (Hoving et al. 2004), suggesting that population changes in hares and lynx resulted from human-induced habitat change. Clearcut harvesting has significantly decreased since the early 1990s (Figure 3.2) (Maine Forest Service 1994, 1997, 2003), resulting in a decline in the cumulative increase of HQHH (Figure 3.3), which has important implications for lynx conservation in the contiguous U.S. These results provide insight into the role that forest management has played and will continue to play as an important process that determines the quantity and distribution of habitat for lynx in the forested landscapes of the sub-boreal region.

The development of the regenerating forest from preemptive and salvage harvests (1970-1988) led to the broad-scale and rapid increase 1986-2004 (Figure 3.3) in regenerating forest conditions associated with high snowshoe hare densities in Maine (Robinson 2006, Homyack et al. 2007). On average, even-aged regenerating forest with high stem densities of conifer saplings in Maine supports 7x the over-winter hare density (mean = 1.8 hares/ha) relative to mature forest (mean = 0.25 hares/ha) (Fuller and Harrison 2005, Robinson 2006, Homyack et al. 2007), which sets the Acadian Forest

apart from the other southern areas of the lynx range in the contiguous United States where hare densities rarely exceed 0.6 hares/ha (Orr and Dodds 1982, Apps 2000, Griffin 2004). Mean hare densities at the scale of lynx home ranges increased across a large proportion of the study area 1988-2004 and the extent of forestland with hare densities exceeding previously published minimum thresholds for supporting a lynx population (≥0.5 hares/ha) increased from <1% to 65% of the landscape. Previous research has further suggested that if a lynx population is non-cyclic, as has been suggested for populations <49º N (e.g., Hodges 2000), the minimum hare density required for positive population growth may be much greater (>1.5 hares/ha; Steury and Murray 2004). However, hare densities in my study area rarely exceeded 1 hare/ha at the scale of a lynx home range, even though stand-scale hare densities commonly exceed 1.5 hares/ha within conifer-regenerating forest stands (Robinson 2006, Homyack et al. 2007). This suggests that *landscape-scale* hare densities do not need to be as high as 1.5 hares/ha to ensure the persistence of a southern lynx population. In fact, estimated lynx densities in northern Maine (Vashon et al. 2008b, Chapter 2) are comparable to some more northerly populations during the cyclic high (Brand et al. 1976, Parker et al. 1983, O'Donoghue et al. 1997).

Lynx POC increased rapidly through the 1990s to 2004 in central and northern regions of the study area (Figure 3.6) as increased landscape-scale hare densities generally offset the continued loss of mature conifer forest during this period. However, increases in area with ≥80% POC were most pronounced where both mature conifer remained (Figure 3.4) and landscape-scale hare densities were high (Figure 3.5). Thus, the strongly positive influence of the interaction between mature conifer and HQHH on

lynx occurrence in Maine (Chapter 2) emphasizes that lynx require a mosaic of HQHH and mature forest within their home ranges (Parker et al. 1983, Koehler and Brittell 1990, Mowat et al. 2000). Previously researchers have speculated that lynx may require mature conifer forest for denning (Koehler 1990); however, recent studies from Maine indicate that lynx will use a variety of structures with a range of forest types and age classes for natal dens (Organ et al. 2008). Thus, the positive association of mature conifer forest with lynx occurrences may instead be related to enhanced foraging opportunities along edges between regenerating and residual conifer stands (Staples 1995, Mowat et al. 2000).

The broad-scale distribution of both mature conifer and HQHH ca. 2007 were a product of the interaction between the distribution of mature conifer at the start of the 1970s and the large harvest blocks that were created in many of these areas during the salvage period that would eventually become HQHH. Another result of this interaction was the positive spatial association of mature conifer and HQHH within areas occupied by lynx. A *post hoc* comparison of the edge density between mature conifer and HQHH conducted as part of a companion second-order habitat selection study (Chapter 2), indicated that occupied lynx home ranges (mean = 7.692 meters/ha; SD = 4.207) had almost 2x the edge density of unoccupied ranges (mean = 3.998 meter/ha; SD = 3.883). This result strongly suggests that it is not simply the presence of mature conifer that is important for influencing lynx occurrence in Maine, but the juxtaposition of this habitat type with regenerating conifer-dominated forest (Chapter 2). Researchers have previously noted the importance of the edges between regenerating forest and mature conifer as providing foraging opportunities, potentially allowing lynx to hunt more successfully than within dense regenerating forest (e.g., Staples 1995, Mowat et al. 2000). Further,

studies in northern Maine have indicated that patch (Fuller et al. 2007) and within-patch (Fuller 2006) habitat selection by lynx is influenced by both prey accessibility and prey density. Thus, the salvage logging period and the resulting loss of mature conifer likely contributed both to the increase in HQHH and the creation of potentially valuable edge habitat within lynx home ranges.

A new spatiotemporal pattern started to emerge 2004-2007, characterized by a substantially reduced rate of increase in the lynx POC across my study area (Figure 3.7). HQHH continued to accumulate during this period, but at a slower rate (Figure 3.3). This decline occurred because of decreases in *heavy* harvesting starting in 1988 (Figure 3.3) and from thinning operations. The decrease in *heavy* harvests was a reflection of the 1989 enactment (12 MRSA §8867-A to §8888 & MFS Rules Chapter 20) of the Maine Forest Practices Act (MFPA). The MFPA set forth Maine's first definition of a "clear-cut" and required that landowners adhere to green-up and adjacency standards. The immediate effects of this legislation were that between 1989 and 1991 the number of acres harvested by clear-cut on Maine's commercial forestlands declined by almost 50% (Maine Forest Service 1995). The annual rate of heavy harvesting on my study area declined by 28% 1988-1991 followed by an additional 32% 1991-1993 (Figure 3.2). From 2004 to 2007, the annual rate of mature conifer harvest and the rate of thinning increased compared to 2001-2004; consequently, coupled with the decline in regenerating forest ingrowth there was only a small increase in the total area with lynx POC ≥50% or with POC ≥80% during the interval 2004-2007 (Figure 3.7). The first areas of decline in POC also emerged 2004-2007 (Figure 3.6) and the largest area of decline occurred in the central portion of the study area where both thinning in HQHH and harvest of mature conifer

occurred in close proximity (Figure 3.6). Further, although the NDMI-based methodology has been shown to be 87-91% accurate for mapping clearcut vs. partial harvests in the Acadian Forest (Sader et al. 2003), the omission error rate associated with detecting precommerical thinning in regenerating forest is undoubtedly higher than for detecting harvest of mature forest since the method was not originally developed for that purpose. This is an important consideration because thinning regenerating stands has been shown to result in a ~50% reduction in snowshoe hare density compared to unthinned regenerating stands in northern Maine (Homyack et al. 2007). A preliminary assessment suggested that the omission accuracy associated with using NDMI to identify areas where PCT occurred was <50%, which suggests that a larger proportion of the regenerating forest within my study area was likely thinned 1970-2007.

It is important to note that estimates of regenerating forest ingrowth from *heavy* harvests should be viewed cautiously because the time series only provided harvest information back to 1970. Consequently, regenerating forest created by clearcuts in the 1960s, for example, would not be mapped or included in estimates of HQHH. However, timber harvesting in the 1940s through the 1960s occurred primarily as diameter limit cuttings (Hart 1963), which like most current partial harvesting techniques are not expected to create the regenerating forest conditions that support high snowshoe hare densities (Robinson 2006). It is, however, likely that small proportion of harvests classified as *light* (1991-2004) have resulted in regenerating forest conditions favorable to snowshoe hares (Chapter 2). As pointed out in Chapter 2, this situation could arise, for example, in the case of an overstory removal if the understory conifer stem density prior to harvest is high (>7,000 stems/ha; Robinson 2006), which may under certain

circumstances be classified as a *light* harvest even though it is effectively a stand-replacing harvest.

Based on the harvesting patterns that followed the salvage period, the spatial distribution of lynx foraging habitat is expected to change substantially 2007-2022 (Figure 3.10). The quantity of habitat, however, may actually change relatively little over this period, which is consistent with the shifting mosaic steady-state concept first put forth by Bormann and Likens (1979). Based on this concept, the seral stage present at any given location within a landscape changes over time due to succession, but averaged over a large enough scale (spatial and temporal) the proportion of the landscape in each seral stage will remain relatively constant in time. Lynx foraging habitat is also likely to be less aggregated in 2022 as a result of the decrease in clearcut size that occurred after the passage of the MFPA (Maine Forest Service 1995). Consequently, it is estimated that an increasing proportion of forestland will contain <20% HQHH at the lynx home-range scale. These changes in location and configuration will be reflected in an expansion of the area with ≥30% probability of occurrence in the southern region of the study area, but an overall decrease in the area with ≥50% probability of occurrence and a loss of connectivity (Figure 3.11) throughout the larger study area.

Although the shift in HQHH will increase landscape-scale hare densities in the southern region of the study area, the potential for lynx densities to increase in the southern region of the study area may be constrained by extrinsic factors, including the presence of competitors and less favorable climatic conditions. Researchers have speculated that because of their similarity in body size and the potential for a high degree of overlap in their diet (Buskirk 2000) that interference competition or resource

competition is particularly likely to occur between lynx and bobcats (*Lynx rufus*) (Parker et al. 1983). Although direct competition has yet to be documented, geographic-scale modeling efforts in Maine have suggested that lynx occurrence at this larger scale is negatively influenced by bobcat presence (Robinson 2006). Additionally, fisher (*Martes pennanti*) might also compete with lynx for snowshoe hares in the winter (Arthur et al. 1989), and fishers have been documented to kill female lynx and their kittens in northern Maine (J. Vashon unpublished data). Thus, because bobcats and fisher have higher foot-loading and are more limited by snow (Krohn et al. 2005) and therefore occur at higher densities in southern Maine where annual snowfall is lower, if the lynx distribution shifts south in response to the shift in resources, this is might increase competition with bobcats and fisher. Further, lynx occurrence at the regional scale in the Northeastern USA is strongly influenced by annual snowfall (Hoving et al. 2005), and it has been suggested that lynx distribution is likely to contract northward in some areas if temperatures increase and annual snowfall declines in the future as a result of climate change (U.S. Department of Interior 2008). Under those conditions, bobcat and fisher distributions might also be expected to expand northward, which could also increase competition and thereby exacerbate the negative effects of habitat loss and climate change on the lynx population in northern Maine.

CONSERVATION AND MANAGEMENT IMPLICATIONS

This study indicates that timber harvesting can create favorable conditions for both snowshoe hares and lynx in northern Maine. However, it is important to remember that the broad-scale increase in lynx foraging habitat within the study area was an unplanned byproduct of the preemptive and salvage logging that occurred as a

consequence of the last spruce budworm outbreak, which also lead to the loss of 31% of the mature conifer leading up to the implementation of the Maine Forest Practices Act (MFPA). The change in harvesting patterns that resulted from the MFPA will mean that lynx foraging habitat is not likely to continue to increase as it did 1985-2004. Projections suggest that the quantity of habitat could remain relatively stable in the study area 2007-2022; however, this potential outcome is predicated on the assumption that the rate of stand thinning in HQHH does not increase. The recent increase 2004-2007 in stand thinning warrants future attention, particularly because the actual magnitude of loss is underestimated by the methods used here. Further, recent increases in the rate of harvest of the remaining mature conifer in the study area warrants future consideration because of the synergistic role that this forest type plays by positively influencing lynx POC, and because only 50% of the mature conifer forest that was present in the study area ca. 1975 remained in 2007.

In 2007 only a few townships were estimated to support adult lynx densities of >4 lynx/100km^2; nonetheless, these estimated densities along with previous research (Vashon et al. 2008a) suggest that habitat in Maine can potentially support lynx densities that are similar to more northerly lynx populations (i.e., <49º N) (Brand et al. 1976, Parker et al. 1983, O'Donoghue et al. 1997). However, the spatial distribution of HQHH is certain to change over the next 15 years, which may result in increased competition with bobcats and fisher. Future habitat management to maintain lynx populations in Maine will require coordination across many of Maine's private forestland owners to effectively address both habitat supply and habitat connectivity. Areas targeted for lynx conservation should be located in areas that provide favorable habitat conditions for lynx

and are likely to provide future HQHH. Forest management should emphasize even-aged management and silvicultural techniques that promote high conifer stem densities (Robinson 2006). Precommerical thinning should be avoided as a strategy for accelerating stand development in lynx management areas unless sufficient habitat is otherwise available. Commercial thinning of older regenerating forest (>35 years old) may be less detrimental to landscape-scale hare densities than precommerical thinning if it occurs after hare densities have already started to decline because of succession-induced reductions in cover and/or forage. Additional study is needed to help better understand the temporal pattern of snowshoe hare density in HQHH in the Acadian Forest.

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CHAPTER 4

INFLUENCE OF ALTERNATIVE MANAGEMENT STRATEGIES ON LANDSCAPE-SCALE TIMBER HARVESTING PATTERNS AND FUTURE (2007-2032) HABITAT SUPPLY FOR CANADA LYNX AND AMERICAN MARTENS

ABSTRACT

Umbrella species have been proposed as a single-species approach that can be used for simplifying biodiversity conservation for land and wildlife mangers, which are expected to address the impacts of land-use activities on numerous species. Two species that have shown great potential as umbrella species in the Acadian forest of the Northeastern U.S. are the American marten (*Martes americana*) and Canada lynx (*Lynx canadensis*). Regional habitat conditions for martens and lynx have changed significantly in Maine over the last 30-40 years as a result of broad-scale forest management. The goal of my research was to provide a better understanding of how past forest management legacy will influence the outcomes associated with future forest management, and to help identify conservation planning alternatives for these important umbrella species and the species that they represent. I used the Remsoft Spatial Planning System to develop alternative forest management scenarios. Scenarios were compared based on projected timber volume harvested and projected habitat supply and population density for lynx and martens over the next 25 years across 1,215 km^2 of commercial forestlands. Forest management scenarios were developed to simulate relatively realistic forest practices and patterns and the effects of specific modifications to management plans, including changes in aspatial and spatial constraints on clearcut harvesting. Allocation of harvest to different

silvicultural treatments and total acreage harvested varied between scenarios, which had important implications for habitat supply and densities for lynx and martens. The scenario that benefited lynx and martens the least 2007-2032 was the baseline scenario, which projected recent (2001-2007) trends in harvest rates including an aspatial limit (~4% of the total acreage harvested) on clearcut harvesting to mimic existing patterns and effects of current regulations on forest management. The scenario that provided some benefit to both species projected recent harvest trends but removed the limit on clearcutting. Marten habitat was benefited by a reduction in total acreage harvested and acreage partially harvested; lynx foraging habitat increased in latter periods as a result of the additional regenerating forest that was created by increased clearcut harvesting under this scenario. Increasing the maximum allowable size for clearcuts had little effect on total acreage harvested or habitat supply. Under the strategic management objective to maximize sustainable volume, habitat supply for lynx was benefited but habitat supply for martens declined more drastically than under other scenarios. Habitat supply for martens is only expected to increase significantly if timber harvesting were to stop altogether. Overall, modifications to forest management plans caused relatively little change in the trajectory of habitat supply for lynx or martens and both habitats are expected to decline over the next 5-20 years as a result of past forest management legacy (1970-2007). This suggests that delisting criteria for the federally-threatened lynx need to incorporate the anticipated loss of habitat supply for lynx, and that marten harvest management needs to be reconsidered to avoid threatening a population that is likely to experience continued habitat loss in the future.

INTRODUCTION

There is a growing need among land and wildlife managers for tools to quantitatively assess effects of land-use decisions on habitats. Regulations are often designed to protect species at risk from localized habitat destruction caused by specific land uses, but managing for sustainability and connectivity of habitat for those species and protecting biodiversity at larger scales continues to be an unmet challenge. Forecasting changes in wildlife habitat is an increasingly important objective of the forest-management planning process, relying on species-habitat relationships as a fine-filter strategy to measure the effects of land use activities. Thus, spatial forest planning models are emerging as an essential tool for developing management plans to meet multiple natural resource goals (Kurttila 2001, Bettinger and Sessions 2003, Bettinger et al. 2003). Progress has begun on developing algorithm-derived forest management plans that consider spatial as well as aspatial habitat goals. However, much research attempting to evaluate the effects of alternative resource-use strategies (e.g., Bettinger et al. 1997, Bettinger et al. 1998, Kliskey et al. 1999, Marzluff et al. 2002) has focused on relatively small scales (but see Brown et al. 2007). Consequently, it remains important to better understand how tactical forest management decisions may scale-up and influence large-scale landscape pattern (Wickham et al. 2007) and the resulting spatiotemporal variation in wildlife habitats.

Spatial forest planning differs from conventional planning because the spatial patterns of management activities are explicitly integrated into the otherwise temporal (e.g., optimizing timber yield) decision-making process (Baskent and Keles 2005). Research evaluating large-scale (e.g., >50, 000 ha) effects of forest harvest planning on

landscape pattern (Mehta et al. 2004, Gustafson et al. 2006, Radeloff et al. 2006, Zollner et al. 2008) and wildlife habitat suitability (Larson et al. 2004, Shifley et al. 2006) has not yet utilized spatial forest planning models; rather, this research has been based on stochastic simulation generally using the program LANDIS (Mladenoff et al. 1996, Mladenoff and He 1999, Gustafson et al. 2000). A shortcoming of LANDIS, however, is that it is not designed to develop operational forest management plans (Gustafson et al. 2000, Mladenoff 2004), and recent research has indicated that the program should not be used to develop spatially-explicit forest management plans (Radeloff et al. 2006). The stochastic nature of LANDIS also limits its utility for addressing the effects of forest management on species that are influenced not only by habitat amount, but also by the spatial and temporal arrangement of habitat patches (Bissonette et al. 1989, Thompson and Harestad 1994). Forest management guidelines generally address habitat requirements for species by invoking spatial constraints on harvests (e.g., adjacency and green-up). Considerable effort has been directed to develop algorithms that can optimize tactical harvesting plans under these types of constraints, including mathematical optimization techniques (e.g., mixed integer programming) and heuristic approaches (e.g., simulated annealing). A number of heuristic techniques have been applied to forest planning with objectives to maintain habitat for single species, including elk (*Cervus elaphus roosevelti*) (Bettinger et al. 1997, 1999), red-cockaded woodpecker (*Picoides borealis*) (Boston and Bettinger 2001), northern flying squirrel (*Glaucomys sabrinus*) (Calkin et al. 2002), spotted owl (*Strix occidentalis*) (Bettinger et al. 2003), and woodland caribou (*Rangifer tarandus caribou*) (Brown et al. 2007). Land and wildlife managers are, however, expected to monitor and manage the environmental impacts of

management activities on numerous species in order to address the risks to terrestrial biodiversity from landscape change, which limits the utility of spatial forest planning based on separate simultaneous applications directed at single species.

Umbrella species have been proposed as a single-species approach that can be used for simplifying biodiversity conservation through focusing on protecting the minimum habitat requirements of species whose protection should also maintain the viability of an array of other species with similar habitat associations (Murphy and Wilcox 1986, Noss 1990). Although species as diverse as Bay checkerspot butterflies (*Euphydryas editha bayensis*; Launer and Murphy 1995) and black rhinos (*Diceros bicornis*; Berger 1997) have been evaluated as umbrella species, medium and large sized terrestrial carnivores are often proposed because they tend to have large spatial requirements and are often closely associated with a particular habitat type (Noss 1996). Two species that have shown great potential as umbrella species for conservation planning in the Acadian forest of the Northeastern U.S. are the American marten (*Martes americana*) and the Canada lynx (*Lynx canadensis*) (Hepinstall and Harrison *In preparation*). Because the two species have different habitat associations, early- and mid-to-late successional forests respectively, they also represent complementary groups of species for which they can serve as umbrella species (Lambeck 1997). In an analysis of 130 resident forest vertebrates Hepinstall and Harrison (*In preparation*) showed that 86% could be benefited by conservation planning on Maine's commercial forestlands for lynx and martens. Regional habitat conditions for martens (Chapter 1) and lynx (Chapter 3) have changed significantly in Maine over the last 30-40 years as timber harvest rates and patterns have been influenced by both past natural disturbance events and changes in

forest policy (see Chapter 1). In the 1970s and 1980s, clearcut harvesting increased as large areas of spruce-fir forest were preemptively and salvage harvested in response to the 1973-1985 spruce budworm (*Choristoneura fumiferana*) outbreak. In 1989, the Maine Forest Practices Act (MFPA) was passed (12 MRSA §8867-A to §8888 & MFS Rules Chapter 20), which increased regulatory standards and requirements associated with clearcut harvesting. In the first year following the MFPA, the number of acres annually harvested by clearcut declined by 36% and the number of total acres harvested increased 19%, and habitat conditions for martens and lynx changed significantly over a relatively short period of time (Chapters 1 and 3). Thus, broad-scale conservation planning is needed to ensure continued habitat supply for those important umbrella species.

Since the late 1990s, approximately 500,000 acres of commercial forestland have been harvested annually (Maine Forest Service 1994, 1997, 2003, 2006) over the ~17 million acres of commercial forestland in Maine and forest management has increasingly come to rely on a variety of partial harvest treatments that result in a wide range of residual forest conditions (Robinson 2006). The goal of my research was to evaluate the effects of forest management strategies on habitat supply for lynx and martens in this complex landscape to provide a better understanding of past forest management legacy on outcomes of future forest management and conservation planning alternatives. Recently, systems based on hierarchical spatial forest-management planning have been developed that take advantage of the processing strengths of both linear programming and heuristic techniques to create an optimized spatial forest-management plan that can incorporate spatial constraints (Boston and Bettinger 2001, Bettinger et al 2005). The objectives of this study were to: 1) design and generate a forest stand map using satellite

and forest inventory information that could successfully model the outcomes of forest management using a hierarchical spatial forest-planning system; 2) model a set of alternative forest management scenarios that would simulate realistic timber harvesting rates and patterns under aspatial and spatial constraints; 3) compare the broad-scale outcomes of alternative forest management scenarios on timber harvesting rates and patterns, and on current and future habitat supply for lynx and martens; and 4) evaluate the interaction between past legacy and future forest management on outcomes of alternative management scenarios.

STUDY AREA

The 1,215 km^2 study area was defined within the geographic ranges of American marten and Canada lynx (Figure 4.1). This area occurs within the Acadian forest ecoregion, which is an ecological transition zone in the northeastern U.S.A. between the southern temperate deciduous-dominated forests and the northern boreal forests (Seymour and Hunter 1992). This area includes 14 unorganized townships in northern Maine that comprise 21 individual parcels owned by nine forestland owners, including the state on Maine. The study area includes approximately 129,454 ha of commercial forestland and commonly occurring tree species include: balsam fir (*Abies balsamea*), white (*Picea glauca*), red (*P. rubens*), and black (*P. mariana*) spruce, white pine (*Pinus strobus*), white (*Betula papyrifera*) and yellow (*B. alleghaniensis*) birch, red (*Acer rubrum*) and sugar (*A. saccharum*) maple, and American beech (*Fagus grandifolia*). Forest harvesting is the primary form of forest disturbance within this area and forest harvesting practices are regulated under the Maine Forest Practices Act (12 MRSA

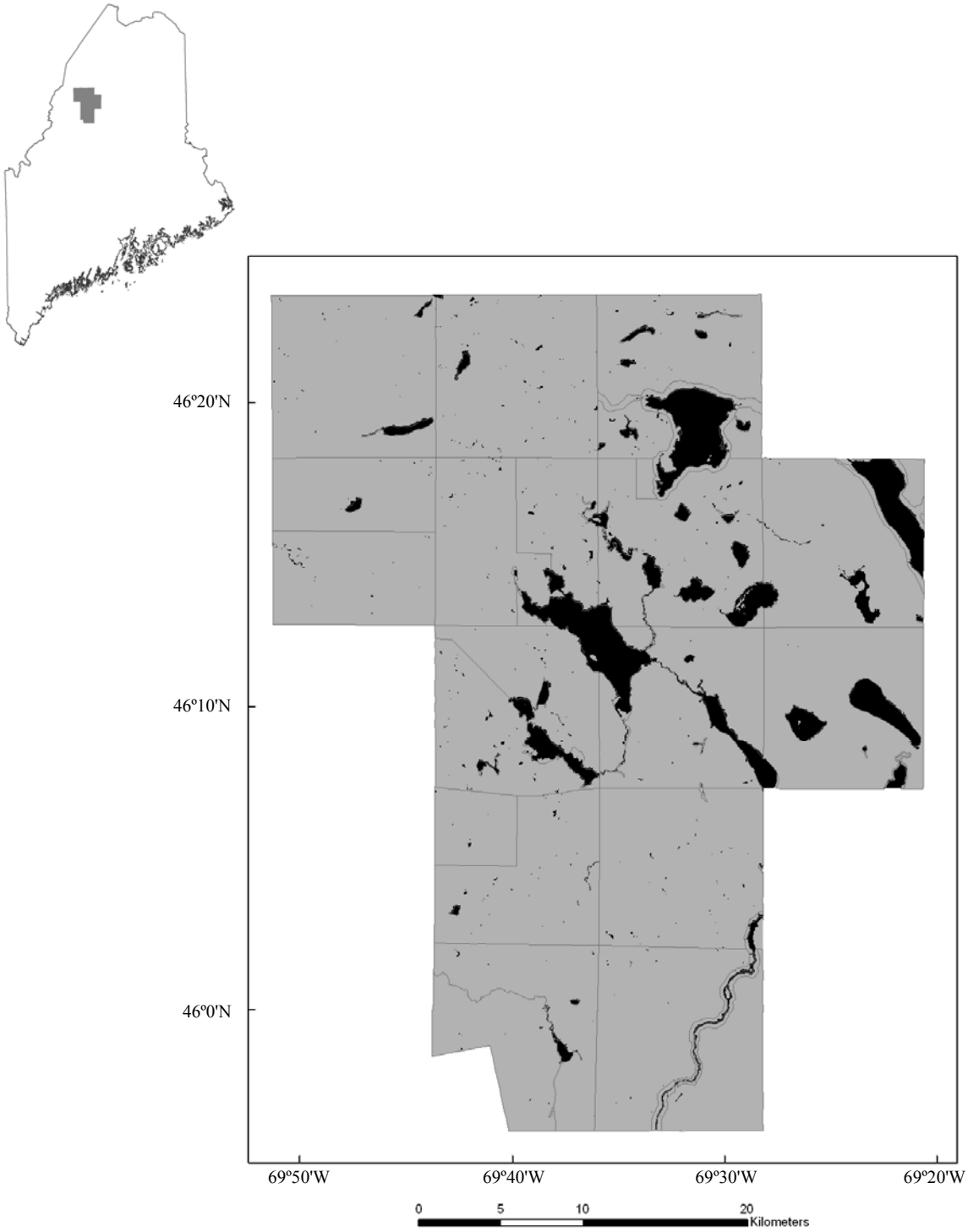

Figure 4.1. The 14 township study area (shown in gray) was located in northwestern Maine. This area included approximately 129,454 ha of commercial forestland divided among 21 parcels owned by nine forestland entities.

§8867-A to §8888 & MFS Rules Chapter 20). Elevation is generally low (average = 369 m) and varies relatively little across the study area (range = 282 - 731 m).

METHODS

Overview

I used the Remsoft Spatial Planning System to develop alternative forest management scenarios to simulate timber harvesting activities and resulting habitat supply for lynx and martens. Scenarios were designed to simulate realistic forest harvesting practices and patterns in northern Maine, which were then modified through changes to either aspatial (e.g., proportion of annual total harvest by clearcut) or spatial harvest constraints (e.g., clearcut harvest size). Trends in habitat supply and potential population densities within the study area were determined based on predictive species occurrence models developed as part of previous companion studies evaluating lynx (Chapter 2) and marten (Hepinstall et al. *In preparation*) landscape-scale occurrence (2nd-order habitat selection; *sensu* Johnson 1980) in northern Maine. The effects of both harvest legacy (1970-2007) and future forest management (2007-2032) on habitat supply were evaluated at the scale of the study area and at the scale of the ownership parcel.

Marten habitat suitability

Hepinstall et al. (*In Preparation*) developed resource selection probability functions (RSPFs; Manly et al. 2002) to evaluate the effects of habitat amount and habitat configuration on the landscape-scale occurrence of male and female martens on commercial forestlands in north-central Maine. Location data from radio-collared adult, resident male (n=25) and female (n=35) martens collected between 1994 and 1998 (May - October) (Katnik 1992, Phillips 1994, Chapin et al. 1998, Phillips et al. 1998, Payer

1999, Fuller and Harrison 2005) were used to generate annual home ranges (95% minimum convex polygon). The Maine GAP Vegetation and Land Cover map (MEGAP) served as the base map for developing year-specific habitat maps that captured habitat change caused by timber harvesting activities 1994-1998. At the patch-scale, suitable habitat for marten was defined *a priori* based on the results of previous studies in Maine (Chapin et al. 1998, Payer 1999, Payer and Harrison 2003, Fuller and Harrison 2005) as patches of forest ≥2.7 ha with tree height >6 m. According to the MEGAP, approximately 89% of the study area was comprised of mature forest ca. 1993 that was mapped with >94% accuracy (Hepinstall et al. 1999). Habitat maps were used to calculate landscape metrics for occupied marten home ranges (n=121) and simulated unoccupied home ranges areas (n=86) selected based on previous studies in Maine (Katnik 1992, Chapin et al. 1998) and elsewhere (Hargis et al. 1999). Metrics were then used to construct *a priori* candidate models which were evaluated separately for male and female martens using model selection criteria based on the corrected Akaike's Information Criterion (AIC_c; Burnham and Anderson 1998) to rank binary logistic regression model performance. Models were evaluated with reserved test data (n=66) based on standard error matrix statistics and receiver operating characteristic (ROC) curves.

The top-ranked models for both females and males included measures of habitat amount and habitat configuration (Tables 4.1 and 4.2). In both cases, probability of marten occurrence was positively influenced by the amount of habitat and negatively influenced by an increase in configuration metric at low to intermediate values of habitat amount. The top-ranked model for predicting female marten occurrence (Table 4.1)

Table 4.1. Parameter estimates and associated odds ratios for the top-ranking model for female martens (Hepinstall et al. *In preparation*). This model included the predictor variables: percent suitable habitat in home range (PHR), suitable habitat patch density (PD), and the interaction (PHR*PD).

Parameter	**Estimate**	**95% Lower**	**95% Upper**	**Odds Ratio**
Constant	0.113	-4.927	5.153	
PHR	-0.001	-0.066	0.064	0.999
PD	-7.558	-14.742	-0.374	0.001
PHR*PD	0.111	0.008	0.213	1.117

Table 4.2. Parameter estimates and associated odds ratios for the top-ranking model for male martens (Hepinstall et al. *In preparation*). This model included the predictor variables: percent suitable habitat in home range (PHR), landscape shape index (LSI), and the interaction (PHR*LSI).

Parameter	**Estimate**	**95% Lower**	**95% Upper**	**Odds Ratio**
Constant	-25.835	-54.253	2.583	
PHR	0.187	-0.061	0.436	1.206
LSI	-0.867	-3.769	2.035	0.420
PHR*LSI	0.073	0.006	0.140	1.076

included: the proportion of suitable habitat within home range (PHR), suitable habitat patch density (PD), and the interaction term (PHR*PD). Hosmer-Lemeshow statistic value (0.28) and McFadden's rho-squared (0.403) for this model suggested that the data fit the logistic regression model and that the variables included in the top model explained a high proportion of variability in the data. This model received 45% of the weight of evidence (w_i = 0.45) and no candidate model had a $\Delta AIC_c \leq 2$ relative to the top model. The area under the ROC curve (AUC) for this model based on independent validation was 0.94, suggesting that there is an 94% probability that an occupied female home range will have a higher PHR and lower PD than an unoccupied home range. The top-ranked model for predicting male marten occurrence (Table 4.2) included: the proportion of suitable habitat within home range (PHR), landscape shape index (LSI) of suitable habitat patches, and the interaction term (PHR*LSI). Hosmer-Lemeshow statistic value (0.55) and McFadden's rho-squared (0.810) for this model suggested that data closely fit the logistic regression model and that the variables included in the top model explained a high proportion of variability in the data. This model received 66% of the weight of evidence (w_i = 0.66) and only one candidate model had a $\Delta AIC_c \leq 2$ relative to the top model (ΔAIC_c = 1.5). The AUC for this model based on independent validation was 0.89, suggesting that there is an 89% probability that an occupied male home range will have a higher PHR and lower LSI than an unoccupied home range. Results highlight the important role suitable habitat amount appears to play in marten occurrence, which has been previously noted (Katnik 1992, Chapin et al. 1998, Hargis et al. 1999).

Lynx habitat suitability

A similar process was used to develop a RSPF for predicting landscape-scale occurrence of lynx in northern Maine based on forest structure (Chapter 2). Location data was based on snow track surveys (January-March) conducted by the Maine Department of Inland Fisheries and Wildlife (MDIFW) 2003-2006. Snow track surveys were conducted to establish the status of the lynx population in Maine (Vashon et al. 2003) and were targeted at a stratified-random sample of unorganized townships based on the predicted probability of lynx occurrence (low, medium, high) using the model results of Hoving et al. (2004). All survey routes and the locations of lynx track crossings were recorded with a GPS. Surveyed areas were only included in subsequent analyses if a minimum survey intensity of 0.55 km/km^2, which MDIFW identified as the minimum required to detect a resident lynx (MDIFW *unpublished data*). Simulated occupied (n=18) and unoccupied (n=25) home ranges were randomly located based on the lynx tracks recorded during the surveys. Unoccupied home ranges were located in surveyed areas with 1) no lynx detections and 2) equal to or greater than the minimum survey distance traversed within the occupied home ranges (i.e., 0.24 km/km^2). The habitat map used in the lynx modeling analysis was developed as an update to the MEGAP following the methods of Sader and Legaard (2008). Forest harvest 1970-2004 and 2004 forest overstory composition data were generated using Landsat satellite imagery in a companion study (Legaard et al., Maine Image Analysis Laboratory, University of Maine, *In preparation*) and combined with MEGAP in order to derive a ca. 2004 forest cover type map reflecting both harvest history, age structure, and current overstory composition (Chapter 2). Habitat-based predictor variables and *a priori* candidate models

were chosen to evaluate the alternative hypotheses that 2nd-order habitat selection by lynx was based on: 1) home range composition, 2) landscape-scale hare density, 3) landscape-scale hare density and home range composition, 4) landscape-scale hare density and habitat configuration, and 5) habitat configuration (Chapter 2). Analyses were again based on binary logistic regression and models were ranked using AIC_c.

The probability of lynx occurrence showed a strong positive association to both mean hare density and percent of mature conifer forest at the scale of a lynx home range (Table 4.3). The top-ranked candidate model received 59% of the weight of evidence (w_i = 0.59) and included the predictor variables: mean landscape-scale hare density (HARES), percent of mature conifer (C), and the interaction (HARES*C). Hosmer-Lemeshow statistic (0.89) and McFadden's rho-squared (0.272) suggested that the data fit the binary logistic regression model and that the variables included in the top model explained a high proportion of variability in the data. No candidate model had a $\Delta AIC_c \leq 2$ relative to the top model. The AUC for this model based on the leave-one-out cross-validation method was 0.69, suggesting that there is an 69% probability that an occupied home range will have a higher mean hare density and percentage of mature conifer than an unoccupied home range.

Spatial forest management planning

Developing a spatially-feasible harvest plan was a primary objective; therefore, I used the spatial forest planning system developed based on the work of Jaminick and Walters (1993) to model the outcomes of the alternative forest management scenarios. The Remsoft Spatial Planning System includes an integrated set of programs that utilize a hierarchical solution approach to timber harvest planning, and which support both

Table 4.3. Parameter estimates and associated odds ratios for the top-ranking model for predicting occurrence or non-occurrence of lynx (Chapter 2). Model included the predictor variables: mean snowshoe hare at the lynx home-range scale (HARES), the percent of mature conifer at the lynx home-range scale (C), and the interaction between these two variables (HARES*C).

Parameter	**Estimate**	**95% Lower**	**95% Upper**	**Odds Ratio**
Constant	-1.268	-5.545	3.010	
HARES	-1.271	-7.880	5.337	0.280
C	-0.378	-0.930	0.173	0.685
HARES*C	0.926	-0.025	1.877	2.525

[a] Candidate predictor variables were derived from a combination of timber harvest data used to map stand-level harvest operations 1970-2004 (Legaard et al., Maine Image Analysis Laboratory, University of Maine, Orono *In preparation*) and a 2004 forest cover type map (Chapter 2).
[b] Mean snowshoe hare density was included as a candidate variable to evaluate the cumulative effect of home-range composition on prey density and lynx occurrence. Values for occupied and unoccupied home ranges were calculated by applying stand-scale hare densities (Table 3.1; Chapter 3) to forest types identified by harvest history and 2004 composition.
[b] Percent mature conifer was included as a candidate variable because of the important role that this forest type appears to play in supporting lynx populations in some areas of the boreal forest (e.g., Murray et al. 1994, Poole et al. 1996). Variable was defined as "mature" based on the timber harvest data (i.e., uncut since 1970).

strategic forest planning (Woodstock) and tactical harvest-block scheduling and layout (Stanley). Woodstock uses a stratum-based linear programming (LP) approach to first find an optimal solution for the long-term harvest scheduling problem based on the strategic objective and subject to aspatial constraints (e.g., harvest even flow) (Remsoft Inc. 1999). Stanley then uses the LP solution to guide stand blocking and harvest allocation using a Monte Carlo integer programming (MCIP) algorithm subject to spatial constraints, including adjacency delay and maximum harvest block size (Remsoft Inc. 2000).

Stanley requires a stand boundary map and in order to use a common classification scheme that could be applied to all ownerships included in the study area. I used forest harvest (Legaard et al., Maine Image Analysis Laboratory, University of Maine, *In preparation*) and composition information provided by satellite imagery to derive the initial stand map. Forest harvest data were generated from multi-temporal Landsat satellite imagery spanning the time period 1988-2007 based on the Normalized Difference Moisture Index (NDMI) and for 1973-1988 based on the Normalized Difference Vegetation Index (NDVI). Areas of biomass reduction created by timber harvesting activities 1988-2007 were classified into two classes ('light' and 'heavy') based on the magnitude of NDMI change (Legaard et al., Maine Image Analysis Laboratory, University of Maine, *In preparation*). *Light* harvest entries were interpreted as partial harvests or tending operations of the current mature growing stock, and *heavy* harvest entries were interpreted as stand-replacing or regeneration harvests. Only *heavy* harvest entries were mapped 1973-1988, which coincided with the spruce budworm salvage era when even-aged management and clearcut harvests predominated in the

spruce-fir forest. Generalized forest composition information was provided by the MEGAP for areas where no harvest occurred 1973-2004, and an unsupervised classification of a 2004 Landsat satellite image for harvested areas. Forested areas ca. 2004 were categorized as 'softwood', 'mixed', or 'hardwood' unless recently disturbed by forest harvesting; these areas were assigned to a 'disturbed' class.

Forest harvest and composition data were spatially combined and stands were delineated based on contiguous pixels of a common harvest history and composition. I then summarized Forest Inventory and Analysis (FIA) field data (United States Department of Agriculture Forest Service 2007) for the plots that overlapped with the Landsat satellite imagery used to map forest change (Legaard et al., Maine Image Analysis Laboratory, University of Maine, *In preparation*) to derive the frequency distributions of forest area by size class (seedling, sapling, poletimber, sawtimber), stocking density (relative no. of trees per acre), and age for forest >40 years stratified by dominant cover type. I used these distributions to populate initial forest conditions for uncut and *light* harvest stands as a spatially-random process. For regenerating stands resulting from *heavy* harvests, size class and stocking density frequency distributions by site quality were derived using the Forest Vegetation Simulator (FVS) (United States Department of Agriculture Forest Service 2002) and FIA plot data for the same overlapping region. Minimum stand age ca. 2007 was estimated based on the number of years elapsed since the *heavy* harvest event and I used the frequency distributions to populate initial forest conditions for regenerating stands by age. Because elevation varies little across the study area, stand-level site quality was indexed based on slope calculated using a 30m Digital Elevation Model (DEM). Thus, initial conditions for stands within

the study area associated with size class, stocking density, and age (in the case of mature forest) matched the distributions associated with the FIA field data, but the spatial patterning was random. It is important to note that, although the accuracy of the uncut forest is expected to be high (>89%), because there is no harvest information prior to 1970 there is a potential for some degree of commission error associated with the assumption that all uncut and *light* harvest stands are >40 years old. Thus, estimates of the amount of forest area with mature forest conditions and regenerating forest conditions should be considered an overestimate and an underestimate, respectively. As a final step, I intersected the derived stand map with a 2007 parcel ownership map. Stand size ranged between a minimum of 2 ha to a maximum of 250 ha.

Over the planning horizon, Stanley models stand-level forest dynamics based on initial stand conditions and user-defined rules of harvest effects and stand development. Harvests are applied to entire stands and stand eligibility for harvest is also user-defined and differs by stand conditions and structural attributes such as basal area (BA). FIA data was also used to guide estimates of initial forest structure and to project residual stand attributes post-harvest. During the blocking phase, a forest stand eligible for harvest is chosen as a "seed" at random. Neighboring stands are then examined to determine if any are also eligible for harvest, and if so are aggregated with the seed stand to form a potential harvest block. This process continues until no more eligible neighbors are found or the maximum harvest block size is reached. If the potential block exceeds the minimum block size it is assigned a block number, a harvest period, and the harvest treatment. The algorithm continues until Woodstock's LP solution has been fully allocated or an acceptable percentage of output targets have been achieved. Stanley

produces a new map that incorporates harvest activity and growth during each operational period (5-years).

Simulation scenarios

My approach for developing scenarios first simulated realistic forest practices and patterns and then modified the forest management plan to enhance understanding of the effects of a set of specific alternatives on wildlife habitat relative to a benchmark based on current harvesting trends and patterns. The strategic objective for all harvest scenarios was to maximize volume subject to even-flow harvest and ending inventory constraints while maintaining 95% growing stock over a 100-year planning horizon. The baseline scenario (BASE; Table 4.4) was designed to project recent ownership-level harvest rate trends (2001-2007) and the effects of current forestry regulations (12 MRSA §8867-A to §8888 & MFS Rules Chapter 20) on overall harvesting patterns across commercial forestlands while still maintaining the overall strategic objective. Ownership-level, annual harvest rates for *heavy* and *light* harvests (area harvested/yr) were estimated based on the satellite-derived forest harvest data (Legaard et al., Maine Image Analysis Laboratory, University of Maine, *In preparation*) and were used to proportionally allocate acreage by harvest types to parcels. Additionally, the proportion of the total harvest implemented by clearcut was aspatially constrained to approximately 4% (+/-2%) to mimic the current proportion reported by Maine's forestland owners (Maine Forest Service 2003, 2005, 2007). In the remainder of the scenarios I removed the aspatial constraint on clearcut harvesting, which was the only modification to the BASECC scenario. The MAX scenario simply followed the strategic objective, without incorporating recent harvesting trends. In the BASECC500 and MAX500 scenarios, the

Table 4.4. Alternative forest management scenarios used to enhance understanding of the potential effects of annual harvest rate, regulation of clearcut size, and proportion of annual acreage harvested by clearcut on future habitat supply and potential population densities of martens and lynx.

Scenario	Harvesting strategy[a]	Max. clearcut[c] size (ac)	Limit clearcut harvesting[d]
BASE	continue recent trends[b]	250	Yes
BASECC	continue recent trends	250	No
MAX	maximize sustainable	250	No
BASECC500	continue recent trends	500	No
MAX500	maximize sustainable	500	No
NOHRV	NA	NA	NA

[a] The strategic objective for all harvest scenarios was to maximize volume subject to even-flow harvest and ending inventory constraints while maintaining 95% growing stock over a 100-year planning horizon.
[b] 'Continue recent trends' projected recent (2001-2007) trends for *heavy* and *light* harvesting rates per ownership, while still maintaining the overall strategic objective.
[c] A clearcut in Maine based on current forestry regulations (12 MRSA §8867-A to §8888 & MFS Rules Chapter 20) is defined as "any timber harvesting on a forested site greater than 5 acres in size that results in a residual basal area of trees over 4 1/2 inches in diameter measured at 4 1/2 feet above the ground of less than 30 square feet per acre." Current maximum harvest block size for clearcuts is 250 ac.
[d] The proportion of the interval harvest allocated to clearcut harvesting limited to 4% (±1-2%) based on landowner reports of annual harvest activities (Maine Forest Service 1994, 1998, 2004).

allowable clearcut size was increased from 250 ac to 500 ac to evaluate the effect that increase in regulatory size limit might have on future habitat conditions. Finally, a final no harvest scenario was included (NOHRV; Table 4.4) to simulate effects of immediate cessation of all timber harvesting activities.

All harvest scenarios shared several characteristics. Harvests were applied to entire stands and annual harvest rates were used to guide the acreage harvested in each period across 6 silvicultural treatments: 1) clearcutting; 2) shelterwood harvesting (establishment); 3) uneven-aged management; 4) overstory removal (OSR); and 5) partial harvesting. *Heavy* harvests included clearcutting, shelterwood harvesting, and OSRs. *Light* harvests included uneven-aged management and partial harvesting. Clearcut harvest blocks were considered adjacent if they were within 250 feet of one another; blocks were subject to a 10-year green up delay, and a minimum acceptable block size of 5 acres. The harvested area at the ownership-level was not held rigidly constant between periods but was allowed to fluctuate +/- 20% of the average to provide greater opportunity to achieve optimized solutions.

Analysis of model outputs

Woodstock software was used to derive aspatial estimates of volume and acreage harvest over the planning horizon, and forest management plans for each alternative scenario were created for 25 years into the future (5 five-year periods) using Stanley software. Spatially-optimized harvest block layouts were output at the end of each period. I compared the aspatial target volume identified by Woodstock with the spatial volume estimated based on the Stanley harvest block to determine the percent reduction associated with the addition of spatial constraints. I also calculated the total area

harvested and the area harvested by silvicultural treatment for each scenario from the spatially optimized harvest plans.

I calculated the total area of marten habitat and lynx foraging habitat in the study area (Figure 4.1) 2007-2032 and at the end of each 5-yr period to compare the effects of the alternative forest management scenarios on habitat amount. At the stand-scale, marten habitat was defined *a priori* based on previous research in Maine. Martens select habitats with complex structure, and research has suggested that the minimum threshold for a forest stand to become suitable habitat for adult, resident martens is 18 m^2/ha (80 ft^2/ac) basal area (BA) of live trees with mean height of 9 m (30 ft) for trees ≥7.6 cm (3 in) diameter at breast height (dbh) (Payer and Harrison 2003). To provide martens with sufficient cover, it has further been suggested that, in addition to maintaining ≥18 m^2/ha BA, >30% canopy closure also be maintained during summer and winter (Fuller and Harrison 2005). Thus, forest stands were only considered as marten habitat at the end of each 5-yr period if: BA was ≥18 m^2/ha and mean height was ≥30 ft for trees ≥7.6 cm dbh, and canopy closure was >30%. Finally, researchers in Maine concluded that martens only use forest stands ≥2.7 ha (6.7 ac) in size; so, only stands or groups of stands meeting the above criteria that were also ≥2.7 ha were included as marten habitat. Additionally, I calculated the amount of marten habitat 2007-2032 with the one additional criterion of mean stand dbh ≥15.24 cm (6 in). This was based on previous research that showed that the minimum stand dbh associated with mature, second-growth forest and partially harvested forest selected for by marten in Maine was ≥15 cm (Fuller et al. 2004, Fuller and Harrison 2005).

Additionally, I estimated the area of marten habitat and lynx foraging habitat 1970-2007 for the 14 townships using the habitat time series developed for martens (Chapter 1) and lynx (Chapter 3). Lynx foraging habitat was defined in the same way for both the retrospective (1970-2007) and prospective periods (2007-2032) as softwood or mixed regenerating forest (16-35 years old), which is the forest type that supports the highest snowshoe hare densities in northern Maine (Homyack et al. 2007, Robinson 2006, Fuller et al. 2007). Composition (softwood, mixed, hardwood) of regenerating forest ca. 2007 previously created by *heavy* harvest (1970-2007) was classified based on 2004 forest composition (see *Spatial forest management planning*). If regenerating forest was classified as 'disturbed' due to recent activity, I assumed that future stand composition for these areas would be determined by site index and so only included regenerating forest on medium and low quality sites as potential high-quality hare habitat. Composition of projected clearcuts (2007-2032) was based on a combination of mature forest composition prior to harvest and site quality.

The definition of marten habitat used in the current study was more rigorous than was used during model development (see *Marten habitat suitability*) or the development of the 1970-2007 habitat series (see Chapter 1), because neither analysis was able to consider BA or stand height classes >6 m (22 ft).Consequently, it was necessary to rescale the 1970-2007 habitat estimates for marten habitat to better match the estimated habitat amounts 2007-2032, which were based on the previously published threshold criteria (see above). To rescale the 1970-2007 habitat estimates, I first estimated the quantity of marten habitat ca. 2007 for the 14 townships based on the criteria used in the retrospective time series (e.g., 80,000 ha). I then calculated the quantity of marten habitat

ca. 2007 based on the more refined structural characteristics that were incorporated into the stand maps (see above *Spatial forest management planning*) (e.g., 50,000 ha). Finally, I compared the two values to determine the proportional difference in habitat quantity resulting from the refined criteria (e.g., (80,000-50,000)/80,000 = 37% reduction in habitat quantity). The difference was then applied to each of the habitat estimates 1970-2007 to scale these quantities to be more comparable to 2007-2032 quantities. Because subsequent analyses (see below) were only based on the 2007-2032 projections, the rescaling only affected graphical output used to illustrate the general habitat for the 14 townships 1970-2032.

I estimated the lynx and marten densities for the study area using the previously developed lynx (*Lynx habitat suitability*) and marten (*Marten habitat suitability*) RSPFs to evaluate the effects of harvest scenario on future density. At the end of every period, I generated each of the predictor variables included in the marten (Tables 4.1 and 4.2) and lynx (Table 4.3) RSPF. For this analysis I defined marten habitat using the ≥7.6 cm (3 in) dbh definition. I used the same hare density estimates associated with different forest types as were used in the development of the lynx RSPF (Table 2.2; Chapter 2). Conifer forest was considered "mature" ca. 2007 if it was left unharvested 1970-2007. As previously mentioned, because there was no harvest information prior to 1970 there is a potential for some degree of commission error associated with mature forest; thus, estimates of the quantity of mature conifer forest at the home-range scale for lynx should be considered an overestimate. Once the necessary predictor variables were generated, I applied the RSPF and used the resulting probability surfaces to estimate density (Manly et al. 2002). I used a fixed grid to calculate the mean probability value (x_{ij}) for each *i* grid

cell, the size of which was based on the estimated exclusive area occupied by an adult, resident animal. Grid sizes used in this analysis were previously estimated based on the spatial ecology of male and female martens (Chapter 1) and lynx (Chapter 2) in Maine. The mean probability calculated for a grid cell can be thought of as the likelihood (0.01 - 1.0) of an individual occupying grid *i* at time *j*. Grid values can then be summed (Manly et al. 2002) and divided by the total area of forestland (*A*) to estimate density (d), such that $d = \Sigma x_{ij}/A$. Finally, to evaluate the effects of the alternative forest management scenarios on habitat amount and density, I ranked the estimates of habitat quantity and densities of martens and lynx ca. 2032 across harvest scenarios.

Additional to evaluating the broad-scale and cumulative effects of the alternative forest management scenarios on future trends in habitat quantity and estimated densities of lynx and martens, I assessed the influence of past forest management legacy (1973-2007) on the outcomes of future forest management (2007-2032). I categorized the privately-owned parcels (n=21) within the study area into three classes of harvest legacy: >50% total acreage harvested occurred as *heavy* harvest 1973-1988 (n=6); >50% of total acreage harvested occurred as *light* harvest 1988-2007 (n=9); or 25-50% of total acreage harvested as *heavy* 1973-1988 and 25-50% of total acreage harvested as light 1988-2007 (n=6). I then calculated the percent change in marten and lynx habitat amount between 2007 and 2032 for each parcel. Variation in the percent change in marten and lynx habitat was compared across the legacy and scenario groups using repeated measures Analysis of Variance (ANOVA). Standardized residuals were checked to identify outliers and influential points, and to verify adherence to assumptions.

RESULTS

Strategic harvest planning using Woodstock resulted in aspatial harvesting targets of 143 to 180 million cubic feet of total volume from the study area 2007-2032. Per 5-year period harvest rates were 25 to 43 million cubic feet across the 5 harvest scenarios (Table 4.5). The targeted harvest volume increased in the BASECC scenario compared to benchmark scenario (BASE) as the 4% limit on the proportion of harvesting by clearcut was removed, and again in MAX scenario when the overall harvesting strategy was to maximize sustainable harvest without being constrained to follow recent trends. No difference was seen in the targeted volume of harvest for the BASECC500 or MAX500 scenarios when the allowable clearcut size was increased from 250 ac to 500 ac (Table 4.5). Greater than 78% of the target volume estimated by Woodstock was achieved by Stanley via the process of spatial optimization across all periods and scenarios (Table 4.5). An increase of 4-5% was observed in the allocated volume with an increase in the allowable clearcut size.

Average area harvested by the different silvicultural treatments used by Stanley varied greatly between the BASE, BASECC, and MAX harvest scenarios (Figure 4.2). The average area harvested per period was greatest in the BASE scenario and the majority of the harvesting occurred as shelterwood establishments or partial harvests as a result of the limits on clearcut size and extent. The average area harvested per period was approximately 18% less under the BASECC scenario with the removal of the limits on the proportion of the harvest by clearcut. This was accompanied by a greater than 6-fold increase in the area clearcut and an almost 5-fold decrease in the area harvested by shelterwood establishment. The area clearcut increased to an even greater degree when

Table 4.5. Aspatial target volume (ft^3) identified as sustainable harvest by Woodstock, and the total volume and proportion spatially allocated by Stanley during stand blocking and harvest allocation across 14 townships in northern Maine, 2001-2032.

	Period[a]	Target Volume[b]	Allocated Volume[c]	% Allocated
BASE	1	33,237,080.0	27,646,809.8	0.83
	2	26,657,060.7	24,732,623.6	0.93
	3	27,611,923.1	24,946,705.5	0.90
	4	28,288,848.6	24,092,485.0	0.85
	5	28,070,061.4	29,439,800.6	1.05
	Total	143,864,973.8	130,858,424.5	0.91
BASECC	1	35,182,513.0	30,378,527.0	0.86
	2	28,534,406.3	23,645,150.6	0.83
	3	29,234,252.8	23,848,323.4	0.82
	4	29,604,225.0	24,784,097.4	0.84
	5	29,506,646.6	28,606,939.9	0.97
	Total	152,062,043.7	131,263,038.2	0.86
MAX	1	42,931,633.2	35,237,206.9	0.82
	2	34,345,306.7	28,004,399.5	0.82
	3	34,345,306.6	27,547,275.9	0.80
	4	34,345,306.7	26,724,744.8	0.78
	5	34,345,306.7	28,033,710.0	0.82
	Total	180,312,859.9	145,547,337.1	0.81
BASECC500	1	35,182,513.1	30,769,979.6	0.87
	2	28,534,406.3	25,251,946.7	0.88
	3	29,234,252.8	27,092,313.7	0.93
	4	29,604,225.0	25,855,960.2	0.87
	5	29,506,646.6	29,572,994.3	1.00
	Total	152,062,043.7	138,543,194.4	0.91
MAX500	1	42,931,633.2	35,787,063.8	0.83
	2	34,345,306.7	30,079,478.2	0.88
	3	34,345,306.6	28,862,953.5	0.84
	4	34,345,306.7	28,314,093.3	0.82
	5	34,345,306.7	29,807,047.7	0.87
	Total	180,312,859.9	152,850,636.4	0.85

[a] Period 1 = 2007-2012; Period 2 = 2012-2017; Period 3 = 2017-2022; Period 4 = 2022-2027; Period 5 = 2027-2032.
[b] Target sustainable harvest volume identified by Woodstock.
[c] Total harvest volume spatially allocated to stands satisfying the spatial constraints associated with each of the future scenarios (See Table 4.4).

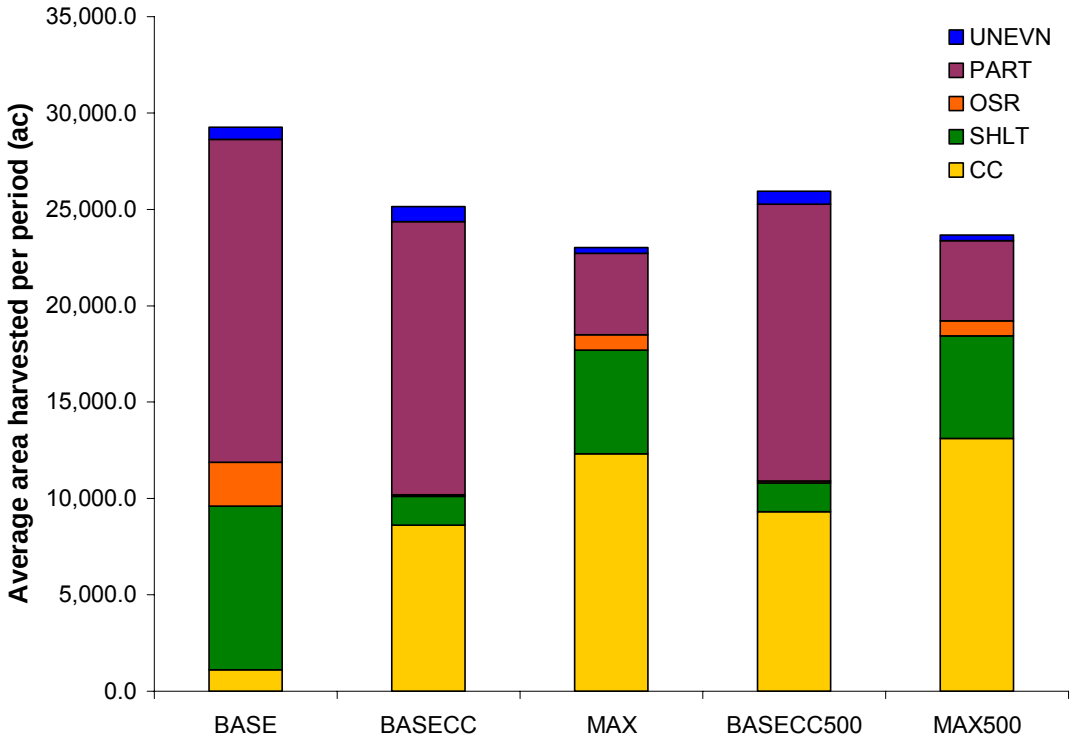

Figure 4.2. Average area harvested per period allocated to the different silvicultural treatments used by Stanley the harvest scenarios across 14 townships in northern Maine, 2002-2032. Treatments include uneven-aged management (UNEVN), partial harvest (PART), overstory removal (OSR), shelterwood establishment harvest (SHLT), and clearcut (CC).

the strategy was to maximize sustainable harvest (MAX), and was accompanied by a >65% decline in the partial harvest area. There was relatively little difference between BASECC and BASECC500 or between MAX and MAX500 in terms of area harvested per period or proportion of harvest by treatment; consequently, I focused on harvest scenarios BASE, BASECC, and MAX and the no harvest (NOHRV) scenario for the remainder of analyses.

Marten habitat decreased in the 14 townships by approximately 25,000 ha (30%), and lynx foraging habitat increased by approximately 18,000 ha (22%) during the 27 years preceding my projections (1970-2007; Figure 4.3). Temporal patterns associated with the projected changes in quantity of habitat for lynx and martens across the 14 townships were consistent among the three harvest scenarios from 2007-2032 (Figures 4.3 a-c). Quantity of future marten habitat was projected to decline slowly 2007-2022, but to remain between 55,000 and 60,000 ha. Slight increases (6-7%) were projected for martens 2022-2027. The 3 harvest scenarios resulted in slight differences in projected marten habitat 2017-2032, and ranged from increase (MAX; Figure 4.3c) to stabilizing (BASECC; Figure 4.3b) to a return to habitat decline (BASE; Figure 4.3a). Lynx foraging habitat was projected to remain relatively constant 2007-2012 at 21,000-23,000 ha under the three harvest scenarios (Figures 4.3 e-g), but is projected to decline substantially from 2012 to 2027. Projections of habitat quantity for lynx under the MAX scenario differed from the other two harvest scenarios 2027-2032, with lynx foraging habitat leveling off under the BASE and BASECC scenarios (Figures 4.3 a and b) but reversing to a slightly increasing trend for the MAX scenario (Figures 4.3c). Under the NOHRV scenario, marten habitat increased 4,938-9,544 ha (7-13%) in each 5-yr period 2007-2032, and

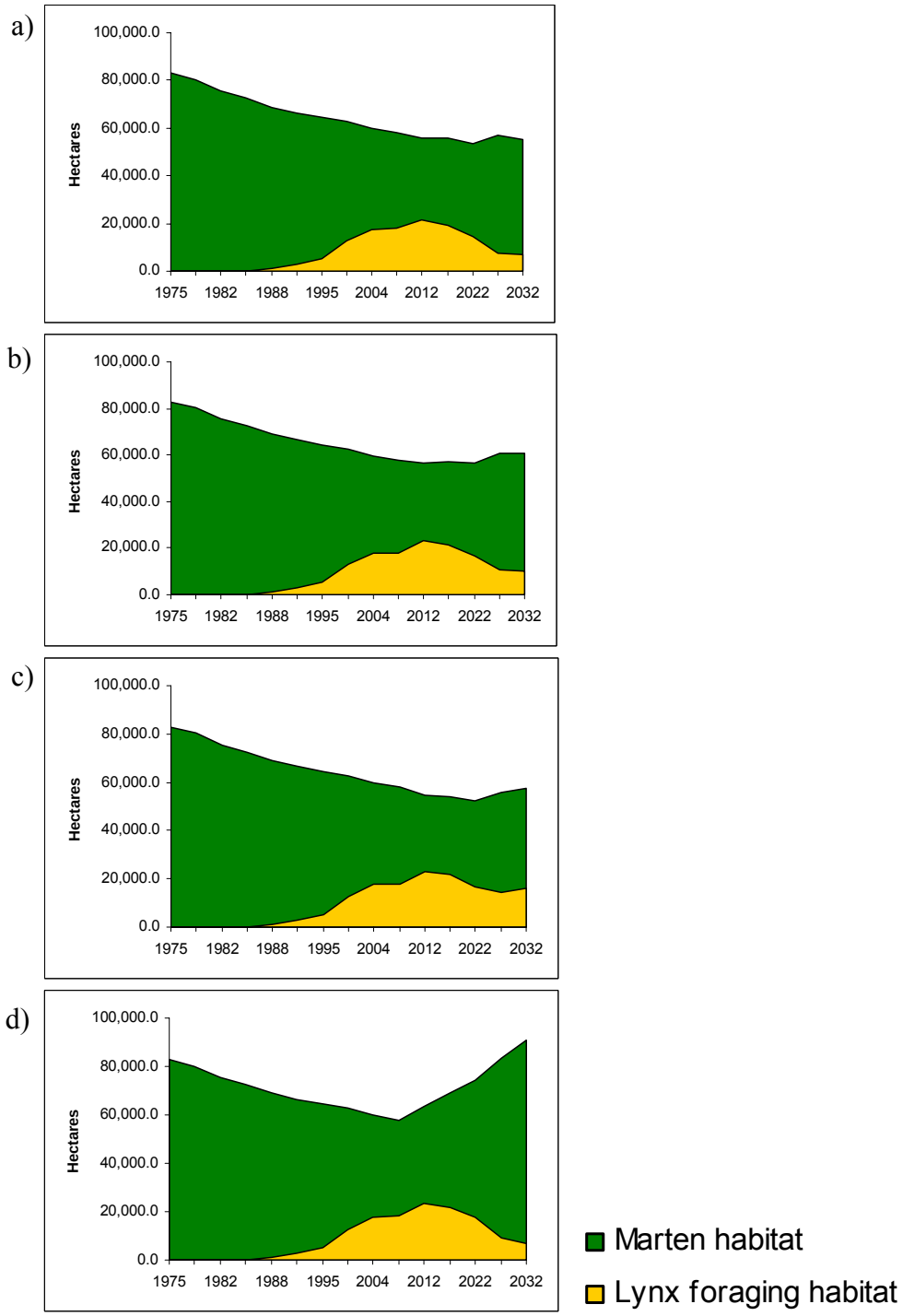

Figure 4.3. Retrospective and future trends in habitat quantity for martens (green) and lynx (yellow) 1970-2032 under the scenarios a) BASE; b) BASECC; c) MAX; and d) NOHRV.

lynx foraging habitat followed the same trends projected with the BASE and BASECC scenarios (Figure 4.3d).

The effect of including the additional criterion of mean stand dbh ≥15.24 cm (6 in) on the total estimated amount of marten habitat 2007-2032 was an average 21% reduction (range = 16-31%) in any given period (Figure 4.4). Overall, however, temporal patterns were not dramatically different compared to the trends based on the original criteria (i.e., ≥18 m^2/ha BA and mean height ≥30 ft for trees ≥7.6 cm dbh, leaf-on canopy closure was >30%, forest patch size ≥2.7 ha). Across all of the 3 harvest scenarios marten habitat decreased monotonically 2007-2032 (Figures 4.4 a-c), without the 2022-2027 increase that was observed with the original criteria. Patterns were also similar for the NOHRV scenario, with an increase in the marten habitat amount starting in 2007 (Figure 4.4d).

Estimated marten and lynx densities (Figure 4.5) followed very similar temporal patterns as the marten and lynx habitat change 2007-2032 (Figure 4.3). Marten densities declined slightly 2007-2022 and then increased slightly 2022-2027, ultimately remaining at approximately 0.2 martens/km^2 under each of the harvest scenarios. Marten densities increased under the no harvest scenario to >0.6 martens/km^2 (Figure 4.5d). Lynx densities declined 2007-2032 by >50% under each of the harvest scenarios, while under the no harvest scenario the onset of the decline was delayed until 2017. Presumably this time lag resulted from the absence of mature conifer harvest and precommercial thinning of regenerating forest, both of which negatively influence probability of lynx occurrence and potential density (Chapter 2), under the NOHRV scenario. Ranking each of the scenarios based on the final outcomes ca. 2032 for habitat and densities indicated that the

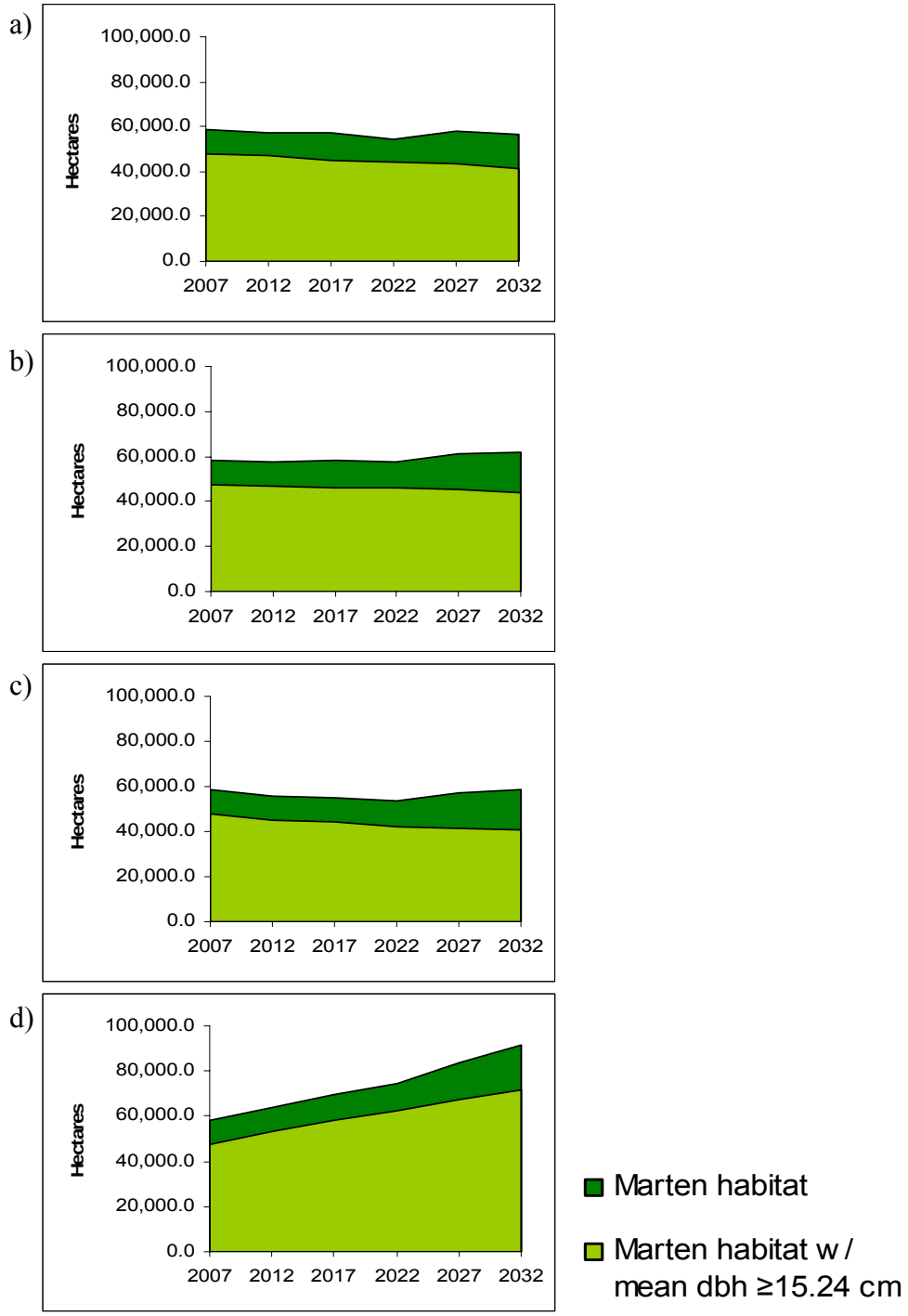

Figure 4.4. Projected trends in marten habitat, 2007-2032, under the scenarios a) BASE; b) BASECC; c) MAX; and d) NOHRV. Habitat quantity calculated based on refined criteria (dark green) and with the added criterion of mean stand dbh ≥15.24 cm (6 in) (light green).

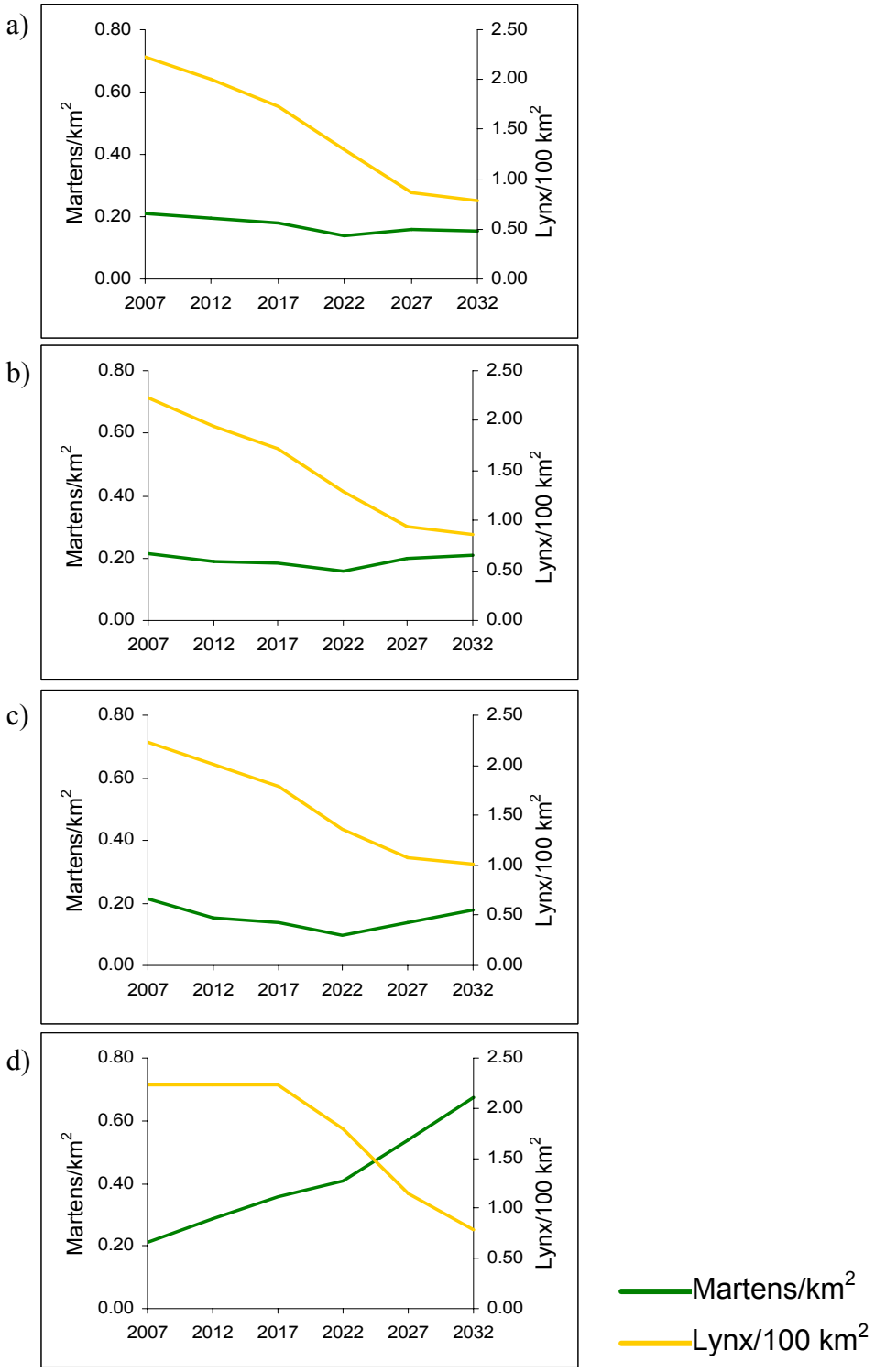

Figure 4.5. Projected trends in marten (green line) and lynx (yellow line) densities, 2007-2032, under the scenarios a) BASE; b) BASECC; c) MAX; and d) NOHRV.

top-ranked scenario for maintaining or increasing marten habitat and densities was NOHRV, while the top-ranked scenario for lynx habitat and densities was MAX (Table 4.6). ASIS was the 2nd-ranked scenario for both lynx and marten habitat and densities, suggesting that this scenario provided some amount of tradeoff between lynx and marten habitat maintenance over the next 25 years. ASISCC was the 4th-ranked scenario for all but one outcome (Table 4.6).

For both martens and lynx, the percent change in the quantity of habitat was significantly affected by parcel LEGACY ($F=5.93 - 6.99$, $p \leq 0.009$), which suggests that the timing and harvest intensity of past forest management will continue to strongly influence future changes in habitat quantity, 2007-2032 (Table 4.7). For martens, changes in habitat quantity for parcels with a legacy of predominantly *heavy* harvesting 1973-1988 were significantly different from both parcels with a legacy of *light* harvesting 1988-2007 (Tukey's HSD Test, $p<0.0001$) and parcels with a combined legacy of *heavy* (1973-1988) and *light* (1988-2007) harvesting (Tukey's HSD Test, $p<0.0001$), but the latter two legacies were not significantly different from each other ($p=0.130$). SCENARIO was also a significant factor ($F=78.76$; $p<0.0001$) influencing percent change in marten habitat; however, only the NOHRV scenario was significantly different from the other 3 scenarios (Tukey's HSD Test, $p<0.0001$). The interaction between LEGACY and SCENARIO ($F=1.91$; $p=0.094$) was not significant (Table 4.7).

SCENARIO was a significant factor ($F=16.32$; $p<0.0001$) influencing percent change in lynx habitat; however, the interaction between LEGACY and SCENARIO was also significant ($F=11.16$; $p<0.0001$) (Table 4.7). Pairwise comparisons indicated that changes in habitat quantity for parcels with a legacy of *light* harvesting 1988-2007 were

Table 4.6. Comparison of alternative forest management scenarios with respect to maintaining or increasing the quantity of habitat and densities for lynx and martens 2007-2032 across the entire 14 townships study area. Each scenario is ranked 1-4 for each of the outcomes, with the value 1 reflecting the highest value.

Scenario	Marten habitat	Marten habitat (mean dbh ≥6")	Marten/km^2	Lynx habitat	Lynx/100km^2
BASE	4	3	4	4	4
BASECC	2	2	2	2	2
MAX	3	4	3	1	1
NOHRV	1	1	1	3	3

Table 4.7. Results from repeated measures ANOVA testing for the effects of LEGACY and SCENARIO on the percent change in the quantity of habitat for martens and lynx across the entire 14 township study area between the years 2007 and 2032.

Response variable	Source	d.f.	Mean squares	*F*	*p*
MARTEN	LEGACY	2	6.606	5.931	0.009
	Error[a]	20	22.275		
	SCENARIO	3	2.081	78.760	<0.0001
	SCENARIO × LEGACY	6	0.050	1.908	0.094
	Error[b]	60	0.026		
LYNX	LEGACY	2	11.162	6.988	0.005
	Error[a]	20	1.597		
	SCENARIO	3	3.517	16.321	<0.0001
	SCENARIO × LEGACY	6	2.679	11.160	<0.0001
	Error[b]	60	0.216		

[a] Between-subject error from repeated measures ANOVA.
[b] Within-subject error from repeated measures ANOVA.

significantly different from both parcels with a legacy of predominantly *heavy* harvesting 1973-1988 (Tukey's HSD Test, $p<0.0001$) and parcels with a combined legacy of *heavy* (1973-1988) and *light* (1988-2007) harvesting (Tukey's HSD Test, $p<0.0001$), but that the latter two legacies were not significantly different from each other ($p=0.769$). Only the MAX scenario was significantly different from the other 3 scenarios (Tukey's HSD Test, $p<0.0001$). When the effects of LEGACY and SCENARIO were combined, the only significant differences occurred when parcels with a legacy of *light* harvesting 1988-2007 were coupled with the MAX scenario, which resulted in an overall increase in the amount of lynx habitat under the MAX scenario (with the exception of one parcel).

DISCUSSION

Forest projection models provide land and wildlife managers with a valuable tool for quantitatively assessing the trends in wildlife habitat supply from past and future landscape change. My results indicate that the cumulative effects of past forest management significantly affect the outcomes of future forest management by influencing both long-term strategic planning and harvest-block scheduling. In turn, this management legacy influences future habitat supply for two important umbrella species in the Northeast. Retrospective changes in marten and lynx habitat supply 1970-2007 have been largely driven by two factors. The first of these was the spruce budworm outbreak of the 1970s and 80s that led to increased rates of clearcutting during the preemptive and salvage logging period, which lasted into the early 1990s (Chapter 3). Subsequently, the Maine Forest Practices Act (12 MRSA §8867-A to §8888 & MFS Rules Chapter 20) was implemented and along with the end of the outbreak contributed to the reduction in clearcut harvesting on commercial forestlands in Maine and an

increase in the acreage partially harvested (Maine Forest Service 1995). These two factors resulted in the broad-scale decline in marten habitat of at least 435,000 ha (Chapter 1) and the substantial increase of ~189,000 ha in lynx foraging habitat (Chapter 3) 1975-2007. Similar trends were also reflected across the 14 township study area included in these analyses 1975-2007 (Figure 4.3). The alternative forest management scenarios differed with respect to the overall magnitude of future habitat change 2007-2032 (Figure 4.3), but the predominant trends in habitat quantity for martens and lynx over the next 25 years will be strongly influenced by the legacy of past forest management.

Timber harvesting rates and patterns differed between the harvest scenarios, resulting in variability in the targeted volumes and areas harvested. When the proportion of the total harvest removed by clearcutting was constrained to ~4%, the total target volume (BASE; 143,864,974 ft^3) was reduced compared to the harvest without the 4% limitation (BASECC; 152,062,044 ft^3), but the average area harvested was larger, averaging 29,253 ac and 25,132 ac respectively. The difference in the harvest footprint resulted in >20,000 additional acres being harvested 2007-2032 under the BASE scenario, represented primarily by shelterwood establishment harvests or overstory removals (Figure 4.2). The target volume increased when maximizing the sustainable harvest was the strategic objective (MAX; 180,312,860 ft^3). Under the MAX scenario there was an additional reduction in area harvested because an increasing proportion of the acres were harvested via clearcut (Figure 4.2). This inverse relationship between acres harvested by clearcut and total acres harvested is the same process as was previously noted as occurring on Maine's commercial forestlands in the 1990s (Maine Forest

Service 1995); in the 10 years after the passage of the Maine Forest Practices Act the total acreage harvested increased by 48% as the acreage harvested by clearcut decreased by 85%. When I increased the maximum clearcut size from 250 ac to 500 ac, I observed few effects beyond those resulting from removing the aspatial constraint on proportion of acreage clearcut (in the case of either the BASECC or MAX scenarios). This suggested that silvicultural opportunities for creating larger clearcuts in spruce-fir forest are somewhat limited in this landscape. Thus, the aspatial constraint of limiting the broad-scale proportion of harvest clearcut appears to be a more influential factor than maximum allowable clearcut size on future silvicultural outcomes and habitat supply in Maine's commercial forestlands.

Projected trends for marten habitat will generally mirror retrospective declines, as habitat loss resulting from forest management continues to outpace habitat gain from growth in previously harvested areas (Figure 4.3). Results indicate that habitat loss for martens will tend to be greatest in areas where stands that were partially harvested 1988-2007 are re-entered in the future to harvest residual mature trees. It is important to note, however, that estimates of continued loss of marten habitat 2007-2032 may be overestimated if areas previously receiving a partial harvest 1988-2007 no longer retained sufficient structure to be considered marten habitat ca. 2007, which I was unable to directly assess (Chapter 2). Only under the no harvest (NOHRV) scenario will marten habitat supply increase in the near future (Figure 4.3), which agrees with previous research that has compared the effects of forest management strategies on marten habitat (Kliskey et al. 1999). In fact, by 2032 amount of marten habitat would exceed the amount in 1975 by ~10% under the NOHRV scenario. Marten habitat quantity is also expected to

increase under the harvest scenarios but not until 2022 as the forest that regenerated in areas that were heavily harvested during the 1970s and 80s spruce budworm outbreak matures. These results are, however, dependent on assumptions about the generalized rates of average growth for commonly occurring tree species in northern Maine. These estimates were based on overstory stand composition and site quality and so should capture general patterns of growth, however, because stand characteristics were randomly assigned based on FIA-derived distributions, the exact timing of marten habitat gain in specific areas should be viewed with caution.

Marten density trends (Figure 4.5) followed a similar temporal pattern as the habitat trends under the 3 harvest scenarios (Figure 4.3), showing a slow decline until 2022. Only under the NOHRV scenario is the density of marten expected to exceed the 2007 density (214%). Thus, regardless of whether or not future harvesting rates follow recent trends, marten density will remain near 2007 levels. Estimated marten density hovered around 0.2 martens/km^2 in all 3 of the harvest scenarios, which is relatively low especially considering that the density estimates do not take potential trapping loss into account. A density of 0.2 martens/km^2 is considerably lower than has been reported for Maine's largest forest reserve (i.e., 0.62 martens/km^2), Baxter State Park, which was actually considered an underestimate because the road-based trapping design may not have been adequate to capture all resident female martens (Payer 1999). Further, average marten density on commercial forestlands adjacent to Baxter State Park that were closed to marten trapping was reported to be 0.31 martens/km^2, which was ~40% greater than an adjacent area that was open to trapping (0.19 martens/km^2) (Payer 1999). Thus, if trapping can be expected to reduce density by 40%, then the actual marten density across

the 14 townships can be expected to be closer to 0.1 martens/km^2, and, in fact, 2006 trapping data suggests >40% removal within the study area (MDIFW *unpublished data*).

Differences between harvest scenarios were not apparent for marten habitat trends when the additional criterion of mean stand dbh ≥15.24 cm (6 in) (Fuller et al. 2004, Fuller and Harrison 2005) was included as part of the habitat definition (Figure 4.4). The initial reduction in estimated marten habitat amount ca. 2007 (mean=21%; range = 16-31%) created by this criterion actually increased in latter periods because the stands from the 1970s and 80s harvests that contributed to marten habitat starting in 2022, as described above, apparently were still too young to exceed a mean stand dbh of 15.24 cm (6 in). Thus, it is important for forest manager to consider that marten habitat amount estimated based on previously published thresholds for martens may tend to overestimate suitable marten habitat in regenerating forest. Additionally, results presented here are also based on a single simulation run for each scenario. Inferences could be made based on multiple runs for each scenario to better understand landscape-scale variability in habitat quantity for martens and lynx. However, the relative stability of the results across the scenarios clearly indicates that the legacy of past forest management strongly influences the outcome of future forest management and the resulting effects on habitat quantity and densities of martens and lynx habitat over the 25-year period, 2007-2032.

Lynx foraging habitat will continue to increase in the near future as a consequence of past forest management (Figure 4.3). However, forests that regenerated in areas that were heavily harvested during the 1970s and 80s spruce budworm outbreak, which has provided the majority of high-quality lynx foraging habitat 1970-2007 (Chapter 3), continues to mature. Thus, lynx foraging habitat will start to decline

precipitously after 2012. In this analysis I assumed that regenerating forest >35 years would no longer function as high-quality habitat based on research in Maine that has suggested that hare densities on average start to decline as a consequence of succession-induced reductions in cover and/or forage when the maximum stand age exceeds 35 years post-harvest (Fuller et al. 2007). Additionally, a small proportion of habitat will be lost prior to the effects of advancing succession from the application of intensive timber management techniques such as precommerical thinning, which is known to reduce snowshoe hare densities (e.g., Sullivan and Sullivan 1988, Griffin and Mills 2007, Homyack et al. 2007). However, this effect is small relative to the influence of reducing the annual acreage clearcut on the future supply of lynx foraging habitat. The increase in the clearcut harvest in the BASECC scenario would have provided for creation of additional lynx foraging habitat over the 25 years when compared to the BASE scenario, although not as much as the MAX scenario (Figure 4.3). Declines in quantity of lynx foraging habitat from 2007-2032 are least severe (-12%) under the MAX scenario because of a greater increase in clearcutting and an increase in shelterwood harvesting relative to the other scenarios (Figure 4.2). This conclusion, however, is based on the assumption that advanced regenerating conifer stands created after the overstory is removed from a previous conifer shelterwood establishment harvest will ultimately provide the same habitat type as regenerating stands created by clearcutting in Maine (Sendak et al. 2003, Saunders and Wagner 2008). Even under the MAX scenario, however, lynx density is expected to decline by ~55% from ~2.2/100km^2 to 0.75-1.0/100km^2 (Figure 4.5) from 2007-2032, compared to an expected decline of 65%, 61%, and 65% under the BASE, BASECC, and NOHRV scenarios.

CONSERVATION AND MANAGEMENT IMPLICATIONS

Habitat supply trends for martens and lynx will continue to be strongly influenced by the legacy of past forest management rates and patterns, but the differences between outcomes associated with the alternative management scenarios provide insight into the important role that the aspatial constraints associated with strategic forest planning objectives play in determining volume and acreage harvested, and the future habitat supply for lynx and martens. Different scenarios were top-ranked for marten (NOHRV) and lynx (MAX) (Table 4.6); however, the same scenario (BASECC) ranked 2nd for both, suggesting that it would benefit both marten and lynx in the future if the proportion of the acreage harvested by clearcut was greater than 4%. Increasing the acreage harvested by clearcut to ~30% of the harvest had the effect of reducing the acreage partially harvested and the total acreage harvested, which helped slow the decline in marten habitat. The BASECC scenario also provided some additional lynx foraging habitat as the regenerating forest created from future clearcuts 2007-2017 developed into high-quality habitat 2022-2032 (Figure 4.2). Conservation planning for these two species, and the other species that they represent, clearly requires a broad-scale perspective and in the future will require coordination between land and wildlife managers in order to ensure habitat sustainability.

Current habitat conditions for lynx are a consequence of the preemptive and salvage logging the occurred as a consequence of the 1973-1985 spruce budworm outbreak (Chapter 3), and forest management will have little opportunity to change the trajectory of lynx habitat supply in the near future. The potential for the creating lynx foraging habitat in the next 15-25 years appears to be greatest at the parcel-level in areas

with a history of predominantly partial harvesting, but only if rates of clearcutting increase. Overstory removal harvests may also have the potential to create high-quality lynx foraging habitat, but additional research is needed to better understand the residual forest structure, successional patterns, and snowshoe hare densities associated with regenerating forest stands created by overstory removals with and without a preceding shelterwood establishment harvest. Nonetheless, as a result of the changes in harvesting rates and patterns that have occurred since the passage of the MFPA, habitat supply will decline over the next 10-20 years, within the 14 townships and in the larger landscape currently occupied by lynx in northern Maine (Chapter 3). This will be an important consideration in setting recovery goals for the federally-threatened lynx.

At the time of listing, available data were not adequate to determine the size or trend of the lynx population in Maine (USDOI 2000). Since then, however, research (Vashon et al. 2008, Chapter 2) has suggested that habitat in northern Maine can support lynx densities that are substantially higher than some western populations (Koehler 1990) and even similar to some more northerly lynx populations during the cyclic high in the snowshoe hare cycle (Brand et al. 1976, Parker et al. 1983, O'Donoghue et al. 1997). These findings highlight both the importance of the Northeast to the recovery of the Distinct Population Segment (DPS), and the potential danger of setting recovery goals based on the status of a population at a snapshot in time. Lynx densities will decline as habitat supply declines; thus, the recovery team should consider that the spatial distribution of lynx habitat will change over time when setting delisting criteria (this study; Chapter 3). I further recommend that the USFWS strongly encourage the development of a regional conservation plan that enlists the support of private

landowners to maintain habitat in areas that are currently occupied by lynx in the Northeast.

The future for marten habitat appears to be best in parcels with a history of salvage harvesting during the 1970s and 80s spruce budworm outbreak and limited partial harvesting. Maintaining habitat supply for marten will be dependent on continued reduced rates of partial harvesting in these areas to maintain the vertical and horizontal structure martens prefer (Payer and Harrison 2003, Fuller and Harrison 2005), particularly until the regenerating forest, which is currently providing high-quality lynx foraging habitat, matures and develops the characteristics associated with marten occupancy (Payer and Harrison 2003, Fuller and Harrison 2005). If a mean stand dbh ≥15.24 cm (6 in) is required for a forest patch to be suitable marten habitat, marten habitat supply will continue to decline 2007-2032, as it has since 1975 (Chapter 1). As a consequence of the sustained habitat loss, we will likely be approaching marten densities, at least in some Wildlife Management Districts, that are marginal for sustaining fur harvest under the current harvest regulations, which were established in the early 1990s when habitat conditions for martens in northern Maine were more favorable (Chapter 1). Thus, I recommend that the marten harvest management system be reconsidered to avoid threatening a population that is already facing a 32-54% loss of habitat over the last 37 years (Chapter 1), and which is not likely to regain a substantial quantity of habitat in the next 25 years under current forest management regulations.

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BIOGRAPHY

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