HABITAT USE AND CONNECTIVITY FOR CANADA LYNX IN THE NORTH CASCADE MOUNTAINS, WASHINGTON

by

Carmen Marie Vanbianchi

B.S., Humboldt State University, 2008

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF

THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE COLLEGE OF GRADUATE STUDIES

(Biology)

THE UNIVERSITY OF BRITISH COLUMBIA

(Okanagan)

June 2015

ABSTRACT

Canada lynx (*Lynx canadensis*) populations in the contiguous US comprise the southern extent of lynx range. Lynx were federally listed as Threatened in 2000, and they survive in sub-boreal forests of lower habitat quality than in the core of lynx range in Canada and Alaska. Southern lynx habitat is fragmented by topography, and increasingly by human impacts. Wildfires, which are projected to increase in frequency, size and intensity under climate change, also fragment southern lynx habitat. I used Global Positioning System radio-collar data from 17 lynx in the North Cascade Mountains of Washington collected during 2007 through 2013 to explore southern lynx habitat use in a fragmented landscape impacted by fire. I used Random Forest models to analyze core hunting, resting, and denning habitat, and the habitats lynx select while traveling between patches of core habitat. I also describe lynx use in new and old burns. Finally, based on the core and travel habitat models, I used Least Cost Path modelling to map connectivity linkages for lynx in the North Cascades.

While selecting core habitat, lynx used spruce (*Picea engelmannii*)-fir (*Abies lasiocarpa)*, lodgepole pine (*Pinus contorta*), and mixed sub-boreal-Douglas fir (*Pseudotsuga menziesii*) forests, and avoided dry forests and forest openings including new burns. While selecting travel habitat, lynx used a wider range of habitats, including new burns where fire skips and residual trees offered cover.

In newly burned areas, lynx used areas near the burn perimeter, fire skips, and residual live trees, but avoided severely burned areas. In old burns, lynx used areas where cool and moist microclimates encouraged dense vegetative growth, regardless of the regenerating forest type or burn severity.

My connectivity model reveals important linkages for lynx, connecting areas of currently occupied lynx habitat divided by the Methow Valley and by the 2006 Tripod Burn. The model also revealed linkages connecting currently occupied areas to areas historically occupied by lynx south of Lake Chelan.

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ACKNOWLEDGEMENTS

I owe many thanks to the generous people who supported and contributed to this research. Foremost, I am tremendously grateful to have had the opportunity to work under my supervisor, Dr. Karen Hodges. Karen's extensive knowledge of the boreal ecosystem coupled with her dedication to careful and thoughtful science helped shape this thesis into a more meaningful and scientifically sound contribution to lynx research. In addition to research guidance, Karen has become an important friend and mentor in my life. Her wisdom on navigating the scientific world and happily juggling life and work will undoubtedly help me for the rest of my career.

I also owe many thanks to the rest of my committee, Dr. Bill Gaines and Dr. Jason Pither. Together Karen, Bill, and Jason encouraged me to step out of my comfort zone of field work and into the much scarier world of computers. They answered my millions of questions and helped me to climb the mountain that is learning program R, GIS, and habitat modeling.

I am extremely appreciative of the help I received from Dr. Melanie Murphy. Her expertise in using Random Forest to model habitat selection made collaborating with her an invaluable part of my research. I'd also like to thank Dr. Jeffery Evans and Melanie for giving me the computer code to run the Random Forest model as they have adapted it for ecological use.

From the early stages of brainstorming research ideas to lending me the lynx location data that this project is based on, local biologists at the US Forest Service, Washington Department of Fish and Wildlife, and Washington State Department of Natural Resources lent tremendous help to my research. I would especially like to thank John Rohrer, Robert

Naney, Jeffrey Heinlen, Kent Woodruff, Brian Kertson, and Scott Fisher for their support and help.

Many thanks to those that helped me to find and develop the GIS layers used in this project. I received extensive help from Gary Reed regarding US Forest Service GIS layers and from Heather Roberts and Matthew Gregory regarding the LEMMA land cover GIS dataset. I owe special thanks to Justin Braaten for developing LandTrendr disturbance layers for my study area and for his help interpreting them.

My research was supported by a UBC Okanagan scholarship and by a research grant from the Natural Sciences and Engineering Research Council of Canada awarded to Karen Hodges. I received further financial support from the US Forest Service for which I need to thank Robert Naney and John Rohrer.

Additionally, I thank Courtney Dean and Tyler Ambrose for their grad student camaraderie and for letting me stay in their home while I was on campus.

Finally, I am so grateful to my family for their unwavering support starting with my first Science Fair project in Kindergarten. My parents, Ron and Peggy Vanbianchi, nurtured a love of nature and wildlife in me which in turn gave me the passion and drive to be a wildlife biologist. I will forever owe my dad a favor for the countless papers of mine he has edited including many drafts of this thesis. He taught me how to be a science writer and continues to help me improve my skills. I am incredibly appreciative for Jesse Davis and the solid rock he has been throughout my graduate program. The peaceful home and life in the Methow Valley he has helped me to create kept me a sane and happy graduate student.

CHAPTER 1
LYNX HABITAT IN THE SOUTHERN RANGE PERIPHERY

1.1 INTRODUCTION

As human populations around the world increase, our footprint on the land grows larger with negative consequences for biodiversity. Habitat loss and fragmentation are two of the leading causes of species decline worldwide, and are identified as top threats to mammal diversity within the United States and Canada (Wilcove et al. 1998, Imre and Derbowka 2011). Large carnivores may be particularly sensitive because of their typically long life history, large spatial requirements, and low population densities (Purvis et al. 2000). In North America, nearly all species of large carnivores have experienced range contractions in large part due to habitat loss and fragmentation (Laliberte and Ripple 2004). As human modification of landscapes continues, conserving the remaining carnivore populations in North America largely depends on our ability to provide for habitat connectivity and thus the movements of carnivores throughout their ranges (Noss et al. 1996).

1.1.1 Connectivity Conservation

Habitat fragmentation can have many negative effects on animals. Disconnected habitats can isolate populations and impede gene flow across the landscape, causing inbreeding and loss of genetic diversity (Frankham 2006), and can also physically impede animal movements, making it more difficult for an animal to search for resources such as food and cover, or to disperse to establish a new home range (Wilcox and Murphy 1985, Fischer and Lindenmayer 2007). In addition, fragmentation may impede animals attempting to escape habitat loss or degradation due to human activities such as timber harvest, agriculture, and residential and commercial development (Wilcove et al. 1998).

Connectivity conservation has surfaced as a key strategy to combat the effects of habitat loss and fragmentation so that biological and ecological processes can persist despite increasing habitat fragmentation. Connectivity conservation has been applied around the world to a wide variety of taxa including marine organisms, insects, birds, and terrestrial mammals (Crooks and Sanjayan 2006). Because animals move at varying spatial and temporal scales, preserving species also requires applying connectivity conservation across a variety of scales. For example, animals must move through the landscape at a local scale to access basic needs such as food, shelter, and mates to insure their individual survival. Animals must also move across landscapes on a larger scale to migrate, disperse, and escape degrading habitat (Ims 1995).

1.1.1.1 Structural Versus Functional Connectivity

Landscape connectivity can be described in terms of structural characteristics or functional characteristics. A landscape is considered structurally connected if, based on a simple binary classification of the landscape as habitat or non-habitat, the habitat is contiguous (Tischendorf and Fahrig 2000). This definition is based on the traditional description of fragmented landscapes as patches of suitable habitat within a matrix of inhospitable habitat (Wiens 2006). Under this view, links between habitat patches are identified as corridors or "stepping stones" of suitable habitat acting as bridges through a matrix of inhospitable habitat. While in extreme cases the matrix can isolate habitat patches, in general this view of the matrix is over-simplified (Chetkiewicz et al. 2006). Landscapes are complex and the matrix is usually not an entirely inhospitable environment (Prugh et al. 2008), so that in reality landscapes are better described as continuous spectra of habitat suitability (Chetkiewicz et al. 2006).

A landscape is described in terms of functional connectivity when a species' behavioral responses to landscape features are included (Tischendorf and Fahrig 2000). This definition of connectivity considers the fact that animals respond to habitats on a spectrum rather than as habitat versus non-habitat, and that lower-quality matrix habitat can serve as travel habitat (Haddad and Tewksbury 2005). In this view, a landscape that is not structurally connected may be functionally connected. This definition also accounts for structurally-connected landscapes that are functionally unconnected, for example when the distance between structurally-connected habitat patches is too great for an animal to traverse (With 1997, Tischendorf and Fahrig 2000, Taylor et al. 2006). Using a functional connectivity framework, connections between habitats are viewed as areas in the matrix that facilitate movement and include a spectrum of habitat quality (Chetkiewicz et al. 2006). These areas are often referred to as linkages. Describing a landscape in terms of functional connectivity and linkages incorporates a more realistic representation of habitat and a species' ability to move through the landscape. When adequate information is available about a species' movement ecology, providing for functional connectivity provides greater assurances for the conservation of the species of interest (Tischendorf and Fahrig 2000, Chetkiewicz et al. 2006).

1.1.1.2 Connectivity Modeling

Many methods are used to model and identify areas of connectivity for conservation. To identify areas of connectivity based on habitat structure, methods may be simplistic and coarse, such as identifying the shortest path between two patches, or in the case of an already highly-fragmented landscape, identifying any remaining habitat connections between patches.

However, identifying linkages that facilitate functional connectivity for a focal species or group of species requires that modelers consider the degree to which different landscape features inhibit or facilitate movement. To identify areas of functional connectivity, modelers select landscape features such as habitat types, topography, or human infrastructure that are believed to influence movement of the species in question. The selected features are then assigned numerical resistance values based on an estimation of how difficult each feature is for an animal to move through so that high-resistance values represent one or more of the following costs to an animal: high avoidance of the landscape feature, high cost to fitness, or low survival (Zeller et al. 2012). Often, when species-specific movement ecology is poorly understood, expert knowledge of an animal's habitat preferences is used to assign resistance values (Noss and Daly 2006). Although expert knowledge is sometimes appropriate or is the only option available, the resulting models should be regarded as a working hypotheses and tested with empirical data. Preferably, scientists use a modeling approach that incorporates empirical evidence of habitat selection or movement patterns to determine the amount of resistance each landscape feature presents (Chetkiewicz et al. 2006).

Once resistance values have been assigned to landscape features, Geographic Information System (GIS) mapping software assigns each pixel on the landscape its resistance value to create a resistance surface (Chetkiewicz and Boyce 2009). Using this resistance surface, areas of high quality habitats can be identified and connectivity can be modeled. Least-cost analysis has emerged as the basis for most linkage modeling approaches and calculates the path of least resistance between two points on a landscape by adding the resistance values of consecutive pixels (Beier et al. 2008). Because least-cost analysis will always identify the least cost paths, modelers must qualitatively evaluate the modeled paths since even the least-costly path may not be suitable for animal movement (Beier et al. 2008). For example, pathways may not be wide enough to protect an animal from the surrounding matrix. Similarly, a pathway with many bottlenecks may lower the functional connectivity of a linkage, as will a linkage that is longer than the dispersal capability of the focal species (Beier et al. 2008). By selecting high-quality least-cost paths, areas linking habitat patches can be identified and prioritized for conservation, offering animals a chance to persist on a fragmented landscape.

As an alternative to using expert knowledge for parameterizing a resistance surface, Resource Selection Functions offer scientists a way to use empirical data to assign resistance values (Chetkiewicz and Boyce 2009). Resource Selection Functions in their most basic form quantify habitat selection by comparing habitats used by a species with those available or unused by the species. Resource Selection Function models are usually fit using a parametric analysis such as a linear or logistic regression, the output of which predicts how each habitat feature affects the probability of use by the focal species (Manly et al. 2002). Probability of use can then be translated into a numerical value estimating the resistance to movement each habitat feature presents to the focal species by assuming that habitats with a high probability of use provide low resistance to animal movements while those with a low probability of use present high resistance to movement (Chetkiewicz and Boyce 2009). Most Resource Selection Functions do not explicitly model movement and rarely, if ever, model gene flow (Spear et al. 2010).

In addition to Resource Selection Functions, a relatively new machine-learning algorithm, Random Forest (Breiman 2001), has recently been applied to habitat analysis studies (Wilsey et al. 2012, Mochizuki and Murakami 2013). Random Forest has several advantages over Resource Selection Functions; it is non-parametric, and it accounts for autocorrelation, interactions among variables and across scales, and the complex non-linear relationships common to ecological data (Cutler et al. 2007, Evans and Cushman 2009, Evans et al. 2011). In addition, Random Forest accommodates many predictor variables, does not assume independence of samples, and does not require *a priori* hypotheses regarding the direction of the response variable, thus allowing unexpected interactions to be discovered (Evans et al. 2011). Random Forest often creates highly predictive classification and regression models, but it is criticized for offering limited insight as to the mechanistic relationships between predictor and response variables (Murphy et al. 2010, McCue et al. 2013). However, graphs to help visualize the relationship between predictor and response variables, and recently developed methods for model selection and determining a significance value have helped ease ecological interpretation (Evans and Cushman 2009, Murphy et al. 2010, Evans et al. 2011).

Random Forest has only recently been applied to wildlife habitat studies, and has not yet been used to characterize the habitat use of a wide-ranging carnivore. In this thesis, I use Random Forest to analyze and describe the habitat use of Canada lynx (*Lynx canadensis*). I then demonstrate the novel approach of using results from my Random Forest habitat analysis to parameterize a resistance surface, which I use to model lynx habitat connectivity in the North Cascade Mountains of Washington.

1.1.2 Canada Lynx, a North American Carnivore in Decline

The boreal and sub-boreal forests of North America are home to the Canada lynx, a medium-sized cat uniquely adapted to the challenges of hunting in deep snow. Lynx' disproportionally large feet and low foot-loading allow them to travel easily through deep snow (Murray and Boutin 1991), and give them a competitive advantage over other medium-sized predators such as coyotes (*Canis latrans*) and bobcats (*Lynx rufus*) (Murry and Boutin 1991, Buskirk et al. 2000a). With these adaptations to snow, lynx have carved a niche in the boreal and sub-boreal forest ecosystem ranging from their core in Alaska and Canada southward into the contiguous US where extensions of the boreal forest occupy portions of the Cascade and Rocky Mountains of the west, the north-central and Great Lakes states, and the north-eastern states.

Lynx are specialized predators that eat primarily snowshoe hares (*Lepus americanus*), and within lynx range, higher densities of hares support higher densities of lynx (Koehler 1990, Aubry et al. 2000, Murray et al. 2008). This specialized relationship between lynx and snowshoe hares has resulted in a well-documented synchronized population cycle in the northern core of snowshoe hare and lynx range (Krebs et al. 2001, but see Krebs et al. 2013). Snowshoe hare populations fluctuate in an 8-11 year cycle with a population density peak followed by a decline and 2-4 year low phase before again increasing in numbers (Hodges 2000a, Krebs et al. 2001). In response to the flux in prey base, lynx populations cycle with a 1-2 year lag behind hare populations, reaching peak population densities of 30-45 lynx per 100 km^2 and low densities of 0-3 lynx per 100 km^2 (Mowat and O'Donoghue 2000).

The available evidence suggests less dramatic snowshoe hare and lynx population cycles in the southern portion of their range (Hodges 2000b, Hodges et al. 2009, Ellsworth and Reynolds 2006, McKelvey et al. 2000b). Here, perhaps due to poorer habitat and competition with other species (Apps 2000), lynx numbers remain low and resemble those of northern populations during a cyclic low (Aubry et al. 2000, Murphy et al. 2006, Murray et al. 2008).

1.1.2.1 Lynx Habitat

Across lynx range, the boreal and sub-boreal forests lynx inhabit vary in tree species composition. However, lynx consistently prefer forest stands that provide the dense horizontal cover selected by snowshoe hares. This structure is generally found both during the early, stand-initiation stage of forest development when shrubs and young trees regenerate in dense stands and in the old-growth multilayer forests when canopy openings encourage dense understory growth and low-reaching boughs create additional horizontal cover (Aubry et al. 2000, Buskirk et al. 2000b, Hodges 2000b, Koehler et al. 2008, Maletzke et al. 2008, Squires et al. 2010) (see Appendix A for details on forest stand terminology). Lynx often select old-growth forest stands with large amounts of deadfall and upturned root wads for denning habitat since dense understory cover protects kittens (Koehler 1990, Mowat et al. 2000, Squires 2008). However, lynx also den in dense regenerating stands and slash piles left after timber harvest (Organ et al.

2008, Moen et al. 2008, Mowat et al. 2000). Thus, lynx may be simply selecting for some but not all structural characteristics associated with old-growth forests.

Large-scale disturbances are common in boreal forest ecosystems and have an initially negative impact on snowshoe hares and lynx since the small seedlings and shrubs in the open stand-initiation stage are not thick or tall enough to provide dense horizontal cover and forage for hares. Insect outbreaks, disease, wind, and fire all contribute to boreal forest disturbances, but fire is the dominant disturbance, especially in western boreal forest where fire return intervals are shortest (Agee 2000, Stocks et al. 2003). Fires in lynx habitat typically result in high severity stand replacement fires, initiating secondary succession of forests (Agee 2000). In addition, although most boreal forest fires are small (< 200 ha), the majority of the area burned is the result of a few, large fires (> 200 ha), with an average of 1.8 million ha burning annually across the Canadian boreal region (Agee 2000, Stocks et al. 2003). Fire disturbances alter forest ecosystems by changing the species composition and population structure of trees (Agee 1993), resulting in a landscape mosaic of diverse stand ages and structures (Agee 2000). However, climate change is projected to alter the disturbance regime of boreal forests, increasing wildfire frequency, intensity, and size (Soja et al. 2007, Fauria and Johnson 2007, Balshi 2009, Littell et al. 2010). Fueled by warmer and drier summers, the balance of successional stages across the landscape may be altered so that a larger portion of the landscape is comprised of forest in open stand-initiation and other early-seral stages (Westerling et al. 2006).

Given the prevalence of fire in boreal ecosystems and the increased area burned predicted as a result of climate change, understanding lynx responses to fire is necessary to the development of strategies to conserve lynx populations. However, few studies of lynx responses to fire exist. Fox (1978) examined how fires affect the snowshoe hare-lynx population cycle in

Canada, indicating that lynx and hare populations decline as a result of very recent fires and increase as the burned areas regenerate into quality lynx and hare habitat. Paragi et al. (1997) found that lynx selected a 25 year-old fire over a nine year-old and 100+ year old forests in Alaska. In the Yukon, lynx selected 30-35 year-old burned forest stands (Mowat and Slough 2003). More detailed questions remain unanswered regarding how within-burn habitat conditions affect when and how lynx and snowshoe hares use burned areas. Patterns of post-fire tree regeneration density and growth-rate depend on site-specific conditions including the severity of burn, seed sources, and microclimates (Brand 1991, Turner et al. 1997, Bonnet et al. 2005, Irvine et al. 2009, Crotteau et al. 2013). Thus, a single burn may regenerate a mosaic of stand structure types. Since snowshoe hares and lynx may use differing heights, densities, and arrangements of regenerating stands at different times and for different purposes, information on detailed snowshoe hare and lynx post-fire use patterns could help scientists to better manage fire for lynx and hares.

1.1.2.2 Travel Habitat

While open habitats such as recent burns may not provide denning sites or foraging opportunities for lynx, they may provide travel habitat. Lynx are capable of dispersing long distances, with records of lynx moving up to 1,100 km (Mowat et al. 2000). In addition to dispersal movements, lynx in the south of their range also make long-distance exploratory movements outside of their home range (Aubry et al. 2000, Squires and Laurion 2000, Squires and Oakleaf 2005). To move long distances, lynx must move through areas of less suitable habitat. However, it is unknown what landscape features facilitate or hinder their movements. Although scientists working in the southern range of lynx have noted lynx traveling through habitats otherwise considered unsuitable, such as shrub-steppe (Squires and Laurion 2000), open mature forests and thinned forests (Koehler 1990), and dry forests or recently-burned areas

(Walker 2005), no studies have yet formally analyzed which landscape features lynx select for traveling across matrix habitats (Stinson 2001).

1.1.3 Lynx in Fragmented Habitats

Optimal environmental conditions and habitat are usually found in the core of a species' range where biological needs are met and productivity is high. Conversely, changing environmental conditions at the limits of a species' range can result in less-contiguous and lower-quality habitats than exist in the core (Lawton 1993, Sexton 2009). As a result of less-favorable environmental conditions and fragmented habitats, population dynamics may suffer, limiting a species' abundance at the edge of its range and exposing these populations to a higher probability of extinction than core populations (Shaffer 1981, Lesica and Allendorf 1995, Brown et al. 1996, Gaston 2009).

Lynx populations in the contiguous United States comprise the southern extent of the species' range. Unlike lynx in the core of their range in Canada and Alaska where habitat is high quality and relatively continuous, lynx in the US survive in naturally-fragmented habitat, which is common of animals living in the range edge (Brown et al. 1996, Buskirk et al. 2000b, McKelvey et al. 2000b). The large, continuous expanses of boreal forests that exist at northern latitudes become fragmented as they transition into southern forest types, and in the western US boreal forests are limited to high elevations where topography and climate interact to further fragments lynx habitat (Agee 2000). In addition, lynx face habitat loss as a result of human development, logging, wildfires, and climate change (Buskirk et al. 2000b, Koehler et al. 2008). Laliberte and Ripple (2004) report that the southern edge of lynx habitat has contracted northward towards its core in Alaska and Canada, eliminating 39% of the historic range. Lynx in the contiguous US are federally-listed as Threatened and persist in only seven states: Maine, Minnesota, Colorado, Wyoming, Montana, Idaho, and Washington (US Fish and Wildlife Service 2000).

Southern lynx populations are small and some scientists speculate that southern populations may function as population sinks that rely on dispersal from core populations in Canada to increase genetic variation and prevent local extinctions (McKelvey et al. 2000b, Murray et al. 2008). Schwartz et al. (2002) found high gene flow across lynx range and suggested that after the peak of the lynx and snowshoe hare population cycle in the range core, large numbers of lynx disperse into peripheral populations. Trapping records that show cyclic influxes of lynx into the US corroborate the genetic evidence (McKelvey et al. 2000a, Murray et al. 2008, Schwartz et al. 2002). Thus, increased fragmentation between the core and periphery of lynx range could disrupt the historical immigration from the range core, lowering genetic variation and increasing the risk of extinction in peripheral populations.

1.1.3.1 Climate Change

In addition to the fragmentation and poorer habitat quality found at the limit of a species' range, the impacts of climate change may be felt more strongly than at the range core (Anderson et al. 2009). Southern range limits that are already at the threshold of their species' climatic tolerance may be sensitive to changes in temperature so that as warming occurs, ranges shift northward and upward in elevation (Franco et al. 2006, Root et al. 2003). Evidence already exists for the contraction of the boreal forest at the southern range edge, as warming temperatures are reducing the regeneration of boreal tree species (Soja et al. 2007, Fisichelli et al. 2014). Southern lynx may be forced upward latitudinally and altitudinally to follow this shift in boreal forest range and as their already fragmented and small habitat patches shrink, southern lynx will likely suffer more than populations in the range core (Carroll 2007, Gonzalez et al. 2007). If the frequency and severity of wildfires also increase with climate change, fragmentation and loss of habitat at the range edge may be accelerated as the landscape skews towards recently burned areas in the open stand-initiation stages that lynx avoid for hunting and denning.

1.1.4 Lynx in the North Cascade Mountains of Washington

Washington supports one of the few remaining lynx populations in the contiguous US. Lynx once inhabited several areas of eastern Washington, as indicated by museum records of lynx trapped in the North Cascades, the Kettle Range, the northeastern corner of Washington, and to a lesser extent the southern Cascades (McKelvey et al. 2000a). No verified records exist for lynx west of the Cascades crest (McKelvey et al. 2000a). As a result of over-trapping and habitat loss, lynx were listed by the state as Threatened in 1993 (Washington Department of Wildlife 1993), and in 2008 a statewide model of Washington lynx habitat estimated enough habitat to support only 87 individuals (Koehler et al. 2008). The North Cascades ecoregion now supports the only known breeding population in Washington (Stinson 2001, Interagency Lynx Biology Team 2013). Although lynx have been occasionally reported from the Kettle Mountains and northeastern corner of the state, these animals were likely transient individuals from British Columbia (Stinson 2001).

Lynx habitat in Washington is limited to high-elevation, sub-boreal forests highly fragmented by topography, disturbances, open alpine areas and meadows, timber harvest, roads, and human development (Koehler et al. 2008). Furthermore, in 2006 the Tripod Fire burned most of what was considered the most extensive and high-quality lynx habitat in Washington (Stinson 2001, Koehler et al. 2008).

1.1.4.1 Previous Lynx Studies in Washington

Although several studies identify the habitats lynx select in Washington (McKelvey et al. 2000c, von Kienast 2003, Koehler et al. 2008, Maletzke et al. 2008), these studies were performed a decade or more ago and recent wildfires have dramatically changed the landscape. Also, these studies focused on core habitats that lynx use for daily activities such as hunting, resting, and denning, but they did not explicitly examine the other habitats lynx travel through. Critical questions thus remain concerning the landscape features lynx use to travel and whether, when, and how areas that burned recently are used (Ruediger et al. 2000, Stinson 2001). Characterizing the habitats lynx use for travel is integral to lynx conservation in Washington for several reasons: 1) Washington lynx habitat is highly fragmented, 2) immigration from core populations in Canada may be important to lynx population persistence in the North Cascades, 3) lynx travel long distances to disperse and make exploratory movements, and 4) climate change is projected to increase the frequency and severity of wildfires and thus increase habitat loss and fragmentation for lynx.

Besides characterizing the habitats lynx use for travel, habitat linkages based on empirical data need to be modeled throughout the North Cascades to identify important areas for habitat conservation. Although four studies have examined lynx habitat connectivity in Washington, each study used expert opinion and literature review rather than actual field data to estimate the resistance of habitats to lynx movement. The coarse scale maps of lynx habitat connectivity throughout the Northwest US and Southwest British Columbia area produced by Singleton et al. (2002) and the WWHCWG (2010) do not reveal fine-scale details (e.g., how fires influence movements) of connectivity within the North Cascades region, and although the other two studies of lynx habitat connectivity in Washington provide finer-scale depictions of habitat connectivity, they are peripheral to the central portion of the North Cascades. Begley and Long (2009) modeled lynx dispersal habitat in a limited area around the Stevens Pass area of the North

Cascades. Gaines et al. (in prep) assessed connectivity in Northeastern Washington outside of the North Cascades.

To address these gaps in our understanding of lynx ecology, I addressed the following specific objectives using data from 17 lynx inhabiting the North Cascade Mountains and previously radio-collared by a team of state and Federal government agency researchers.

1. In Chapter 2 my objective was to predict the core habitats lynx regularly select for denning, hunting and resting in the North Cascades. I determined general core habitat selection by creating an Overall Core Habitat Model using all lynx data sets to create a Random Forest model. I also examined differences between core habitat selection in the separate Black Pine Basin and Loomis study areas, during summer versus winter, and between male and female lynx by creating separate Random Forest core habitat models for each.

2. In Chapter 2, I also described the habitats lynx used for traveling by creating a Random Forest model of the landscape features lynx use when traveling across matrix areas.

3. In Chapter 3 I analyzed the habitats lynx used while in burned areas. I used Random Forest to address how burn severity, spatial configuration, and habitats affect lynx use of burned areas.

4. In Chapter 4 my objective was to model lynx habitat connectivity throughout the North Cascades. I created a resistance surface and modeled least-cost linkages based on results of the core and travel habitat models examined in Chapter2.

5. Finally, in Chapter 5, I synthesized the results of my habitat models and connectivity models to expand our understanding of lynx ecology in a landscape with

frequent fires and high fragmentation. I also discuss how my results can help to guide managers working to protect the Threatened population of lynx in Washington.

CHAPTER 2
LYNX HABITAT IN THE NORTH CASCADE MOUNTAINS, WASHINGTON

2.1 LITERATURE REVIEW AND OBJECTIVES

As habitat loss and fragmentation increase in the wake of human population growth and climate change, habitat conservation becomes increasingly important for the conservation of biodiversity. However, to conserve habitat for wildlife we must first know which habitats an animal uses. Linking an animal's behavior to habitat selection is integral to a full understanding of habitat use, since it allows us to distinguish between habitats selected for different activities (Roever et al. 2014). For example, an animal may forage or rest in one type of habitat, and travel through a different type (Dickson et al. 2005, Owen-Smith et al. 2010). The distinction between habitat an animal uses for breeding and foraging and those used for traveling may become especially important in fragmented landscapes when animals travel through less suitable habitats to access patches of foraging habitat (Roever et al. 2014). To conserve animals living in a fragmented landscape, we must conserve not only their core habitats but the habitats they select for traveling between these patches of core habitat. In this chapter, I examine the habitat selection of a population of Canada lynx (*Lynx canadensis*) living in a fragmented landscape in Washington. This lynx population occupies a fragmented landscape that requires individuals to select different habitats to travel between patches of prime habitat.

2.1.1 Predicting and Describing Wildlife Habitat Use

2.1.1.1 Resource Selection Functions

Identifying, managing, and conserving habitat for a species requires that scientists first understand how the animal uses different landscape features. Many methods for estimating an animal's use of space and resources have been developed, but the Resource Selection Function is the dominant tool for describing wildlife habitat use (McLoughlin et al. 2010). A Resource

Selection Function is defined as a function that is proportional to the probability of use by an organism (Manly et al. 2002). To estimate the Resource Selection Function, resource units (for example, pixels in a Geographical Information System [GIS]), are described by predictor variables representing abiotic factors such as elevation, biotic factors such as forest type, or human disturbance factors such as distance to the nearest road. The resource units are sampled as either "used" by the animal or "non-used", or as "used" and "available" when non-use of a resource is uncertain (Manly et al. 2002). "Used" and "available" study designs are employed when telemetry data identify used resources but all other pixels on the landscape could potentially be used as well (Boyce et al. 2002). Thus, a sample of pixels representing resource units are selected as available to the animal for comparison with those used by the animal.

To estimate a Resource Selection Function, binomial generalized linear regression is most often used (Boyce et al. 2002, McLoughlin et al. 2010). Used and available data are fit to a generalized linear regression so that the interaction between the predictor variable(s) and the response variable(s) can be described by a linear function, which is assumed to emulate the relationship found in nature (Boyce et al. 2002, Manly et al. 2002). For example, if in nature the probability of use for a certain animal increases as elevation increases, then a linear model can accurately describe the relationship between the predictor variable (elevation) and the response variable (probability of use). By comparing used and available data with the statistical rigor of mathematical modeling, Resource Selection Functions can be used to estimate the probability of use by a species across its landscape and help reveal the complex reactions of a species to the features in its landscape (Boyce et al. 2002, Manly et al. 2002).

2.1.1.2 Random Forest Models

While Resource Selection Functions may be the predominant methodology for predicting and describing habitat use, a relatively new machine-learning algorithm, Random Forest, (Breiman 2001), has begun to be used for habitat analysis (Cutler et al. 2007, Vezza et al. 2012, Wilsey et al. 2012, Mochizuki and Murakami 2013). Random Forest does not assume independence of samples, accommodates interactions among variables and across scales, and the complex non-linear relationships common to ecological data (Cutler et al. 2007, Evans and Cushman 2009, Evans et al. 2011). Random Forest also accommodates many predictor variables, and *a priori* hypothesis regarding the direction of the response variables are not made, allowing unexpected interactions to be discovered (Evans et al. 2011). Random Forest may be particularly useful when considering spatial scale in a habitat selection model since the scales at which animals respond to habitat are often unknown (Boyce 2006, Cunningham and Johnson, 2006, Carrasco et al. 2014). For this reason, including habitat variables at multiple scales in one model could help to disentangle how spatial scale influences a species' habitat selection. Including many scales in one model quickly grows the number of predictor variables, making Random Forest an attractive option for multi-scale modeling (Carrasco et al. 2014). Indeed, Random Forest and other related machine-learning algorithms often yield better predictions than parametric statistical models, including Generalized Linear Models (Cutler et al. 2007, McCue et al. 2013).

Despite this finding of strong predictive power, Random Forest has yet to enter the mainstream of ecological research (Cutler et al. 2007), perhaps due to the perception that Random Forest offers limited insight into the biological mechanisms by which an organism reacts to its landscape (Cutler et al. 2007, McCue et al. 2013). That is, Random Forest may predict that the probability of use at a certain location is high, but reveals limited insight as to why the organism would select that location. However, recent advances in *post-hoc* Random Forest analysis have eased biological interpretation, making Random Forest a better inferential tool for habitat analysis (Cutler et al. 2007, Evans and Cushman 2009, Siroky 2009, Murphy et al. 2010, Evans et al. 2011). For example, although Random Forest can accommodate many predictor variables, interpreting a model with many variables is difficult. Murphy et al. (2010) developed a model selection procedure for identifying the most parsimonious model including only significant variables, thus increasing ease of interpretation. In addition, partial dependence plots demonstrate how a predictor variable affects the probability of a response variable class (such as use) when all other predictor variable effects are averaged (Cutler et al. 2007, Evans et al. 2011).

The Random Forest algorithm is an extension of Classification and Regression Tree approaches (Breiman et al. 1983). I will limit this description of the Random Forest algorithm to classification trees since the used and available data analyzed in many habitat studies is binary and therefore categorical, whereas regression trees predict continuous variation. Classification trees use binary partitioning to split a dataset into increasingly smaller groups (nodes), based on the predictor variable at each node that best divides the data into two homogenous groups as measured by the Gini Index. Splitting continues until further splitting would not increase the Gini Index, resulting in a hierarchical set of rules for prediction. Random Forest improves the predictive ability of Classification and Regression Trees by using an ensemble of weak learners ("trees") instead of just one tree. In Random Forest for classification, bootstrap samples of the data are used to create many classification trees that, when combined, converge on the best solution. The algorithm runs as follows (Breiman 2001 provides more detail):

1. The researcher chooses a number of bootstrap samples to be drawn with replacement from the original dataset. These bootstrap samples comprise the training dataset, while the unselected data points are referred to as the out-of-bag dataset and are used to assess model fit.

2. A limited number of random predictor variables are tested at each node as candidates for best dividing the response variable into two homogenous groups. The data are split by the best predictor variable until a classification tree is fully grown for each bootstrap sample.

3. To calculate the error rate of the random forest model, the out-of-bag dataset is used to test the model. Each tree in the forest predicts the classification of every out-of-bag observation. For each out-of-bag observation, the classification most often predicted by the trees becomes the observation's final predicted classification, x. The number of times that x is incorrect divided by the number of out-of-bag observations is the error rate.

4. To assess and rank the importance of each predictor variable the values of each variable are randomly permuted for the out-of-bag observations. These modified out-of-bag observations are run down the trees. The misclassification rate of the modified out-of-bag observations is subtracted from the misclassification rate of the unmodified out-of-bag observations. This number divided by the standard error results in a measure of importance for each predictor variable. For example, if the variable "elevation" is randomly permuted but the resulting misclassification rate is not very different from the original misclassification rate, "elevation" is not an important predictor of classification.

Animals likely respond to a large number of landscape features and may respond not only to individual habitat variables, but to different combinations of variables. Further complicating habitat selection, animals may have non-linear responses to habitat features. Habitat selection patterns may be especially complex for wide-ranging species living in fragmented landscapes where many different habitat types are encountered. Random Forest and its ability to accommodate a large number of predictor variables, non-linear responses to predictor variables, and interactions between variables is thus a well-suited method for unraveling the intricacies of how animals react to landscape features in a fragmented and heterogeneous environment.

2.1.2 Lynx in a Fragmented Landscape

Canada lynx in the contiguous US occur at the southern edge of lynx range. The boreal forest that lynx inhabit is relatively continuous in the core of their range in Canada and Alaska, but at the southern edge of lynx range the boreal forest becomes fragmented and patchy as it transitions into southern montane forest types (Agee 2000). Topography, wildfires, and human-caused habitat destruction further fragment lynx habitat at the southern range edge, resulting in scattered, low-density lynx populations (Buskirk et al. 2000b, McKelvey et al. 2000b). In 2000, lynx were federally listed as Threatened in the contiguous US, where they persist in the sub-boreal forest of the north-eastern, Great Lakes, and western states (McKelvey et al. 2000b, US Fish and Wildlife Service 2000).

2.1.2.1 Lynx in the North Cascade Mountains, Washington

The North Cascade Mountains of Washington support one of the few remaining lynx populations in the contiguous US and the only resident breeding population in Washington (Stinson 2001). According to a 2008 population model of Washington lynx habitat by Koehler et al. (2008), the state provided habitat for an estimated 87 lynx. Washington lynx select sub-boreal forest types on moderate slopes at elevations between 1,200 and 2,000 m, where their primary prey, the snowshoe hare (*Lepus americanus*), occur (Koehler 1990, Koehler et al. 2008, McKelvey et al. 2000c). Specifically, lynx in the North Cascades select old-growth multilayer Engelmann spruce (*Picea engelmannii*)-subalpine fir (*Abies lasiocarpa*) forest (the climax sere of the *Abies lasiocarpa* Zone; Franklin and Dyrness 1973), where canopy openings encourage dense understory growth and low-reaching boughs create additional horizontal cover and forage for snowshoe hares (Hodges 2000b, Koehler et al. 2008, Lewis et al. 2011). Lynx also select young lodgepole pine (*Pinus contorta*) forest (often present as an early-seral stage of the *Abies lasiocarpa* Zone; Franklin and Dyrness 1973), where high stem densities support snowshoe hares (Koehler 1990, McKelvey et al. 2000c). However, the topography of the North Cascades naturally fragments high-quality lynx habitat with land cover types that support few snowshoe hares (Lewis et al. 2011). Dry Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*) forests occur on southerly aspects and at lower elevations. At higher elevations, bare rock and subalpine meadows fragment lynx habitat (Koehler et al. 2008).

In addition, recent burns fragment high-quality, core lynx habitat (Koehler et al. 2008). Forest fires are the dominant disturbance in western boreal and sub-boreal forests, and create a landscape mosaic consisting of forest stands with different ages, species, and structures (Agee 2000). Previous studies of lynx in the North Cascades found that lynx do not use new burns for foraging since young seedlings are not dense enough to support high numbers of hares, especially in the winter when snow covers much of the regenerating growth (von Kienast 2003, Koehler et al. 2008). However, patches of unburned forest within a burn may support higher densities of snowshoe hares, and lynx have been observed crossing recent burns to reach these patches (Walker 2005, Koehler et al. 2008).

Historically, fire return intervals in the North Cascades differed between lodgepole pine forests and Engelmann spruce-subalpine fir forests. Lodgepole pine forests generally burn at shorter intervals and regenerate relatively quickly, as their seeds release from serotinous cones, and peak densities of trees develop within 50 years (Agee 1993). Conversely, Engelmann spruce-subalpine fir forests burn at longer intervals, are easily killed by fire, and take decades to centuries to regrow (Agee 2000). If a lodgepole pine seed source is present, early succession of the Engelmann spruce-subalpine fir forest may be dominated by lodgepole pine for 150 years before spruce and fir trees establish (Agee 1993). Sites may remain as lodgepole forest for longer than 150 years if fires repeatedly burn the area before spruce and fir trees can establish (Agee 1993). When spruce-fir forests burn and a lodgepole pine seed source is not present, the site may remain a shrubby meadow for tens to hundreds of years before spruce and fir trees recolonize (Agee 2000).

Climate change will likely change the historical disturbance regime of subalpine forests in the North Cascades. As a result of warmer and drier conditions, fires in western forests are predicted to be more frequent, larger, and higher intensity (Fauria and Johnson 2007, Soja et al. 2007, Balshi 2009, Littell et al. 2010); indeed the 2014 Carlton Complex fires cover the largest area on record for Washington. Increasing fires will dramatically alter and fragment lynx habitat, shifting the North Cascades landscape away from the early stand development and old-growth stages lynx and snowshoe hares select, and towards the open stand-initiation stage they avoid (Appendix A describes stand development stages). In 2006, the 70,644 ha Tripod Fire burned most of what was considered the most extensive and high-quality lynx habitat in Washington (Stinson 2001, Koehler et al. 2008). In addition, the 1994 Whiteface Burn (1,554 ha), the 1994 Thunder Mountain Fire (3,686 ha), the 2001 Thirty-Mile Fire (2,465 ha), and 2001 Farewell Fire (32,278 ha) all burned lynx habitat in the North Cascades.

Human activities such as timber management also fragment lynx habitat (Stinson 2001). Similar to high severity wildfires, clearcuts create forest openings that lynx do not select until tree regeneration provides adequate forage and cover for snowshoe hares (von Kienast, 2003, Hoving et al. 2004, Koehler et al. 2008, Maletzke et al. 2008). Harvest units that are thinned also degrade lynx habitat since the decrease in tree density and understory removal leave little cover and browse for snowshoe hares (Koehler 1990, Hodges 2000b, Koehler et al. 2008).

As a result of fragmentation, the North Cascades provide patchy habitat that forces lynx to cross low quality habitats ("matrix" habitat hereafter), to colonize new home ranges, find mates, and explore. At a finer scale, habitat fragmentation within lynx home ranges forces lynx to cross areas of matrix habitat to reach hunting and denning habitat ("core" habitat hereafter) (Koehler et al. 2008, Maletzke et al. 2008).

Although several studies in Washington identified the habitats lynx select (von Kienast 2003, Koehler et al. 2008, Maletzke et al. 2008), these studies were performed a decade or more ago and wildfires continue to change the landscape. Also, these studies focused on core habitats lynx use for daily activities such as hunting, resting, and denning; habitats used for travel have been little studied. Lynx in the US have been noted to travel through habitats not selected as core habitats such as shrub-steppe (Squires and Laurion 2000), open mature forests and thinned forests (Koehler 1990), and dry forests or recently-burned areas (Walker 2005) indicating that lynx may select a broader spectrum of habitats for traveling than they do for core habitats. It has also been hypothesized that lynx may use ridgelines and draws to travel (Stinson 2001).

Critical questions remain concerning the habitats lynx use to travel across the matrix and whether, when, and how burned areas facilitate or prevent movement (Ruediger et al. 2000, Stinson 2001). In pursuit of understanding how lynx in Washington use habitat, in this chapter I examine a small population of lynx living at their southwestern range edge in the North Cascade Mountains. I use Random Forest to analyze the core habitats lynx use for hunting and denning as well as the landscape features lynx select for traveling between patches of core habitat in a landscape fragmented by topography, wildfires, and human disturbance. I have two specific objectives:

1. to model core habitat use for lynx in the North Cascades. I used Random Forest to develop habitat models that characterize core (hunting and denning) habitat of lynx in the North Cascades. I developed models depicting Overall Core Habitat using the entire lynx dataset, core habitat in Black Pine Basin study area versus the Loomis study area, Male versus Female Core Habitat Models, and Summer versus Winter Core Habitat Models.

2. to model travel habitat for lynx in the North Cascades. I again used Random Forest to create a Travel Habitat Model that characterizes the landscape features lynx use when traveling across matrix habitat. This model was not further subdivided into study area, sex, or seasonal models, due to the smaller number of lynx locations supporting this analysis.

2.2 STUDY AREA

My study took place in the Okanogan portion of the Okanogan-Wenatchee National Forest and the Loomis State Forest, both located on the eastern slope of the North Cascade Mountains in Washington. These forests fall within the Okanogan Lynx Management Zone, as designated by the Washington State Lynx Recovery Plan (Stinson 2001). In the Okanogan-Wenatchee National Forest, I worked in the 250 km^2 Black Pine Basin, spanning from Fawn Peak and Buck Mountain north to the Pasaytan Wilderness, east to the Lost River Gorge, and west to Eight Mile Creek. I also worked in the Loomis study area, which is positioned approximately 15 km east of the Black Pine Basin and is separated by the "Meadows" area, which was considered the best lynx habitat in the state (Stinson 2001) until the 2006 Tripod Fire burned most of it. The Loomis study area ranges from 3 km south of Highway 20 north to the Canadian border, and west to east from the North Twenty Mile Peak to the Sinlahekin Valley. The Loomis study area is a 1,225 km^2 portion of land of which 66% falls in the Okanogan-Wenatchee National Forest and 34% in the Loomis State Forest, managed by the Washington Department of Natural Resources (**Figure 2.1**).

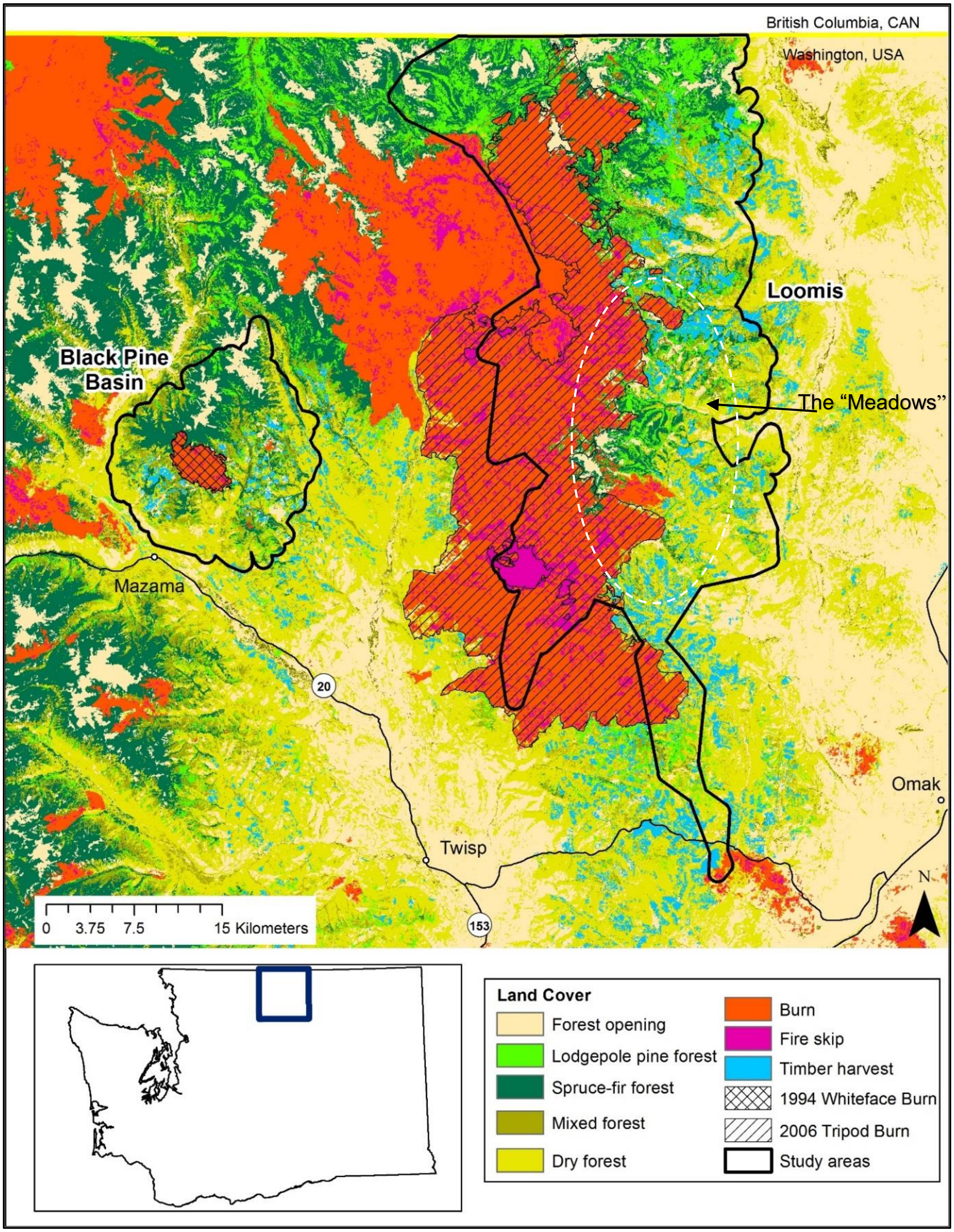


Figure 2.1. The Black Pine Basin and Loomis study areas located in north central Washington. The 2006 Tripod Burn separates the two study areas.

Both study areas are mountainous, with the Black Pine Basin having slightly more rugged terrain (mean slope = 23°) than the Loomis study area (mean slope = 16°). Elevations range from 657 – 2,577 m across both study areas, with 62% and 65% of the Black Pine Basin and Loomis areas respectively in the 1,290-1,925 m elevation range. Average monthly temperatures in nearby Mazama, Washington (elevation: 664 m) range from -10°C to 23°C with average annual snowfall of 305 cm (Western Regional Climate Center, http://www.wrcc.dri.edu/, accessed June 20, 2014).

Forests on the Black Pine Basin and Loomis study areas vary according to site temperature and moisture, which is dictated by topography and aspect. The sub-boreal forest spans from mid-elevation to timberline and consists of Engelmann spruce-subalpine fir ("spruce-fir" hereafter) forest or lodgepole pine forests. Mid-elevation forests vary according to topography with sub-boreal forests generally occupying cool pockets and north-facing slopes (Lillybridge et al. 1995). Forests transitioning from a sub-boreal type into a drier forest dominated by Douglas fir ("mixed forest" hereafter) generally exist on south-facing slopes. Lower elevation forests are dominated by dry Douglas fir-ponderosa pine forests ("dry forest" hereafter), (Lillybridge et al. 1995). Forest openings such as grassy or shrubby meadows and rocky areas comprise a small portion of both study areas (**Table 2.1**).

Table 2.1. Land cover percentages in the Black Pine Basin and Loomis study areas. The % of each forest type listed includes undisturbed forests and regenerating forests disturbed after 1985. The "Other" category refers to unclassified natural disturbances and human infrastructure.

Land Cover	Black Pine Basin	Loomis
% of study area		
Forest opening	10	9
Burned[a]	5	30
Harvested[a]	5	6
Forested[b]	79	54
Other	1	1
% of forested area		
Spruce-fir	35	31
Lodgepole pine	7	30
Mixed forest	18	9
Dry forest	39	30
Deciduous	1	<1

[a] 1985-2012.
[b] Undisturbed from 1985-2012.

Several large fires have burned in the study areas within the last 20 years (since 1994). In the Black Pine Basin, the Whiteface Fire (1,554 ha) burned in 1994 and the Sweetgrass Fire (73 ha) burned in 2003. In the Loomis, the Thunder Mountain Fire (3,686 ha) burned in 1994, the Isabel Fire (1,833 ha) burned in 2003, and the Tripod Fire (70,644 ha) burned in 2006.

In addition to wildfires, timber harvest contributes to forest disturbance in the Black Pine Basin and Loomis study areas. On the Okanogan-Wenatchee National Forest, harvest trends since the early 2000s have emphasized thinning low-elevation dry Douglas fir and ponderosa pine forests, rarely harvesting in the upper elevation forests that lynx use (Kent Woodruff, personal communication). The Loomis State Forest continued to harvest in high elevation forests until 2006, after which harvests have been concentrated in low-elevation dry forests (Scott Fisher, personal communication), (**Table 2.1**).

In the Black Pine Basin, gravel roads are numerous at mid and lower-elevations and total ~375 km or 1.5 km/km^2. In the Loomis study area, there are fewer gravel roads on the Okanogan-Wenatchee National Forest, but roads are numerous on the Loomis State Forest. Across the Loomis study area, road length totals ~1,490 km or 1.2 km/km^2. Roads on the Black Pine Basin and Loomis study areas range from abandoned and closed roads to roads maintained and regularly used. Most roads are accessible during the winter by snowmobile, and some roads are groomed for this purpose.

2.3 METHODS

Lynx were trapped and fitted with Global Positioning System (GPS) telemetry collars in the Okanagan-Wenatchee National Forest and the Loomis State Forest from January 2007 to April 2012. Trapping took place during the winter using box traps (Kolbe et al. 2003) as a collaboration between the Washington Department of Fish and Wildlife, Washington Department of Natural Resources, U.S. Forest Service, U.S. Bureau of Land Management, and the U.S. Fish and Wildlife Service (John Rohrer, personal communication). The collars were programmed to record GPS locations every four hours for one year, except for one collar programmed to record GPS locations every six hours. The average fix rate of collars was 72%. It is possible that dense forest habitats deteriorated the fix rate of the GPS collars, so that lynx locations were recorded less frequently in the densest canopy covers (Hebblewhite et al. 2007).

Data from 17 lynx were obtained, 5 of which were collared in the Black Pine Basin and 12 in the Loomis State Forest. Fourteen of the 17 collared lynx were males. One of the male lynx collared in the Black Pine Basin (number 312) did not appear to have a home range. Instead, he spent two months in the Black Pine Basin and nearby areas before leaving on several long distance movements outside of the Black Pine Basin. Male 312 then returned to the Black Pine Basin and traveled to the Loomis study area, where his collar died (Appendix B). Four of the lynx collared in the Loomis area left the study area and went into British Columbia, Canada. Two of these lynx returned to the Loomis study area and two remained in British Columbia until they were legally harvested. One lynx in the Loomis study area lived in a home range that crossed the border into Canada.

I eliminated GPS locations from 312's long-distance movements outside of the study areas, lynx locations within British Columbia, and any locations that were clearly a result of collar error (locations farther away from the previous and following locations than a lynx could credibly travel). Several of the lynx in the Loomis area made short exploratory movements outside of their home range but within the US (furthest location away from a home range was approximately 35 km). I did not remove locations from these exploratory movements.

After filtering the data, 20,564 lynx locations remained for the analysis, 6,772 of which were in the Black Pine Basin and 13,792 in the Loomis (**Figure 2.2**). Excluding time spent on 312's long-distance movements or time spent in British Columbia, data from 11 of the lynx span one or more years while data from six lynx span less than one year.

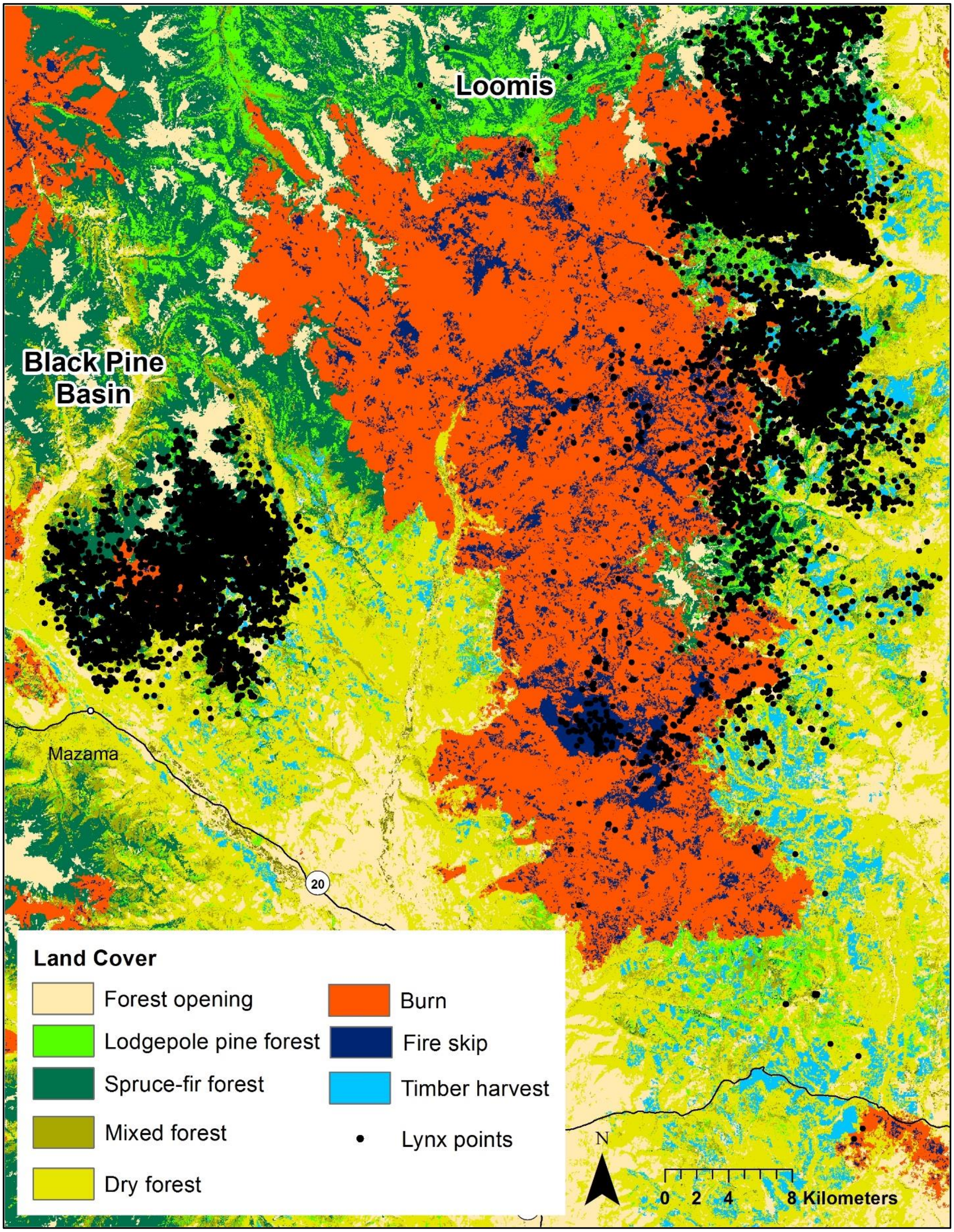

Loomis
Black Pine Basin
Mazama
20
Land Cover
Forest opening
Lodgepole pine forest
Spruce-fir forest
Mixed forest
Dry forest
Burn
Fire skip
Timber harvest
Lynx points
N
0 2 4 8 Kilometers

Figure 2.2. Lynx telemetry points used for the habitat analysis in the Black Pine Basin and Loomis study areas located in the North Cascade Mountains, Washington.

2.3.1 Study Area Delineation for Modeling Available Habitat

To delineate the Black Pine Basin and Loomis study areas, I used ArcGIS 10.1 (ESRI 2012) to create polyline features connecting consecutive lynx locations. I then buffered the lines by 766 m, the average straight-line distance traveled by a lynx in the four-hour period between GPS fix attempts. The outermost edges of the buffered lines were used to delineate the Black Pine Basin and Loomis study areas. The resulting study areas represent the space available to the lynx while using core areas and crossing through matrix habitats, while keeping areas lynx never went to a minimum. To examine lynx habitat use in the Black Pine Basin and Loomis study areas, I used ArcGIS 10.1 (ESRI 2012) to generate random available locations within each study area that were equal to the number of used locations in each study area (Barbet-Massin et al. 2012).

2.3.2 Habitat Variables

I used GIS layers to represent the heterogeneity of North Cascades land cover, disturbance, patch metrics, topography, climate, forest structure, and human disturbance (**Table 2.2**). Using 15 GIS data layers (Appendix C), I used ArcGIS 10.1 (ESRI 2012) to derive continuous representations of each predictor variable using 30 m^2 pixels projected into the 1983 North American Datum Albers coordinate system. To capture habitat selection at different scales, I represented each landscape variable as a percentage within 3x3 and 27x27 pixel windows. I represented the forest structure, topographic, and climate variables and the percent canopy cover as the average value within 3x3 and 27x27 pixel windows. A 3x3 pixel window represents a small-scale area and has a diameter of 90 m. I chose a 3x3 pixel windows since it was the smallest-scale possible to depict as a continuous variable and, based on my field observations, I hypothesized that lynx select habitats at a small-scale. A 27x27 pixel window represents a large-scale area and has a diameter of 810 m. I chose a 27x27 pixel window hypothesizing that this area represented the largest-scale perceived by a lynx operating within its home range.

2.3.2.1 Land Cover

I included land cover variables that may influence lynx habitat use, based on a literature review and on field observations. I selected lodgepole pine forest, spruce-fir forest, and dry forest since previous studies in the North Cascades found that lynx habitat selection was influenced by these forest types (McKelvey et al. 2000c, Koehler et al. 2008, Maletzke et al. 2008). As sub-boreal forests transition into lower elevation dry forests, some forest stands may be comprised of the sub-boreal tree species lynx use and the dry forest tree species, Douglas fir, that lynx do not use. I included this mixed forest type, hypothesizing that lynx may use it less than sub-boreal forest but more than dry forests. Mixed forests have not, to my knowledge, been previously examined for lynx use in the North Cascades. Finally, I included deciduous forests, a forest type unexamined for lynx use in the North Cascades.

In addition to the five forest types listed above, I included three forest opening types to capture the heterogeneity of forest openings and the possible differences in lynx selection between them. I separated rocky or icy areas, grasslands, and shrub lands as distinct categories of forest openings.

Table 2.2. Land cover variables used in Random Forest models of lynx habitat selection.

Variable Class	Variable	Layer Name	Measurement Type
Land Cover	Lodgepole pine	lp	Number of like pixels within a 3x3 or 27x27 window
	Spruce-fir	essf	
	Mixed forest	mixed	
	Dry forest	dry	
	Deciduous forest	decid	
	Ice or rock	rock_ice	
	Grassland	grass	
	Shrub land	shrub	
Disturbance	Old clearcut	old_cut	Number of like pixels within a 3x3 or 27x27 window
	Old, thinned forest	old_thin	
	New clearcut	new_cut	
	New, thinned forest	new_thin	
	Old, high-severity fire	oldhigh_f	
	Old, low-severity fire	oldlow_f	
	New, high-severity fire	newhigh_f	
	New, low-severity	newlow_f	
	Fire skips	fireskips	
Patch Metrics	Area of forest opening	area_fo	Square meters
	Area of harvest	area_cut	Square meters
	Distance to edge of forest opening	distedge_fo	Meters
	Distance to edge of harvest	distedge_cut	Meters
	Distance to edge of fire	distedge_fire	Meters
Topography	Slope	slope	Degrees averaged across a 3x3 or 27x27 window
	Distance to nearest draw	dist_draw	Meters
Climate	Compound Topographic Index	cti	Index, higher numbers indicate wetter areas. Index averaged across a 3x3 or 27x27 window
	Heat Load Index	hli	Index, higher numbers indicate warmer areas. Index averaged across a 3x3 or 27x27 window
	Growing season precipitation	gsp	Average total precipitation (mm) between April and September. Index averaged across a 3x3 or 27x27 window
Forest Structure	Canopy cover	can_cov	Average percent canopy cover in a 3x3 or 27x27 window

2.3.2.2 Disturbance

To examine in detail how lynx respond to fires, I included variables depicting old, low-severity burns (fire years 1985-1997, canopy cover loss of 1-50%), old, high- severity burns (canopy cover loss of 51-100%), new, low- severity burns (fire years 1998-2012), new, high-severity fires, and areas within fire perimeters that did not burn ("fire skips" hereafter).

I also included variables depicting old, thinned forests (harvest years 1985-1997, canopy cover loss of 1-50%), old clearcuts (canopy cover loss of 51-100%), new, thinned-forests (harvest years 1998-2012), and new clearcuts.

2.3.2.3 Patch Metrics

The type, size, and spatial arrangement of a forest opening may affect how a lynx responds to it (von Kienast 2003, Walker 2005, Koehler et al. 2008). To examine how lynx use different opening types and sizes, I included variables depicting patch metrics for forest openings (mostly created by rocky or icy areas, grasslands, or shrub lands), timber harvest, and burns. For forest openings and timber harvest, I calculated their size. I did not include an area variable for burns since there was only one major burn on the Loomis study site and one on the Black Pine Basin study site. These burned in different years, which confounds an analysis of size differences. For each opening type, I also included a metric depicting the distance from each pixel within the opening to the nearest edge.

2.3.2.4 Topography

To incorporate the influence of topography on lynx habitat use, I included a variable depicting the distance to the nearest draw and a variable depicting slope. I did not include elevation as a topographic variable since elevation is a proxy variable that indirectly measures multiple ecological processes. Lynx response to elevation is likely indirect, linked more directly to the shifts in climate and temperature that occur at varying elevations.

2.3.2.5 Climate

Hypothesizing that lynx select north-facing slopes for their cooler, moister climate, I included the Heat Load Index, a measure of temperature based on aspect and slope (McCune and Keon 2002). Since wetness may affect the amount of vegetative cover and the regeneration rate of disturbed areas, I also included the Compound Topographic Index, which measures wetness based on the area of upstream contributing area and slope (Moore et al. 1993, Gessler et al. 1995). Similarly, I included a layer depicting the average total precipitation accumulated during the growing season (April through September).

2.3.2.6 Forest Structure

I used canopy cover to represent the density of a forest stand and as an indirect measure of understory. Although canopy cover density does not directly represent understory cover, Koehler et al. (2008) found that moderate understory and canopy cover were correlated in their North Cascades lynx study.

2.3.3 Model Development

I developed seven core habitat models and one travel habitat model using Random Forest (Breiman 2001) implemented in program R 3.1.2 (R development core 2014) with the package rfUtilities (Liaw and Wiener 2002, Evans and Murphy 2014), (**Table 2.3**). For each model, I used an equal number of used and available points to insure unbiased sampling of each class (Evans and Cushman 2009). To mitigate for autocorrelation and redundant data issues, which are common to GPS location datasets with short time intervals between fixes (Cushman 2010), I sub-sampled the used and available points, extracting 20% of the data for each model. I sub-sampled the used lynx locations using the R program Spatial Intensity Weighted Subsample. This program created a kernel density estimate for each lynx and then sub-sampled each animal's point locations so that the sub-sample drew more points from the areas a lynx used more. I sub-sampled the available points randomly.

Table 2.3. Lynx locations and available locations used to construct each of the seven Core Habitat Models and the Travel Habitat Model. For each model, the number of available points equaled the number of lynx points. Summer = May – October, Winter = November – April.

Model Name	Data Compared:	Number of lynx points before sub-sample
Overall Core Habitat Model	all used points to all available points	20,564
Travel Habitat Model	used points within matrix areas to available data points within matrix areas	2,023
Black Pine Basin Core Habitat Model	used points in the Black Pine Basin study area to available points in the Black Pine Basin study area	6,772
Loomis Core Habitat Model	used points in the Loomis study area to available points in the Loomis study area	13,792
Female Core Habitat Model	all points used by female lynx to an equal number of available points from across both study areas	3,729
Male Core Habitat Model	all points used by male lynx to an equal number of available points from across both study areas	16,835
Summer Core Habitat Model	all points collected during the summer to an equal number of available points from across both study areas	8,818
Winter Core Habitat Model	all points collected during the winter to an equal number of available points from across both study areas	11,746

2.3.3.1 Core Habitat Models

To insure that no one lynx was having a disproportionally large impact on the results of a Random Forest model, I used a jackknife resampling technique. For each lynx included in a model dataset, I ran Random Forest while leaving that lynx' dataset out. Comparing the amount of variance explained by each run could indicate whether a certain lynx used habitat drastically differently than the others. Examining the results of each jackknife test I found that no lynx used habitat significantly differently than the others except in the Female Core Habitat Model. Only one of the three female lynx lived in the Loomis study area, so she was identified as having a different habitat selection pattern from the two Black Pine Basin female lynx. Because the Loomis female's habitat selection pattern was the product of having different available habitat (most importantly, the Tripod Burn), and not unique habitat preferences, I retained the Loomis female's data in the Female Core Habitat Model.

Although Random Forest can accommodate multi-collinear variables, removing multivariate redundant variables can ease interpretation and improve model performance. To eliminate such variables I used methods developed by Murphy et al. (2010) prior to running each habitat model. I also used a Spearman rank test to identify highly collinear variables ($r > 0.8$). Between collinear variables, I retained the variable with a higher importance value as indicated by an initial Random Forest run including all habitat variables. In cases where variables had similar importance values, I retained the variable of higher interest or the variable that would increase the variety of habitat characteristics explored in my models.

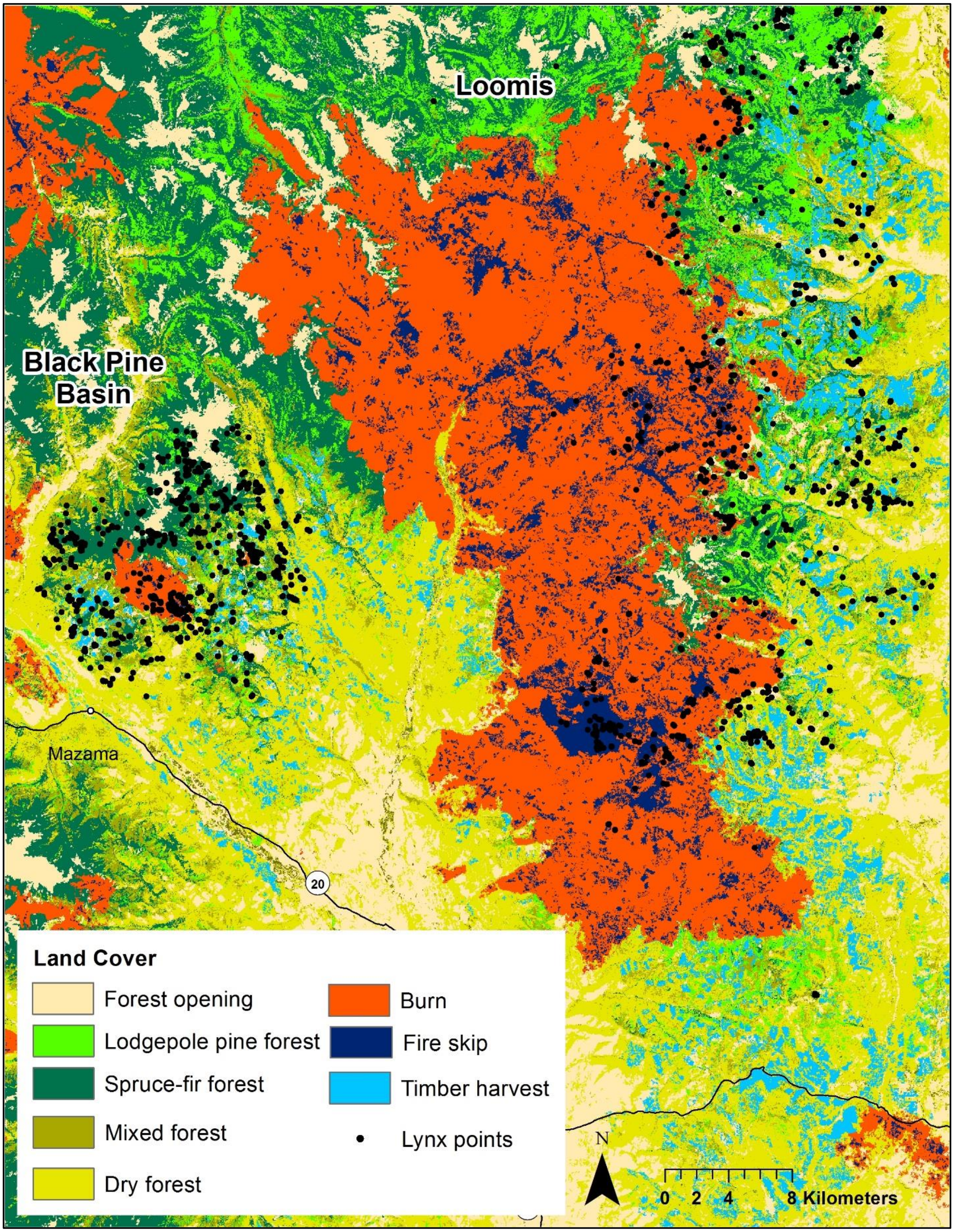
While Random Forest can function with a large number of predictor variables, using only the most important variables in a Random Forest model can identify which variables contribute to model performance and thus improve interpretability and model performance. To identify a parsimonious set of predictor variables for each habitat model, I ran Random Forest using 5,000 bootstrap replicates (trees) and applied a model selection procedure developed by Murphy et al. (2010). The procedure calculated a Model Improvement Ratio for each variable based on each variable's importance to the Random Forest model. Next, variables with Model Improvement Ratios above increasingly high thresholds (thresholds range from 0-1 in 0.1 increments) were grouped. The final group of variables were chosen based on minimizing the out-of-bag error, the within-class error, and the number of variables in the Random Forest model. After selecting a subset of predictor variables for each of the seven habitat models, I again ran Random Forest for each habitat model using the selected habitat variables.

To assess the performance of each habitat model, I examined the model-fit based on the out-of-bag error (Liaw and Wiener 2002, Evans and Murphy 2014). I also performed an independent validation using the withheld used locations and an equal number of withheld available locations to assess accuracy, sensitivity and specificity (the proportion of used locations correctly predicted and the proportion of available locations accurately predicted), the area under the curve of a Receiver Operator Characteristic (AUC), (a measure of how evenly the model predicts sensitivity and specificity), and the Kappa statistic (a measure of how much better the model predicted used and available points than expected by random chance) (Murphy et al. 2010, Evans et al. 2011). Finally, each model's significance was assessed by randomizing the used and available data 1,000 times to create a null distribution of variance for comparison with each habitat model. If the variance explained by a habitat model was significantly greater than the variance explained by the null distribution ($P < 0.05$), I considered the habitat model significant (Murphy et al. 2010).

2.3.3.2 Travel Habitat Model

To create the Travel Habitat Model, I used the output of the Overall Core Habitat Model to identify low-quality, matrix habitat within the Loomis and Black Pine Basin study areas.

Matrix habitat was defined as having a relative probability of lynx use < 45% and core habitat was defined as having > 45% relative probability of use. Although a more conservative definition of core habitat (e.g. > 65% relative probability of use) would have revealed the study areas as quite fragmented and lent more data points to the Travel Habitat analysis, I wanted to ensure that I was exploring lynx habitat use at the lowest end of the habitat quality spectrum where lynx were likely traveling, and not hunting, resting, or denning. To discover how lynx selected habitat while traveling through matrix habitats, I used only the lynx locations that fell within the matrix (outside of core habitat) and generated an equal number of random available points also within the matrix (**Figure 2.3**). Because the Jackknife test for the Overall Core Habitat Model revealed consistent habitat selection patterns among individual lynx, I did not run a Jackknife test specifically for the Travel Habitat Model; I simply included all lynx datasets. I then used the Random Forest procedures described above to compare used versus available lynx locations (**Table 2.3**) within the matrix areas of the Back Pine Basin and Loomis study areas.



Loomis
Black Pine
Basin
Mazama
20
Land Cover
Forest opening
Lodgepole pine forest
Spruce-fir forest
Mixed forest
Dry forest
Burn
Fire skip
Timber harvest
Lynx points
N
0 2 4 8 Kilometers

Figure 2.3. All lynx points retained for travel habitat analysis in the Black Pine Basin and Loomis study areas located the North Cascade Mountains, Washington.

2.4 RESULTS

A majority (71%) of the GPS lynx locations fell within undisturbed forested areas with only 29% of the locations in an open or disturbed area. More than half (58%) of the lynx locations fell within undisturbed sub-boreal forest types and 13% fell within undisturbed dry forest. 20% of the lynx points were located in an area disturbed by fire or timber harvest between 1985 and 2012. 2% of the lynx points fell within a new burn (1998-2012), and 4% fell within an old burn (1985-1997), despite new burns comprising a majority of the burned landscape in the Black Pine Basin and Loomis study areas. 12% of the lynx points fell within an old timber harvest unit and 2% of the locations fell within a new timber harvest unit.

The tests for multivariate redundancy identified and removed growing season precipitation within a small-scale (3x3 pixel) area from all Overall, Loomis, and Black Pine Basin Core Habitat Models, and removed growing season precipitation within a large-scale (27x27 pixel) area from the Travel Habitat Model. In addition, I removed several variables that showed a high degree of collinearity from each of these model based on results of the Spearman-rank test. (**Table 2.4**).

Table 2.4. Collinear variable pairs as determined by Spearman rank tests (r > 0.8). Variable descriptions are given in Table 2.2. In the case of old thins and old clearcuts in the Overall Core and Travel Habitat Models, I removed old clearcuts while in the Loomis and Black Pine Basin Core Habitat Models I removed old thins. The decision to retain one variable over another was based on the importance value of each variable as indicated by an initial Random Forest run using all variables; the more important variable was retained. In the case of collinear variables with very similar importance values, I retained the variable of higher ecological interest or one that added variety to the suite of variables tested in my models. Numbers after the variable name identify it as being portrayed at a large-scale (27x27 pixel area) or small-scale (3x3 pixel area).

Overall Core Habitat Model		**Travel Habitat Model**		**Loomis Habitat Model**		**Black Pine Basin Habitat Model**	
retained	eliminated	retained	eliminated	retained	eliminated	retained	eliminated
distedge_cut	area_cut			distedge_cut	area_cut	distedge_cut	area_cut
distedge_fo	area_fo			distedge_fo	area_fo	distedge_fo	area_fo
distedge_fire	fireskips27	distedge_fire	fireskip27	distedge_fire	fireskips27		
newhigh_f27	fireskips27			newhigh_f27	fireskips27		
newhigh_f27	newlow_f27	newhigh_f27	newlow_f27	newhigh_f27	newlow_f27	newhigh_f27	newlow_f27
		newhigh_f27	newhigh_f3				
oldlow_f27	oldhigh_f27	oldlow_f27	oldhigh_f27				
						oldhigh_f27	oldlow_f27
						oldhigh_f27	fireskips27
						oldlow_f27	fireskips27
						oldhigh_f3	distedge_fire
new_thin27	new_cut27						
				new_cut27	new_thin27		
old_thin27	old_cut27	old_thin27	old_cut27				
				old_cut27	old_thin27	old_cut27	old_thin27
		dry27	dry3	dry27	dry3		
hli27	hli3	hli27	hli3			hli27	hli3

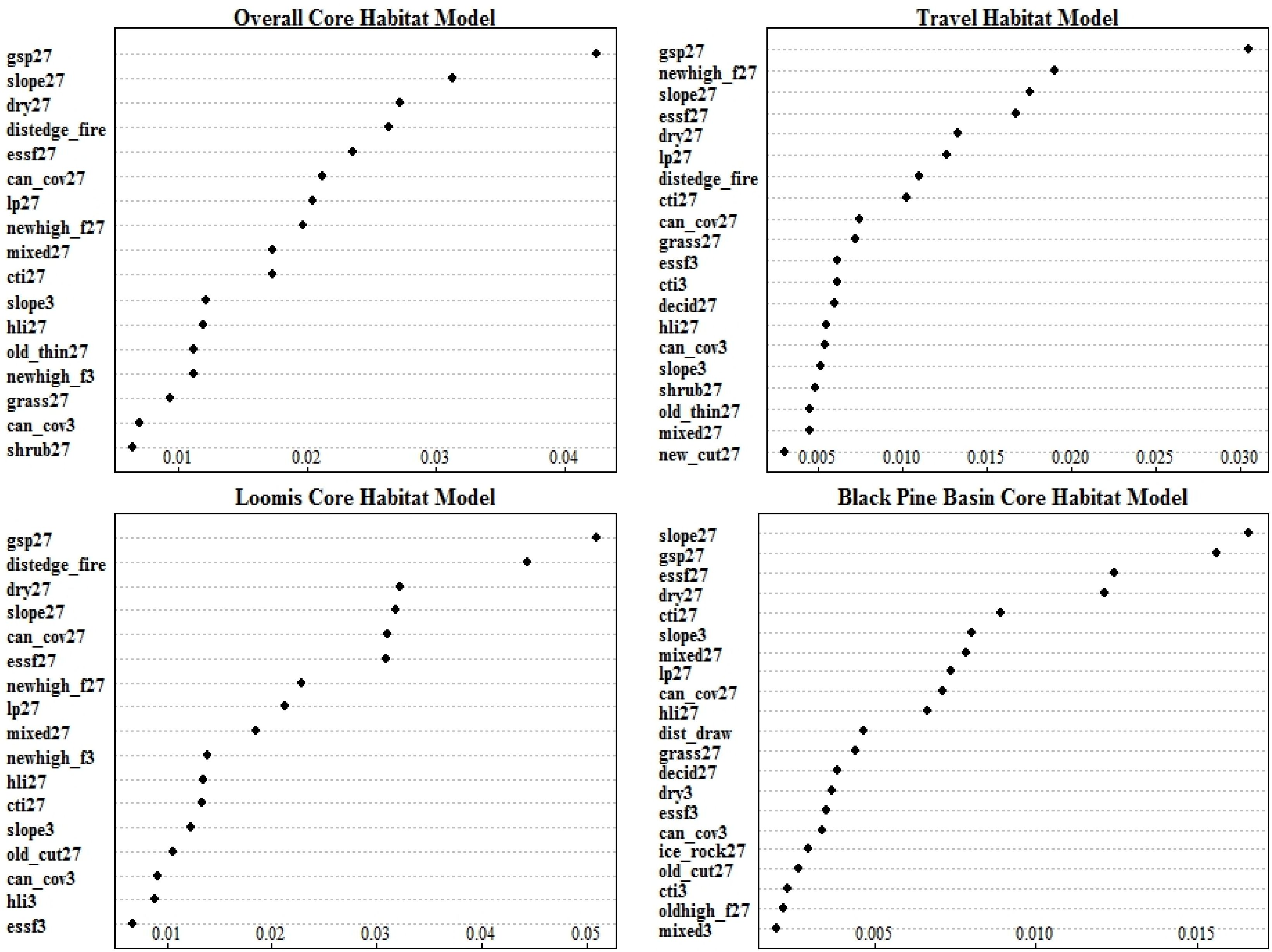
Out-of-bag error rate (fit) was below 35% in all cases (**Table 2.5**). The models also performed well when predicting use versus availability of the 80% data withheld from the subsample; > 69% of the withheld data was predicted correctly by all the models. Accuracy and AUC scores below approximately 80% are expected from Random Forest habitat models of a highly mobile species and for models based on large radio telemetry datasets, which have inherently high amounts of "noise" (Melanie Murphy, personal communication). Indeed, my model's AUC scores were similar or higher to those reported for the only other machine learning habitat model developed for a mammalian carnivore to my knowledge; a boosted regression tree occupancy model for coyotes (*Canis latrans*) (McCue et al. 2013). My AUC scores were also similar or higher to those reported by a Resource Selection Function model for lynx in Maine (Simons-Legaard et al. 2013). The models were all significant at $P < 0.05$ as compared to the null distribution created by randomizing the used and available points. A slightly higher sensitivity value than specificity value for each Core Habitat Model shows that these models predicted used locations more accurately than available locations. The Travel Habitat Model showed even prediction between used and available points. Seasonal and Sex-Specific Core Habitat Models did not show differences between seasons or sexes so their results are not considered further in this chapter (Appendix D).

Table 2.5. Model validation and fit statistics for the Core Habitat Models and the Travel Habitat Model. Accuracy (%) indicates the overall performance of the model when predicting the withheld, validation dataset. Sensitivity and specificity show the proportion of used locations correctly predicted and the proportion of available locations correctly predicted. Area under the curve of a Receiver Operator Characteristic (AUC) scores are a measure of how evenly the model predicts sensitivity and specificity. The Kappa (*k*) statistic is a measure of how much better the model predicted used and available points than expected by random chance. *P* values indicate significance of each model and out-of-bag error rates (%) show the mean misclassification rate of trees when predicting the out-of-bag data.

	Model Validation Statistics						Model Fit
Model	Accuracy (%)	Sensitivity	Specificity	*k*	AUC	*P* value	Out-of-bag error (%)
Overall	76.17	0.803	0.7308	0.5237	0.7617	$P < 0.001$	27.28
Loomis	79.86	0.8459	0.7629	0.5971	0.7986	$P < 0.001$	22.25
Black Pine Basin	69.51	0.7424	0.6633	0.3903	0.6951	$P < 0.001$	34.83
Travel	70.33	0.7114	0.6960	0.4065	0.7033	$P < 0.001$	28.02

2.4.1 General Model Results

Growing season precipitation, slope, and forest types were important habitat variables in all models. In the Overall Core Habitat Model, the Loomis Core Habitat Model, and the Travel Habitat Model, fire variables were also highly important. Habitat selection was better explained by large-scales than small-scales and although small-scale depictions of variables were sometimes included in the habitat models, they were always of less importance than the large-scale depiction (**Figure 2.4**).



Overall Core Habitat Model
gsp27
slope27
dry27
distedge_fire
essf27
can_cov27
lp27
newhigh_f27
mixed27
cti27
slope3
hli27
old_thin27
newhigh_f3
grass27
can_cov3
shrub27
0.01
0.02
0.03
0.04
Travel Habitat Model
gsp27
newhigh_f27
slope27
essf27
dry27
lp27
distedge_fire
cti27
can_cov27
grass27
essf3
cti3
decid27
hli27
can_cov3
slope3
shrub27
old_thin27
mixed27
new_cut27
0.005
0.010
0.015
0.020
0.025
0.030
Loomis Core Habitat Model
gsp27
distedge_fire
dry27
slope27
can_cov27
essf27
newhigh_f27
lp27
mixed27
newhigh_f3
hli27
cti27
slope3
old_cut27
can_cov3
hli3
essf3
0.01
0.02
0.03
0.04
0.05
Black Pine Basin Core Habitat Model
slope27
gsp27
essf27
dry27
cti27
slope3
mixed27
lp27
can_cov27
hli27
dist_draw
grass27
decid27
dry3
essf3
can_cov3
ice_rock27
old_cut27
cti3
oldhigh_f27
mixed3
0.005
0.010
0.015

Figure 2.4. Importance plots for each Core Habitat Model and the Travel Habitat Model ranking each habitat variable retained in the final Random Forest models. Variables are explained in Table 2.2. To determine the importance of each variable, the values of out-of-bag observations are randomly permuted, run down each tree, and predicted as used or available. The misclassification rate of the modified out-of-bag observations is subtracted from the misclassification rate of the unmodified out-of-bag observations and then divided by the standard error. Numbers after the variable name identify it as being portrayed at a large scale (27x27 pixel area) or small scale (3x3 pixel area). Note different x-axes.

2.4.2 Overall Core Habitat Model

Lynx habitat selection was largely defined by the amount of growing season precipitation within a large-scale area. Lynx selected areas receiving more precipitation and avoided areas receiving smaller amounts of precipitation during the growing season. Lynx also selected for large-scale areas with greater moisture accumulations found in drainages (as described by the Compound Topographic Index), and for cooler, moister, northeast-facing slopes as defined by the Heat Load Index (**Figure 2.5**).

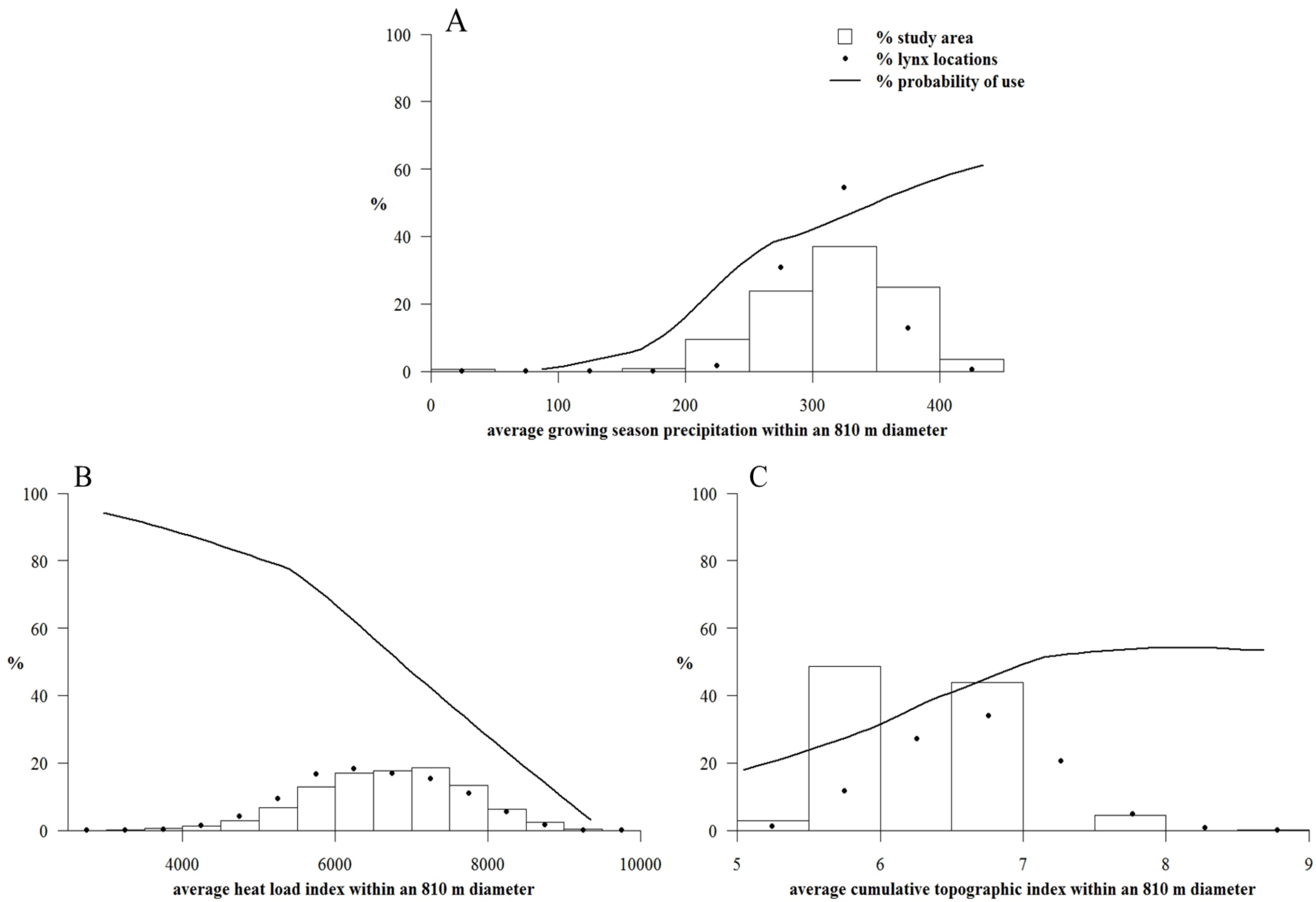

A
% study area
% lynx locations
% probability of use
%
average growing season precipitation within an 810 m diameter
B
%
average heat load index within an 810 m diameter
C
%
average cumulative topographic index within an 810 m diameter

Figure 2.5. Lynx selection of climate variables in the Loomis and Black Pine Basin study areas. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Histograms show the distribution of the focal habitat variable throughout the Loomis and Black Pine Basin study areas. The dots represent the percentage of lynx points found within each histogram category of the focal habitat variable. Panels show lynx selection for A) average growing season precipitation at a large scale; B) average heat load index at a large scale; and C) average cumulative topographic index at a large scale.

Lynx avoided dry forest and selected for moist spruce-fir forest and lodgepole pine forests. The association between probability of lynx use and increasing amounts of spruce-fir or lodgepole pine forest cover reached a threshold of ~ 50%, but probability of use declined at higher amounts (> 50%) of these forest types. Lynx also selected for large-scale areas that included mixed forest types dominated by Douglas fir (**Figure 2.6**).

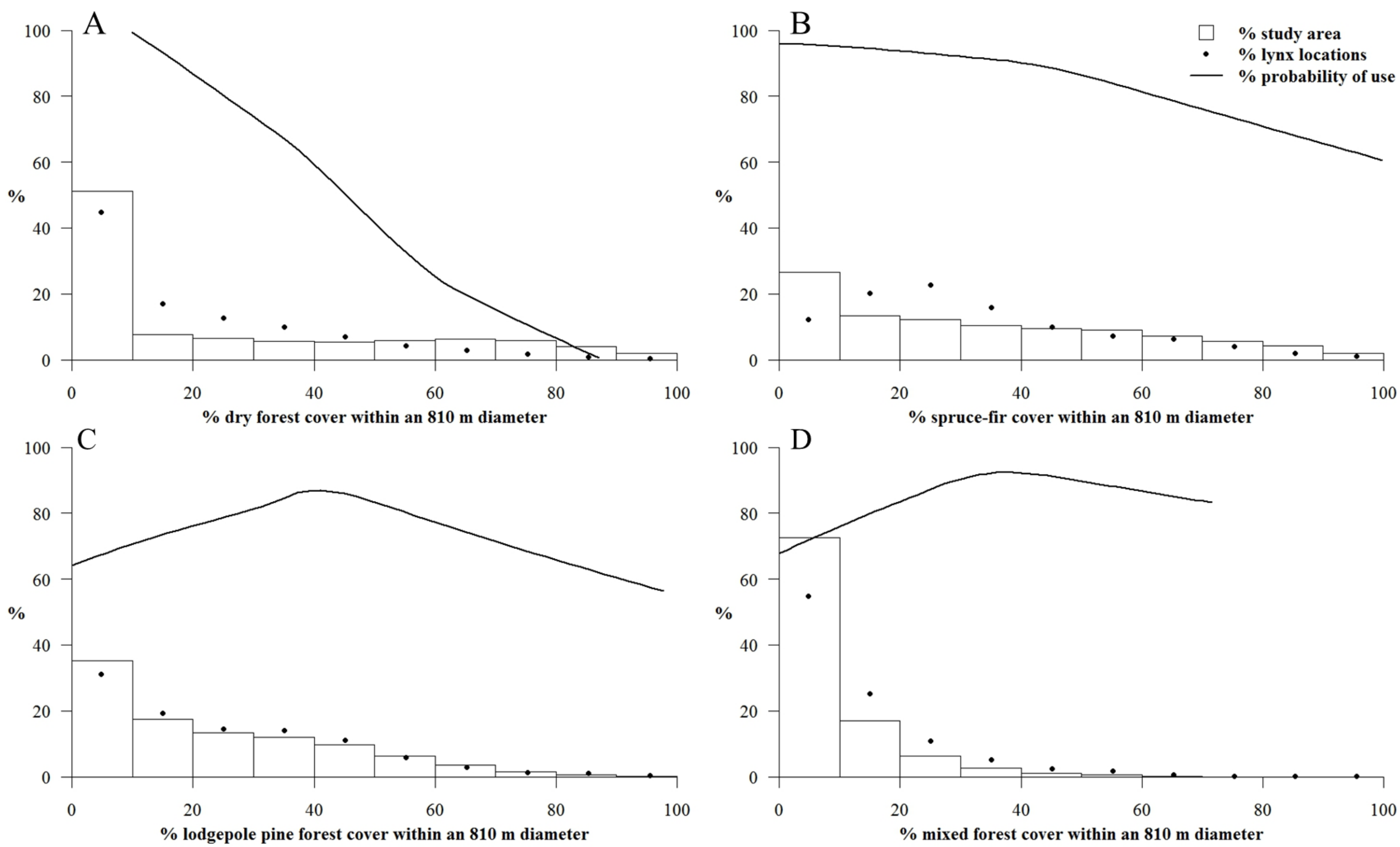

A
B
C
D
% study area
% lynx locations
% probability of use
%
% dry forest cover within an 810 m diameter
% spruce-fir cover within an 810 m diameter
% lodgepole pine forest cover within an 810 m diameter
% mixed forest cover within an 810 m diameter

Figure 2.6. Lynx selection of forest types in the Loomis and Black Pine Basin study areas. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) dry forest at a large scale; B) spruce-fir forest at a large scale; C) lodgepole pine forest at a large scale; and D) mixed forest at a large scale.

Canopy cover was important to lynx habitat selection within large- and small-scale areas. Although lynx use increased with increasing canopy cover, probability of use declined after a threshold of ~ 50% was reached. Probability of lynx use was < 50% at the highest amounts (~ > 70%) of canopy cover within a large-scale area, which was found in < 2% of the study area. Lynx selected against very low amounts of canopy cover, which primarily consisted of open areas such as grassy or shrubby areas, land cover types lynx also selected against within a large-scale area (**Figure 2.7**).

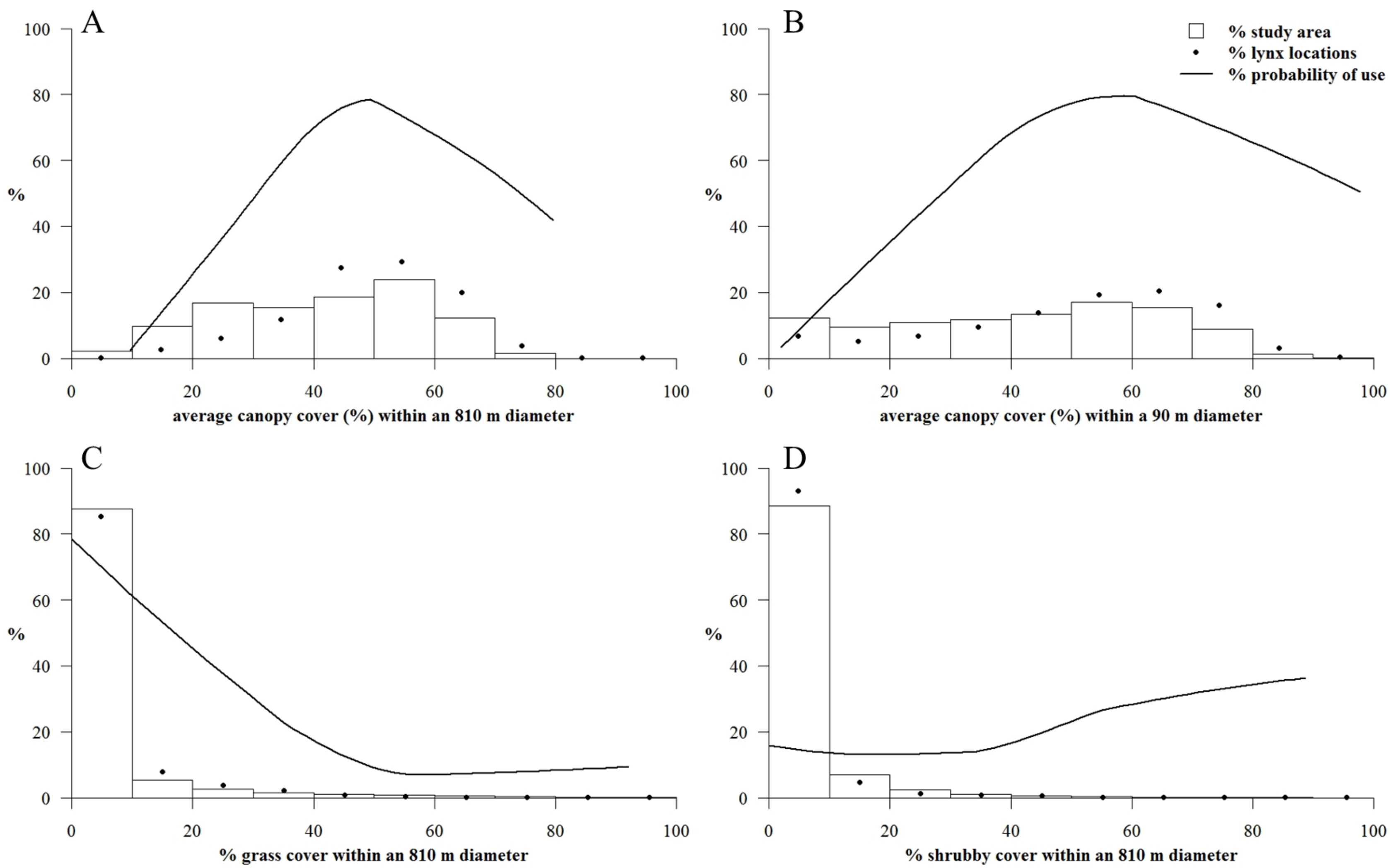
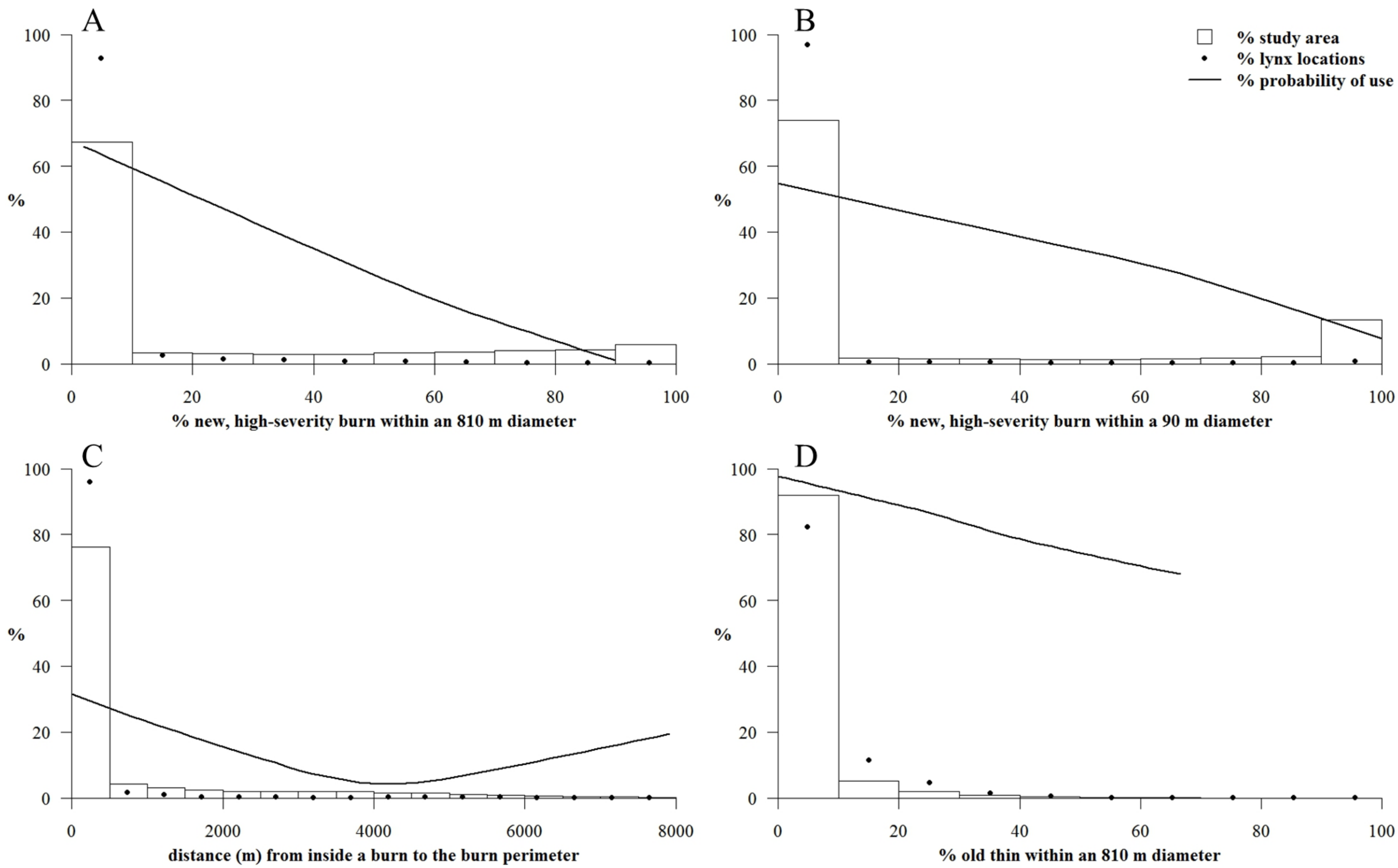

A
B
C
D
% study area
% lynx locations
% probability of use
%
average canopy cover (%) within an 810 m diameter
average canopy cover (%) within a 90 m diameter
% grass cover within an 810 m diameter
% shrubby cover within an 810 m diameter

Figure 2.7. Lynx selection of canopy cover and forest openings in the Loomis and Black Pine Basin study areas. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) average canopy cover at a large scale; B) average canopy cover at a small scale; C) grass cover at a large scale; and D) shrubby cover at a large scale.

Lynx avoided new, high-severity burns within both large- and small-scale areas and avoided venturing within the perimeter of a burn. A slight increase in the probability of lynx using areas over 4,000 m inside the burn is due to one lynx that used a large fire skip in the new Tripod Burn and another lynx that used an old burn (the Thunder Mountain Burn), within the Tripod Burn. Both areas were more than 4,000 m from the burn perimeter. The only harvest variable retained depicted old, thinned forest within a large area. Lynx selected areas where old thins existed, however, there was a negative relationship between lynx use and increasing amounts of old, thinned forest (**Figure 2.8**). The average slope within a large- and small-scale area also affected lynx habitat selection; lynx preferred areas of low slope (< ~20 degrees) (**Figure 2.9**).



A
B
C
D
% study area
% lynx locations
% probability of use
%
% new, high-severity burn within an 810 m diameter
% new, high-severity burn within a 90 m diameter
distance (m) from inside a burn to the burn perimeter
% old thin within an 810 m diameter

Figure 2.8. Lynx selection of disturbed areas in the Loomis and Black Pine Basin study areas. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) new, high-severity burn at a large scale; B) new, high-severity burn at a small scale; C) distance from the edge of a burn; and D) old thins at a large scale.

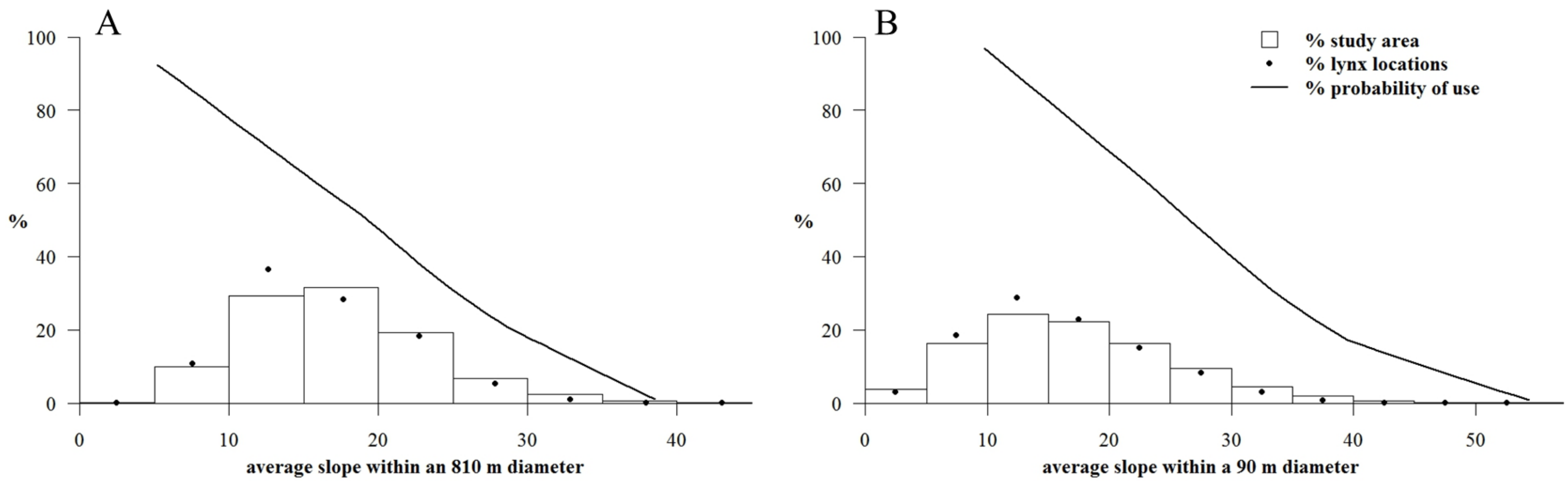


Figure 2.9. Lynx selection of slope in the Loomis and Black Pine Basin study areas. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) average slope at a large scale; and B) average slope at a small scale.

2.4.3 Travel Habitat Model

Core habitat in the Loomis and Black Pine Basin study areas was composed of 75% forested area and 25% open area such as meadows or disturbed areas. Only 7% of the core habitat in the study area was disturbed by fire or harvest in the past 15 years. In contrast, the habitat lynx traveled through between core areas was only 42% forested and was 58% open habitat. 34% of the matrix area was disturbed in the past 15 years with a majority of this disturbance caused by the Tripod Burn. Faced with lower quality, more open habitat in the matrix, lynx preferred habitat features similar to those selected in core habitats but were more tolerant of some adverse habitat features.

New, high-severity burns, namely the Tripod Burn, were still avoided by lynx when selecting matrix habitats, but lynx were more tolerant of new, high-severity burns while using matrix habitats. Lynx preferred to use areas of the Tripod Burn nearer to the perimeter but were also tolerant of areas as far as 500 m inside the burn perimeter. The Travel Habitat Model partial plot depicting distance to the nearest edge shows an increase in use of areas further than 4,000 m inside the burn. This increase in use of areas over 4,000 m from the perimeter is due to a large fire skip and old burn located within the Tripod Burn that some lynx used. Lynx traveling through matrix habitats showed a higher level of use in new, high-severity burns within a large-scale area particularly if fire skips, low-severity burns, or old burns were also within the large-scale areas (**Figure 2.10**). Lynx in matrix habitat showed greater use of grassy openings within a large-scale area, preferring to stay outside a meadow perimeter but also willing to travel through a meadow (**Figure 2.11**).

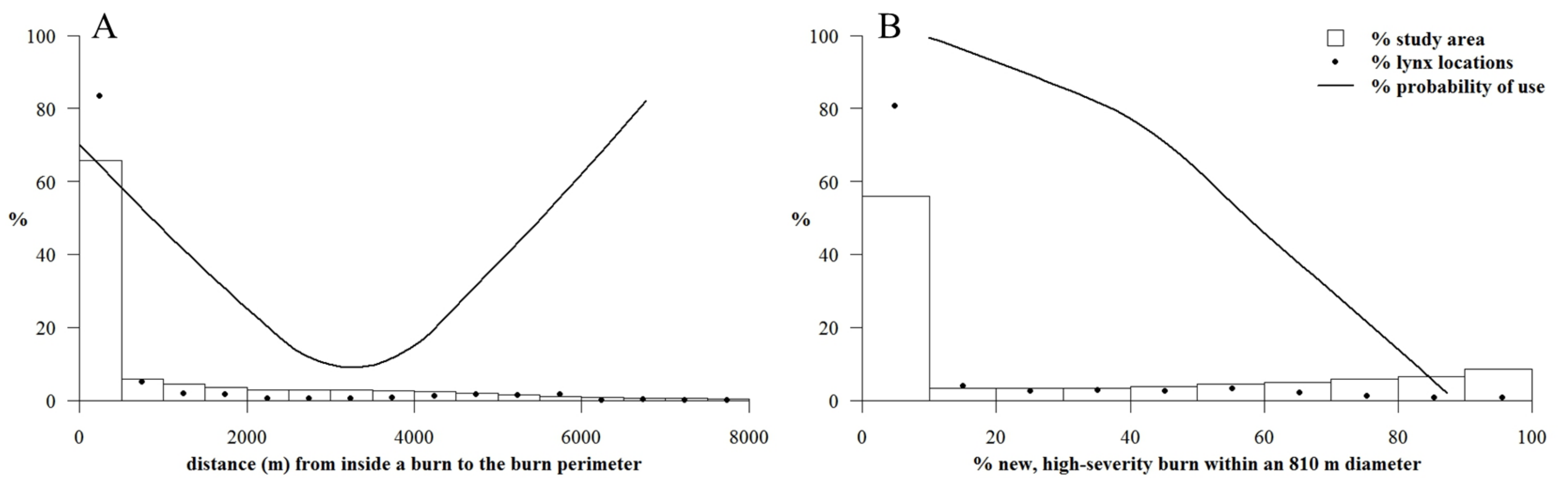


Figure 2.10. Lynx selection of burned areas while in matrix habitats. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) distance from the edge of a burn; and B) new, high-severity burn at a large scale.

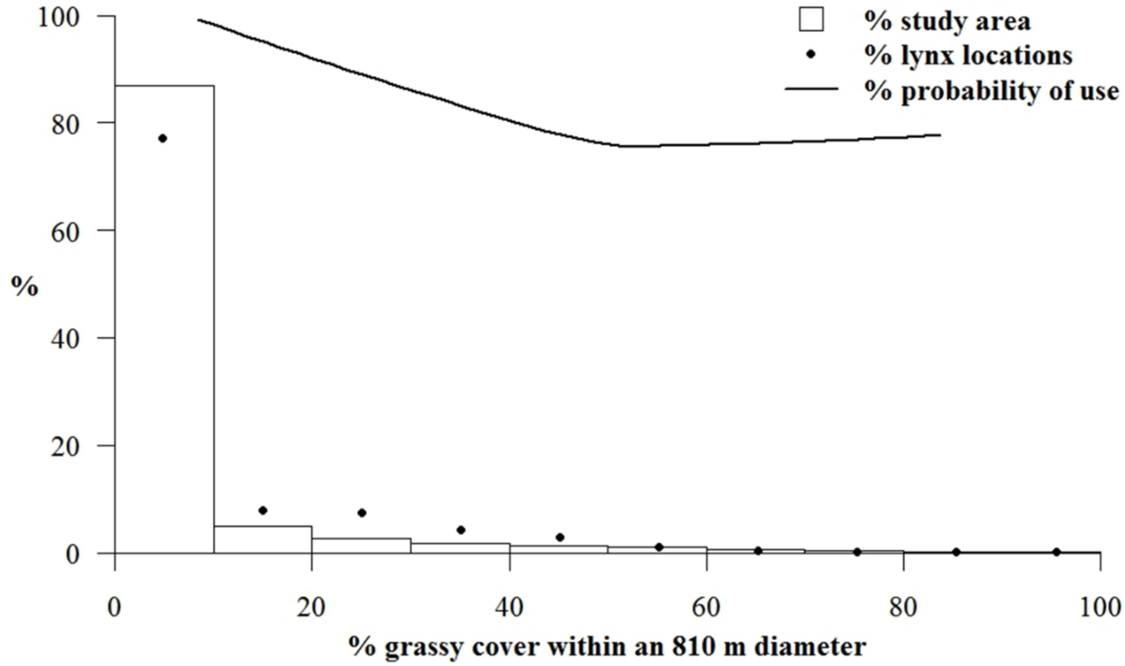


Figure 2.11. Lynx selection of grassy cover at a large scale while in matrix habitats. Probability of use represents the effect of grassy cover on lynx habitat selection when the effect of all other habitat variables in the model are averaged.

Despite demonstrating a higher probability of use for open habitats, lynx still preferred forested cover while traveling through the matrix. Within both large- and small-scale areas lynx selected for areas with > ~ 30% canopy cover and the probability of use continued to increase even at the highest percentages of canopy cover (**Figure 2.12**).

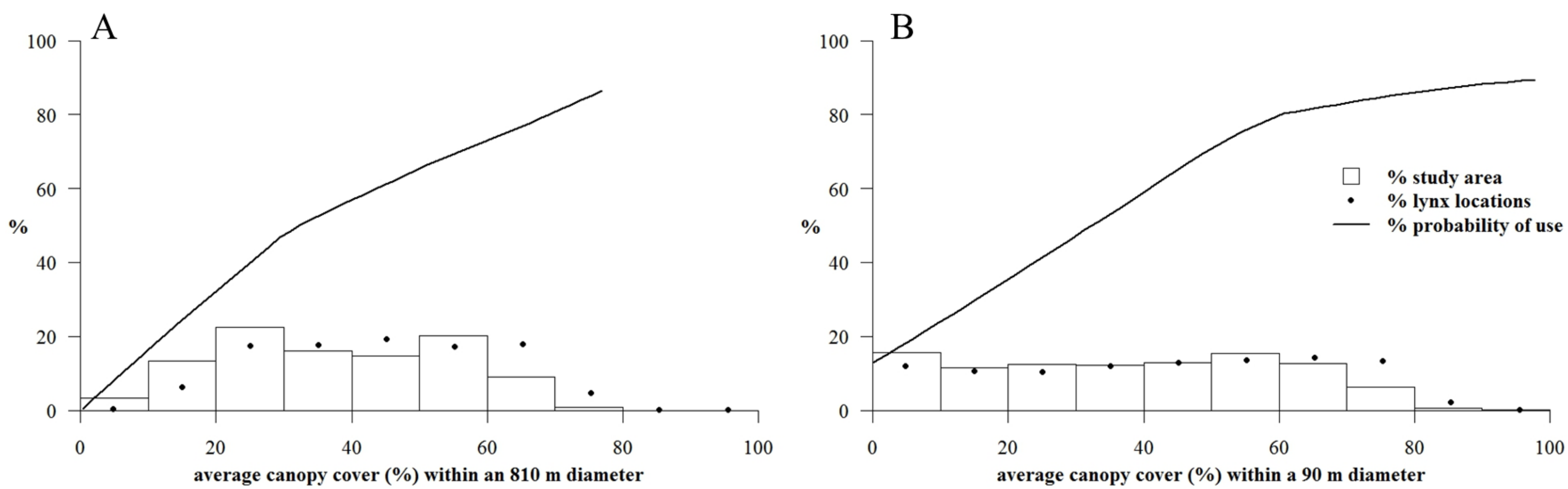


Figure 2.12. Lynx selection of canopy cover while in matrix habitats. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) average canopy cover at a large scale; and B) average canopy cover at a small scale.

Lynx selected for increasing amounts of spruce-fir cover for travel habitats both within and outside of the new Tripod Burn. Lynx also used lodgepole pine forest within a large-scale area, however, the relationship between increasing amounts of lodgepole pine cover and selection was negative and lynx avoided large-scale areas with > 65% lodgepole pine cover. Mixed forest was moderately important to travel habitat selection and, although lynx did not seem to avoid mixed forests, the relationship between increasing mixed forest cover and selection became negative once mixed forest cover reached approximately 20% within a large-scale area. Lynx avoided traveling through increasing amounts of dry forest within a large-scale area, highlighting their aversion to this forest type (**Figure 2.13**).

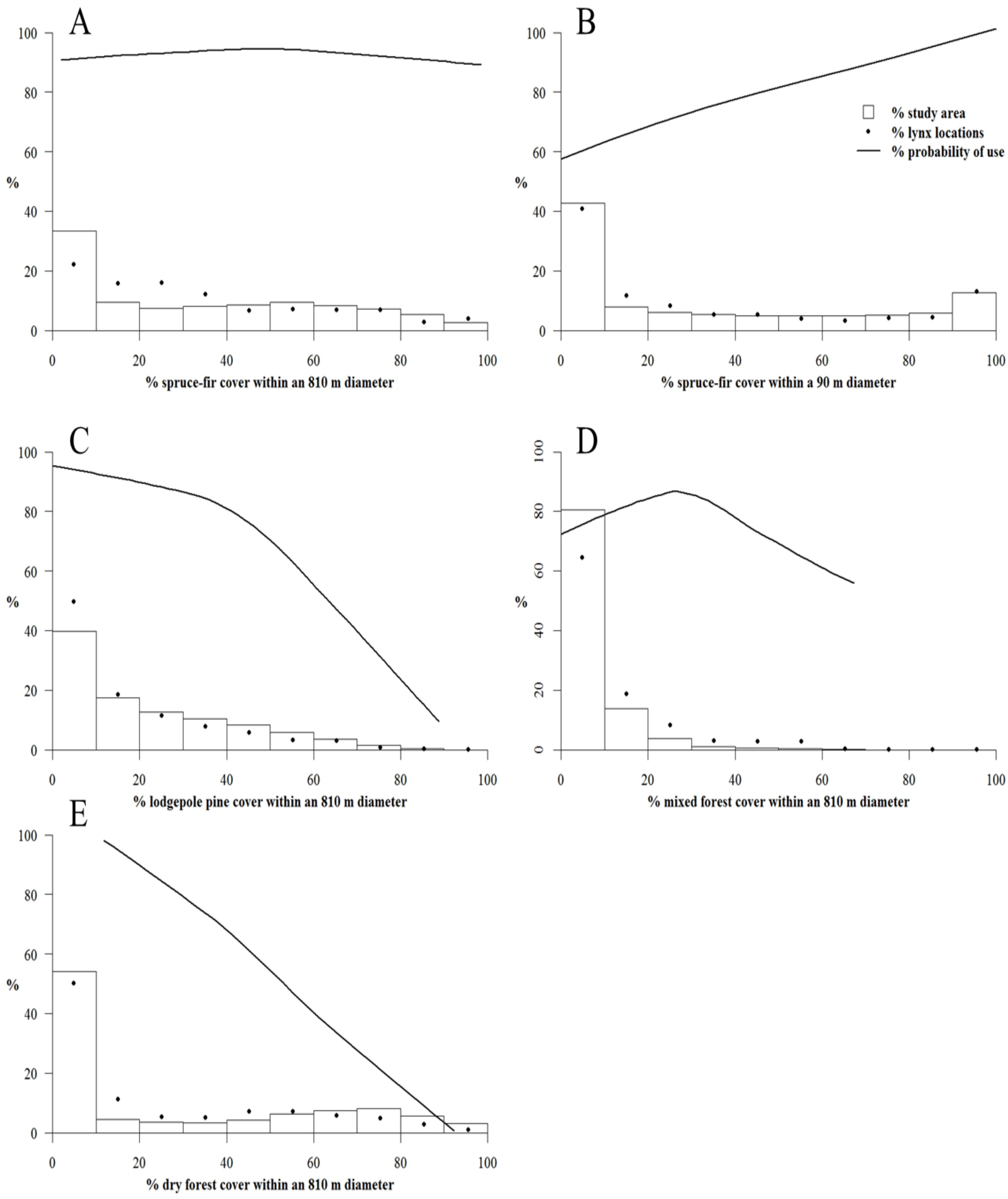

A
B
C
D
E
% study area
% lynx locations
% probability of use
%
% spruce-fir cover within an 810 m diameter
% spruce-fir cover within a 90 m diameter
% lodgepole pine cover within an 810 m diameter
% mixed forest cover within an 810 m diameter
% dry forest cover within an 810 m diameter

Figure 2.13. Lynx selection of forest types while in matrix habitats. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) spruce-fir forest at a large scale; B) spruce-fir forest at a small scale; C) lodgepole pine at a large scale; D) mixed forest at a large scale; and E) dry forest at a large scale.

Lynx avoided traveling through areas with greater than approximately 20% old thin within a large-scale area. Most old thins in matrix habitat are located in dry forest so that the avoidance of old thins may be a result of selection against dry forests. Lynx selected areas with small amounts of new clearcut as travel habitat. However, new clearcuts explained only a small amount of lynx travel habitat selection with an importance value < 0.005 and this result was based on very little data (**Figure 2.14**). Lynx were more tolerant of steep slopes while in matrix habitats (**Figure 2.15**).

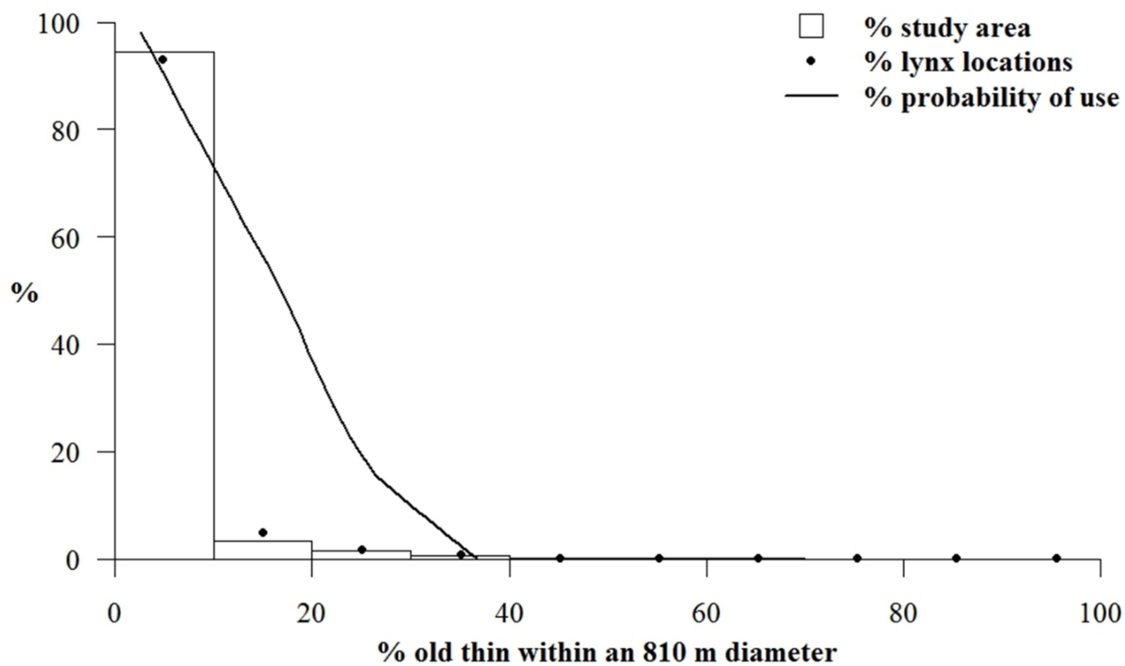


Figure 2.14. Lynx selection of old thins at a large scale while in matrix habitats. Probability of use represents the effect of old thins on lynx habitat selection when the effect of all other habitat variables in the model are averaged.

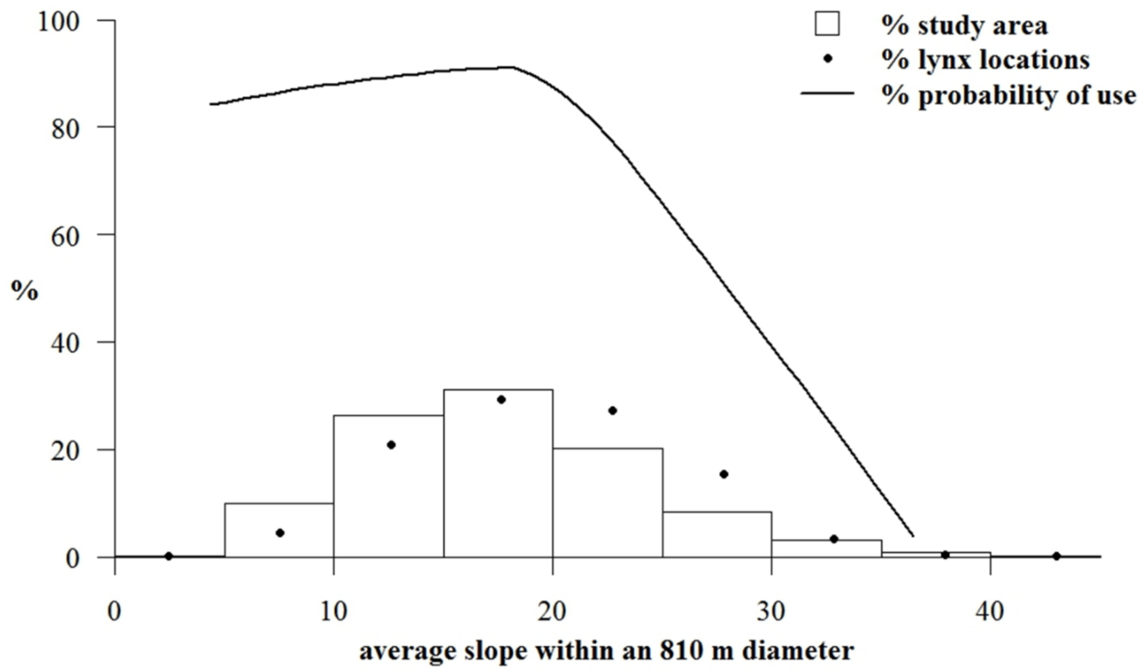


Figure 2.15. Lynx selection of slope at a large scale while in matrix habitats. Probability of use represents the effect of slope on lynx habitat selection when the effect of all other habitat variables in the model are averaged.

2.4.4 Loomis Core Habitat Model

The results of the Loomis Core Habitat Model were similar to those of the Overall Core Habitat Model, which is not surprising since most of the collared lynx lived in that area, thus weighting the Overall Core Habitat Model towards lynx habitat selection in the Loomis study area. As in the Overall Core Habitat Model, lynx in the Loomis study area avoided steep slopes and dry forests and selected moist and cool microclimates and their associated spruce-fir or lodgepole pine forest types. Fire variables were important in describing core lynx habitat in the Loomis study area and clearly demonstrated that lynx avoided new, high-severity burns. Lynx in the Loomis study area avoided areas within the new Tripod Burn perimeter, except for a particular large fire skip and when using an old burn located over 4,000 m inside of the burn.

Lynx avoided areas with greater amounts of new, high-severity burn within large- and small-scale areas. In addition, in the Loomis study area probability of use increased with increasing canopy cover up to ~ 50% canopy cover and then declined. (**Figure 2.16**).

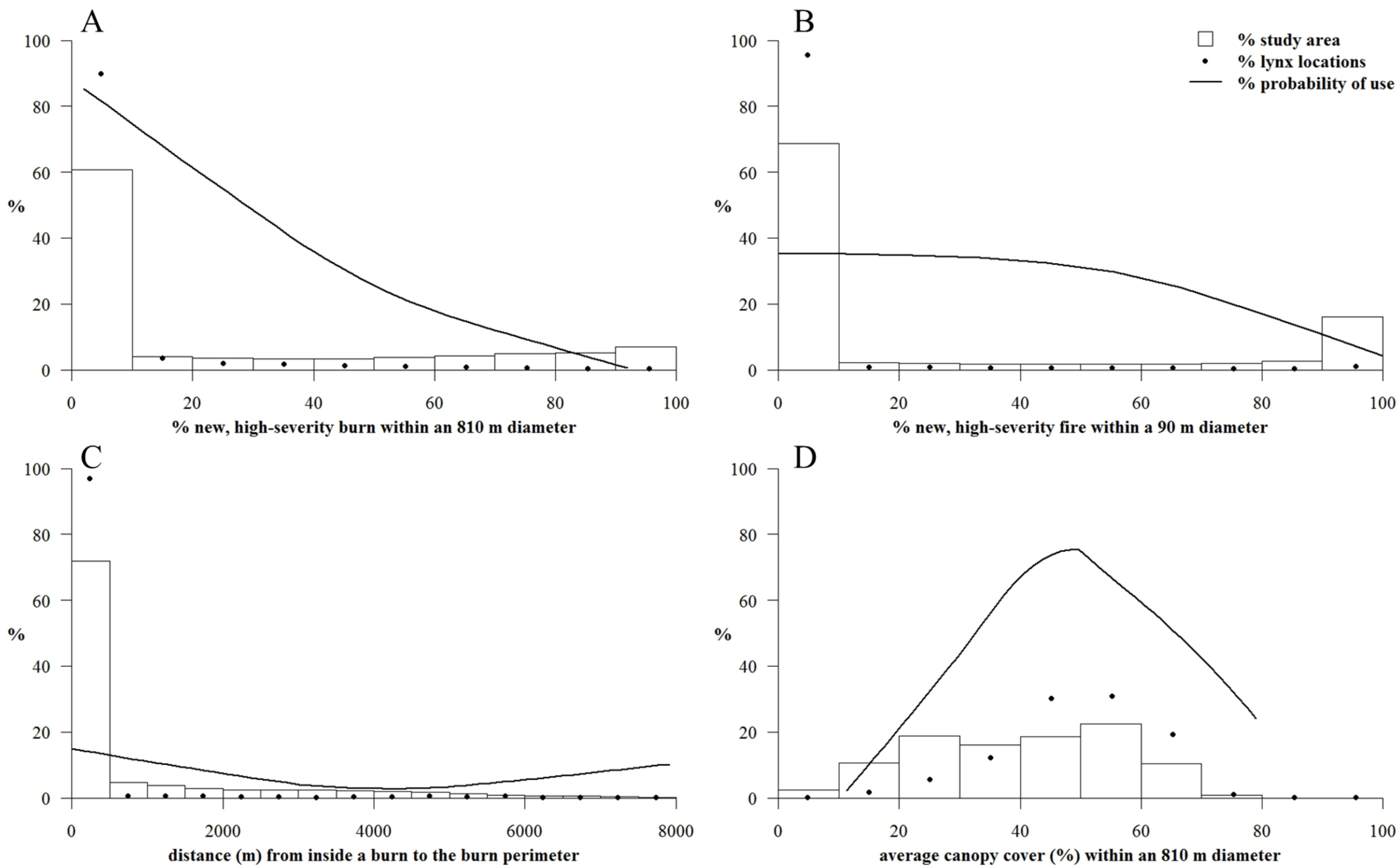

A
B
C
D
% study area
% lynx locations
% probability of use
%
% new, high-severity burn within an 810 m diameter
% new, high-severity fire within a 90 m diameter
distance (m) from inside a burn to the burn perimeter
average canopy cover (%) within an 810 m diameter

Figure 2.16. Lynx selection of burned areas and canopy cover in the Loomis study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) new, high-severity burn at a large scale; B) new, high-severity burn at a small scale; C) distance to the edge of a burn; and D) average canopy cover at a large scale.

Although lynx in the Loomis study area selected for smaller amounts of spruce-fir forest at both scales, the relationship between greater amounts of spruce-fir forest and selection was negative. Lynx selected for increasing amounts of lodgepole pine forest until lodgepole pine cover reached approximately 50% within a large-scale area, beyond which the relationship between lynx selection and increasing lodgepole cover became negative. Mixed forest is uncommon on the Loomis study area and did not significantly contribute to quality, core lynx habitat. Lynx did not select against low amounts of mixed forest cover within a large-scale area, but the relationship between selection and increasing mixed forest cover became negative once mixed forest cover within a large-scale area reached approximately 30% (**Figure 2.17**).

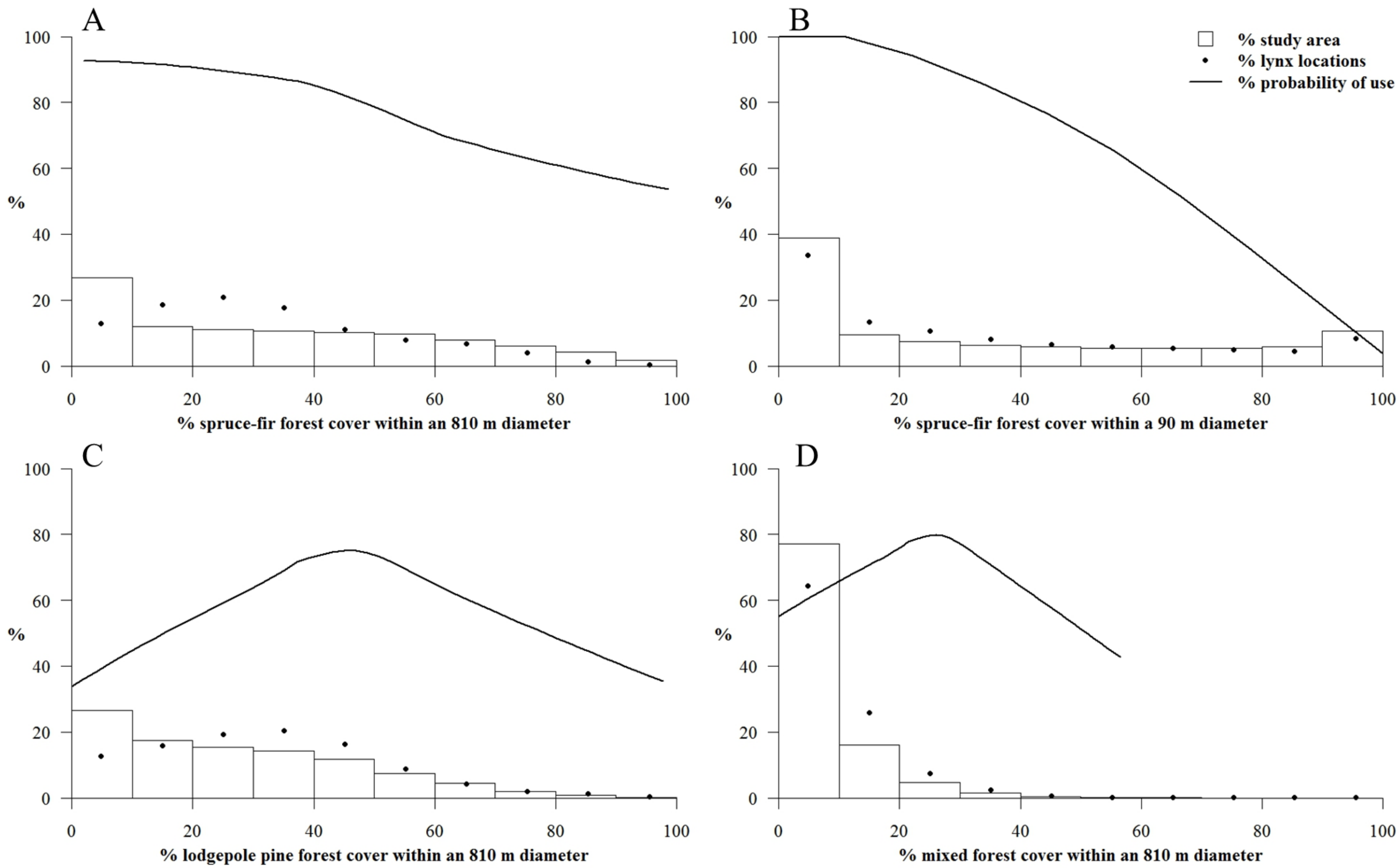

A
B
C
D
% study area
% lynx locations
% probability of use
%
0
20
40
60
80
100
% spruce-fir forest cover within an 810 m diameter
% spruce-fir forest cover within a 90 m diameter
% lodgepole pine forest cover within an 810 m diameter
% mixed forest cover within an 810 m diameter

Figure 2.17. Lynx selection of forest types in Loomis study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) spruce-fir forest at a large scale; B) spruce-fir forest at a small scale; C) lodgepole pine forest at a large scale; and D) mixed forest at a large scale.

As in the Overall Core Habitat Model, timber harvest variables were only somewhat important to lynx habitat selection. Only the variable depicting the amount of old clearcut within a large-scale area was retained and suggests lynx selected areas where old clearcuts are present within a large-scale area. A slight decrease in use was indicated after clear-cuts within a large-scale area reach 25%. However, areas with greater amounts of old clearcut were few on the Loomis study and drawing a conclusion with so little data is difficult (**Figure 2.18**).

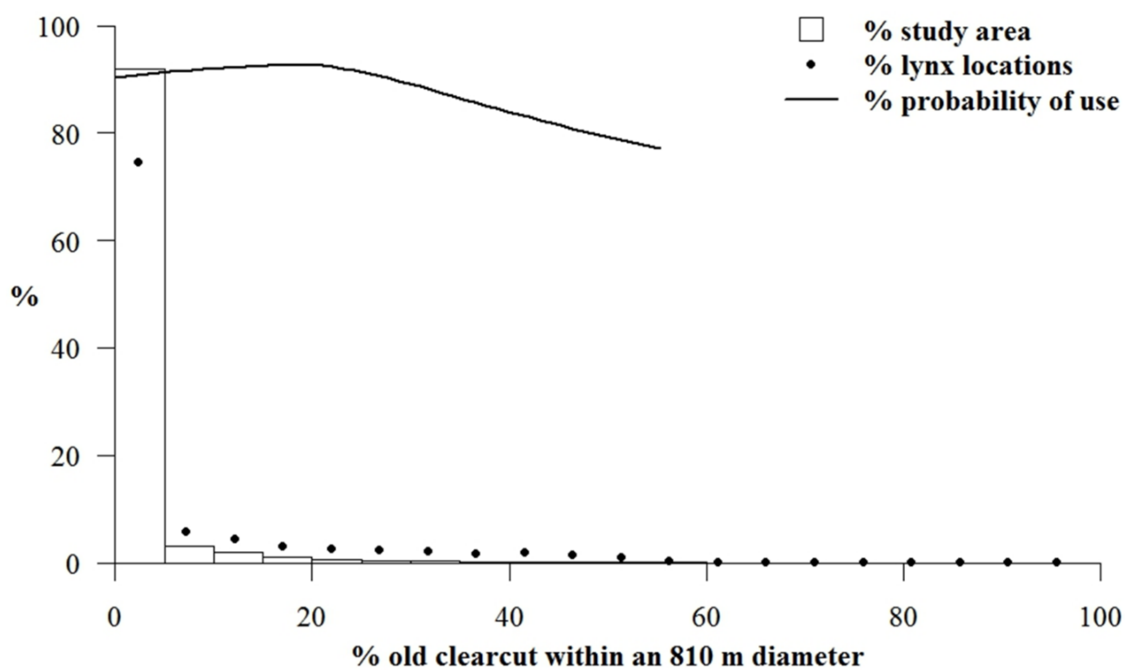


Figure 2.18. Lynx selection of old clearcuts at a large scale in the Loomis study area. Probability of use represents the effect old clearcuts on lynx habitat selection when the effect of all other habitat variables in the model are averaged.

2.4.5 Black Pine Basin Core Habitat Model

In the topographically heterogeneous Black Pine Basin, slope within a large-scale area was the most important predictor of core lynx habitat; lynx selected for lower slopes. Within areas of low slope, lynx selected for cool moist areas with high growing season precipitation, low heat loads, and high moisture accumulation. Lynx in the Black Pine Basin thus used forest types associated with wetter and cooler areas, selecting for increasing amounts of spruce-fir and mixed forest types.

However, unlike in the Loomis study area where lodgepole pine forests were more common, lodgepole pine cover within a large-scale area rarely exceeded 35% in the Black Pine Basin. Although lynx did not avoid the low amounts of lodgepole pine cover found over much of the Black Pine Basin study area, they demonstrated a negative relationship between selection and increasing lodgepole pine cover within a large-scale area and avoided the few areas where lodgepole pine cover was extensive. Additionally, whereas deciduous cover is rare and unimportant to lynx habitat selection in the Loomis study area, lynx in the Black Pine Basin selected for the few large-scale areas with deciduous cover (**Figure 2.19**).

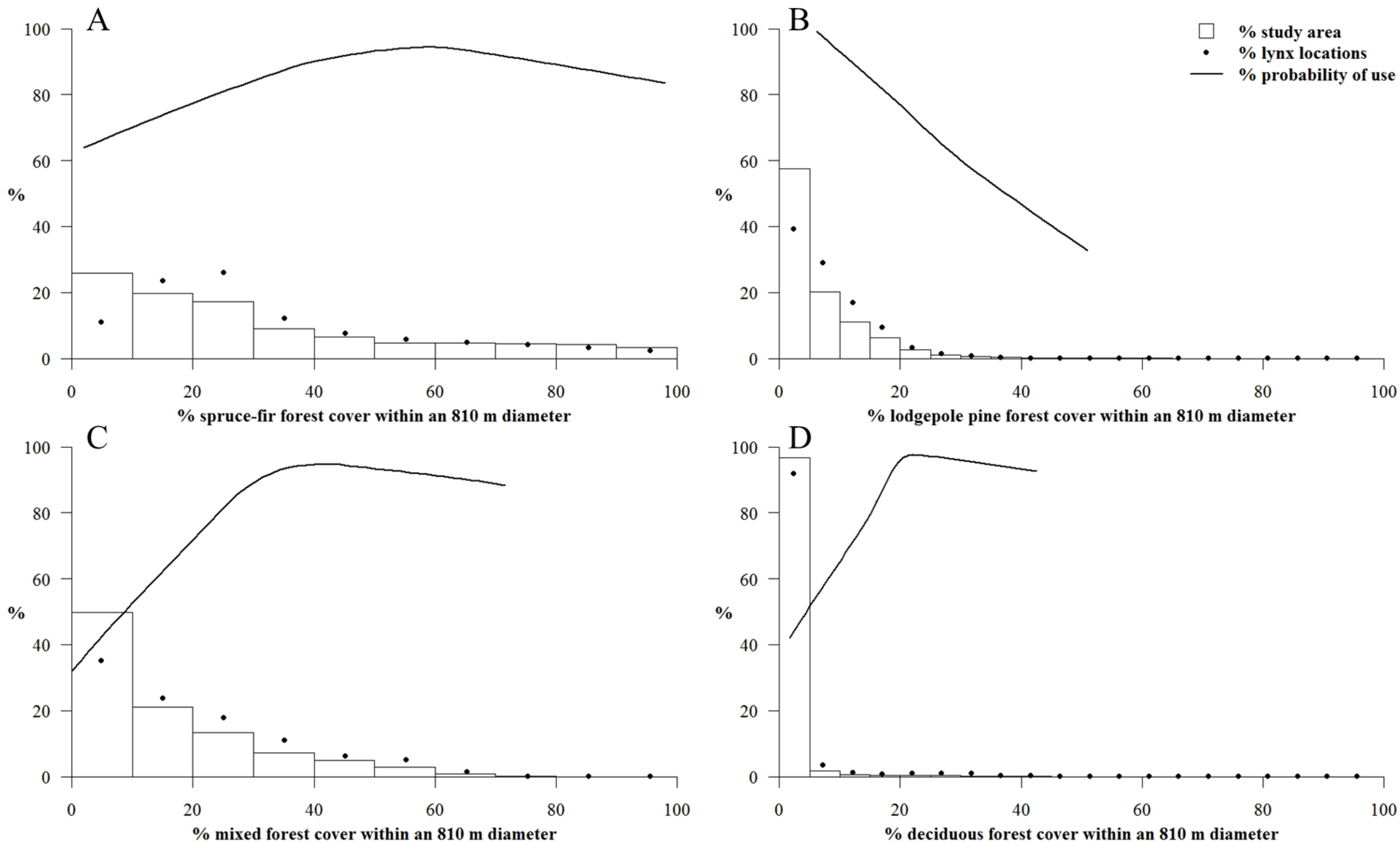

A
B
C
D
% study area
% lynx locations
% probability of use
%
% spruce-fir forest cover within an 810 m diameter
% lodgepole pine forest cover within an 810 m diameter
% mixed forest cover within an 810 m diameter
% deciduous forest cover within an 810 m diameter
0
20
40
60
80
100

Figure 2.19. Lynx selection of forest types in the Black Pine Basin study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) spruce-fir forest at a large scale; B) lodgepole pine forest at a large scale; C) mixed forest at a large scale; and D) deciduous forest at a large scale.

Old disturbances had a positive impact on core lynx habitat in the Black Pine Basin. Lynx selected old, high-severity burns, especially where fire skips or old, low severity burns are also nearby and the Whiteface Burn provided some of the most extensive, high quality lynx habitat in this study area. Additionally, lynx selected for large-scale areas with old clearcuts, although such sites were rare (**Figure 2.20**).

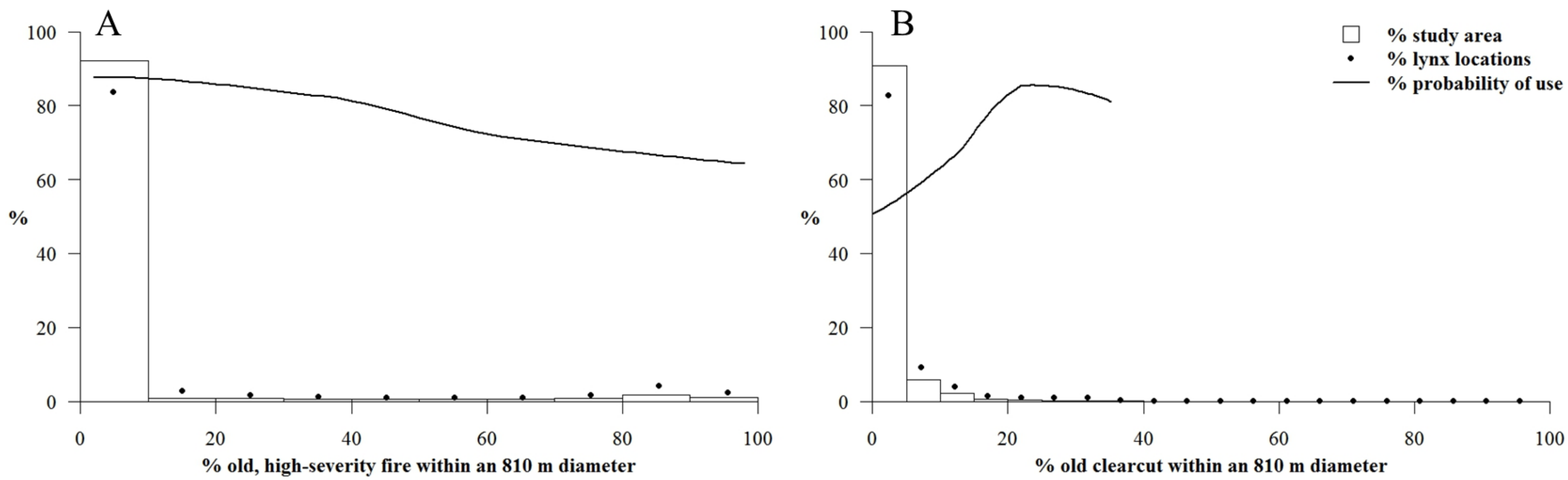


Figure 2.20. Lynx selection of disturbed areas in the Black Pine Basin study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) old, high-severity burn at a large scale; B) old clearcuts at a large scale.

2.5 DISCUSSION

Lynx in the North Cascades selected sub-boreal forests and low slopes as they do in other areas of their range (Vashon et al. 2008, Moen et al. 2008, Squires et al. 2010). I analyzed the first GPS dataset for lynx in Washington and found that among sub-boreal forest types, lynx selected spruce-fir or lodgepole pine forests and that the strength of selection varied with the local abundance of these forest types. These results confirm previous studies showing that lynx in the Loomis area selected locally abundant lodgepole pine forests (Koehler 1990), while lynx in the Black Pine Basin area selected locally abundant spruce-fir forests (Koehler et al. 2008, Maletzke et al. 2008). My results also show that lynx can adjust core habitat selection to take advantage of locally abundant forest types.

However, sub-boreal forests in the North Cascades are fragmented by recent burns, forest openings, timber harvest, and dry forests. Prior to my study, only anecdotal evidence existed to suggest that, while traveling, lynx will use matrix habitats such as burns, open understory forests, and shrub lands (Koehler 1990, Squires and Laurion 2000, Walker 2005). My results reveal that lynx indeed used a wider range of habitats when traveling than when selecting core habitats. Lynx used open areas and took advantage of available cover, such as fire skips within large burns, demonstrating that even this so-called non-habitat was useable. The flexible habitat selection patterns demonstrated in this study by traveling lynx could increase the functional connectivity of the North Cascades landscape.

2.5.1 Core Habitat Selection

Lynx in Washington selected areas of low slope with forest cover to support their hunting and cover needs, corroborating previous lynx research (Koehler et al. 2008, Squires et al. 2010). As Koehler et al. (2008) and Maletzke et al. (2008) found, lynx selected for higher canopy cover and avoided low canopy cover. I suspect this pattern may be primarily driven by understory cover, although I did not have a specific GIS layer for understory. In addition, lynx selected higher growing season precipitation and cooler, moister sites where growing conditions may support diverse and dense understory communities and the sub-boreal forests lynx select (Franklin and Dyrness 1973, Lillybridge et al. 1995). Although some partial plots show that the probability of lynx use declined at the high end of spruce-fir or lodgepole pine forest cover, I believe this result occurs because many of the most expansive stands of spruce-fir and lodgepole pine forest were located within the Tripod Burn. Thus, it was not that lynx avoided large-scale areas with large expanses of spruce-fir or lodgepole pine cover, but rather they avoided new, burned areas where the regeneration of these forests is still in the open, stand initiation stage. Conversely, lynx avoided low growing season precipitation and warmer, drier sites where conditions do not support dense growth but rather the avoided open, dry forests. Previous lynx studies in the North Cascades also found that lynx avoid dry forests (Koehler et al. 2008, Maletzke et al. 2008)

Many lynx habitat studies highlight the importance of post-disturbance forests in the early stand development stage because they provide dense understory cover for lynx (Koehler 1990, Mowat and Slough 2003, Squires 2010, McCann and Moen 2011, Simons-Legaard 2013). Lynx selected regenerating forests as core habitat where they existed in the Black Pine Basin and Loomis study areas. Notably, parts of the old Whiteface Burn provided the most extensive and highest-quality core habitat in the Black Pine Basin. However, few places on my study areas were characterized as old disturbances (those that occurred between 1985 and 1997) and lynx here adjusted their habitat selection patterns to use older forests, demonstrating an ability to exist in a landscape where regenerating forests are rare.

An examination of the influence of timber harvest on habitat selection by lynx provides further evidence that lynx in the North Cascades do not rely on regenerating forests. There was some indication that where old clearcuts were present, lynx selected them as core habitat and that old thins were avoided, which is consistent with previous findings (Fuller et al. 2007, Squires et al. 2010). However, unlike in heavily harvested areas such as northern Maine where regenerating clearcuts provide important core habitat (Fuller et al. 2007), previously harvested forests were rare on my study areas and timber harvest variables were not highly important predictors of core habitat. Lynx in the North Cascades clearly do not depend on regenerating forests created by clearcuts.

The vast 2006 Tripod Burn was generally avoided by lynx. Lynx preferred to stay near to the edge of the 2006 Tripod Burn and to use areas with lower amounts of high-severity burn, such as fire skips. Indeed, one lynx regularly traveled across the Tripod Burn to reach a large fire skip comprised of forest burned 38 years previously in the 1970 Forks Fire. Thus, in agreement with an observation by Walker (2005), fire skips may provide important patches of core habitat for lynx if they are near to a burn edge or are large and attractive enough to lure a lynx deep inside a large burn. In general, though, new high-severity burns result in a loss of core lynx habitat until forests regenerate enough to provide core habitat (Fox 1978, Mowat and Slough 2003).

2.5.2 Travel Habitat Selection

My Travel Habitat model demonstrates that lynx habitat does not exist as discrete patches of used habitat and un-used non-habitat. As a result, a landscape with structurally unconnected core habitat patches may be functionally connected for lynx. My results corroborate those of a recent study that indicates lynx occupancy is affected by habitat loss but not by habitat fragmentation on a landscape scale (Hornseth et al. 2014). These authors suggest that in central

Ontario, lynx adapted their habitat selection patterns so that fragmentation of young spruce-fir forests by other forest types, structural stages, open areas, or development, do not affect lynx occurrence. Instead, lynx were able to adapt to local habitat conditions and use small patches of resources, thus surviving in fragmented landscapes (Hornseth et al. 2014).

Similar to findings by Elliot et al. (2014) on African lions (*Panthera leo*), North Cascades lynx “made the most of a bad situation” when moving through matrix habitats by selecting a wider range of habitat characteristics than when selecting core habitats. Stands of sub-boreal forest that were unsuitable as core habitat due to topography or forest structure were important components of their travel habitat. While traveling, lynx selected sub-boreal forest stands on somewhat steeper slopes, and the densest canopy covers, both of which were negatively associated with core habitat.

Non-forested habitats comprised a majority of matrix areas. Although my results show that lynx traveled through large-scale areas with abundant meadows, perhaps most surprising was lynx use of the new Tripod Burn. My Core Habitat Model clearly demonstrates that the Tripod Burn is not used for core habitat. However, my Travel Habitat Model indicates that lynx selected higher amounts of new, high-severity burn and areas further inside the burn than when selecting core habitats. Lynx used fire skips, areas of old burn, and low-severity burn areas to travel through this extensively burned landscape. (See Chapter 3 for a detailed analysis of how lynx use burned areas).

The results of my Travel Habitat Model indicate that lynx in the North Cascades are not so rigidly specialized that they completely avoid matrix habitats. For example, meadows and open-understory forests were not selected as core habitats yet were used by lynx as travel habitats. Although large, high-severity fires clearly cause loss of core habitats in the short-term, they offer conditions that lynx can use as travel habitat. Within-burn heterogeneity provides lynx with residual habitat structure to facilitate movement across burns and amongst high-quality fire skips.

2.5.3 Loomis and Black Pine Basin Core Habitat Models

The comparison between core habitat selection and travel habitat selection demonstrates that lynx in the North Cascades adjust their habitat selection patterns to travel through matrix habitats. My study also revealed that within core habitat selection, lynx have a nuanced and flexible habitat selection pattern that responds to local habitats. As Koehler et al. (2008) and Maletzke et al. (2008) found, lynx in the Black Pine Basin select the abundant spruce-fir forests as core habitat. In addition, I found that mixed forests composed primarily of Douglas fir mixed with Engelmann spruce, subalpine fir, or lodgepole pine were common in the Black Pine Basin, and lynx responded by selecting mixed forest as another core habitat. Lodgepole pine was not common in the Black Pine Basin study area and was less important to core habitat selection. In the Black Pine Basin lynx selected areas with higher amounts of deciduous cover, much of which was located in the regenerating Whiteface Burn where willow (*Salix* spp.) and alder (*Alnus* spp.) provide thick cover and rich habitat for lynx (Chapter 3 and personal observation); similar results were found for lynx in the Yukon (Mowat and Slough 2003). Conversely, in the Loomis study area, where both spruce-fir forests and lodgepole pine were common but mixed forests were not, lodgepole pine and spruce-fir forests were selected as core lynx habitat. Mixed forest cover was less important to core habitat selection on the Loomis study area and was even negatively associated with habitat selection as the area of mixed forest increased. Similarly, deciduous cover was rare and unimportant to lynx habitat selection in the Loomis study area.

2.5.4 Scale Selection

Habitat selection was better explained by large-scale variables than small-scale variables. This result indicates that lynx select for large-scale areas containing good habitat but are less concerned with selecting particular fine-scale features within that large area, confirming results on lynx scale-selection in Maine (Fuller and Harrison 2010). However, based on my personal observations of lynx habitat selection in the North Cascades and findings by Squires et al. (2010), I believe that while habitat characteristics at a large-scale predict lynx use well, within the selected large-scale areas lynx also select habitat at smaller scales. I think a more plausible interpretation of my scale results is that the marginal importance of small-scale selection suggested by my models is an artifact of lower GIS layer accuracy at this scale and is not a precise depiction of lynx habitat selection.

2.5.5 Seasonal and Sex Specific Models

I did not find differences between the Male and Female Core Habitat Models, which agrees with findings by Mowat and Slough (2003) in the Yukon, but contrasts Burdett (2008) in Minnesota who found small differences in the amount of mature conifer forest used by male lynx versus female lynx with 3-7 month-old kittens. Similarly, my Summer and Winter Core Habitat Models did not reveal differences between seasonal habitat use, whereas Squires et al. (2010) found that lynx in the Rocky Mountains selected older multi-layered forests and avoided openings during the winter, but in the summer used young regenerating forests, smaller amounts of older forest, and did not avoid openings. Mowat and Slough (2003) also found seasonal differences in habitat use indicating that lynx use stands of willow more during the winter than the summer.

I do not believe that my results on seasonal and sex specific habitat use are necessarily conclusive for lynx in the North Cascades; differences may have occurred at a smaller scale than

I included in my models. In addition, differences in sex-specific and seasonal use may have been too slight for my models to detect.

2.5.6 Data Limitations

The travel habitats used by lynx in my study indicate that they use a wider variety of habitats than is often depicted for lynx. But do other kinds of landscape features present lynx with true barriers to movement in the North Cascades? My Travel Habitat Model showed little use of dry forests by lynx, suggesting that this forest type may restrict lynx movement. But because my dataset was limited primarily to lynx moving within their home ranges, I believe this suggestion is a product of using within home-range data and that lynx moving outside their home range area might travel through dry forest. Indeed, data recorded by lynx while on long exploratory movements (and thus excluded from my models), show that these lynx passed through dry forests on several occasions (for an example see Appendix B). Other studies of lynx in the southern portion of their range have observed lynx traveling through open habitats believed to be unsuitable to lynx such as sage-steppe and farmlands (Mech 1973, Squires and Laurion 2000). Similarly, lynx in my study crossed through developed valley bottoms and open sage habitats (Appendix B). This evidence suggests that while my Travel Habitat Model broadens the description of North Cascades lynx habitat, a study of the habitats lynx use while on long-distance exploratory or dispersal movements could reveal an even wider spectrum of used habitats while also revealing any landscape features that present genuine barriers to lynx movement.

While my results show that lynx in the North Cascades have flexible habitat selection, occupancy and habitat selection are not necessarily indicators of general habitat quality since occupied landscapes can act as population sinks where reproduction is lower than survival (Pulliam 1988). Lynx here may have the ability to occupy home ranges and a broader landscape fragmented by disturbances, topography, and human influences, but how different habitats and habitat configurations affect population dynamics is unknown for lynx in Washington. Indeed, a recent study in Montana found that reproductive success was highest for female lynx living in a home range with more continuous amounts of mature spruce-fir forests and only 10-15% dense regenerating forest (Kosterman 2014). Additionally, snowshoe hares in the North Cascades are sensitive to matrix habitat types and hare densities are highest in continuous habitat or habitat patches surrounded by matrix more similar to core forest habitats (Lewis et al. 2011). Using a spectrum of habitat types may allow lynx to exist in the North Cascades, but questions remain regarding how lynx population dynamics are affected by fragmentation, various habitat types, and a prey species that is also sensitive to more open habitats.

2.5.7 Implications for Lynx Management and Conservation

My results reinforce the idea than many animals do not view a landscape simply as habitat and non-habitat but instead view landscapes as a spectrum of habitat quality with different habitats used to carry out different life history functions (Prugh et al. 2008). For lynx in the North Cascades, lodgepole pine, spruce-fir, mixed, and deciduous forests contribute to the array of forest types with potentially dense understory covers that lynx and snowshoe hares select. Only by incorporating all of these forest types into lynx habitat management and conservation can Washington maximize the amount of available core habitat for lynx. In addition to protecting the full spectrum of selected lynx habitat for conserving core areas, broadening the definition of lynx habitat to include travel habitats such as residual trees in new burns or open forests will facilitate connectivity between core areas.

The future of southern lynx habitat is uncertain. There is an urgent need to conserve both core and travel habitats as they are increasingly threatened by degradation and fragmentation due to human development and climate change (Soja et al. 2007, Fauria and Johnson 2007, Balshi 2009, Littell et al. 2010, Fisichelli et al. 2014).

CHAPTER 3

LYNX HABITAT USE IN RECENTLY BURNED AREAS

3.1 LITERATURE REVIEW AND OBJECTIVES

The boreal forest, which spans across the northern areas of Eurasia and North America, accounts for one third of the earth's forests (Perera and Buse, 2014). Boreal forest is characterized by long cold winters, short warm summers and a relatively small assemblage of tree species, mainly spruce (*Picea* spp.), fir (*Abies* spp.), larch (*Larix* spp.), pine (*Pinus* spp.), and deciduous species such as poplars (*Populus* spp.), willow (*Salix* spp.), birch (*Betula* spp.), and alder (*Alnus* spp.) (Goldammer and Furyeav 1996, Perera and Buse, 2014). Near the southern limit of the boreal forest's range, the forest transitions into southern sub-boreal forest types (Agee 2000).

While the boreal forest has a relatively simple assemblage of species, it is also characterized by dramatic and frequent disturbances that create a continually shifting mosaic of successional stages across the landscape (Agee 2000, Perera and Buse 2014). Disturbance agents include wind, disease epidemics, and insects, but the most important boreal and sub-boreal forest disturbance is wildfire (Agee 2000). Wildfires burn millions of hectares per year in the boreal forest, often over large areas and at intensities that initiate stand replacement (Perera and Buse 2014). These dramatic fires drive the boreal landscape's heterogeneity of forest age structure and species assemblages, and ecological functions such as carbon storage or release (Goldammer and Furyeav 1996, Brassard and Chen 2006).

Boreal fires create heterogeneity both at the landscape level and within a single burn perimeter since fire behavior varies greatly according to weather, microclimate, fuels, and topography (Cansler and McKenzie 2014, Perera and Buse 2014). As a result, some areas burn at a high intensity, consuming forest canopies and leaving only burnt snags behind, while other areas burn at a lower intensity such that the understory burns but many trees survive (Brassard and Chen 2006, Perera and Buse 2014). Fire skips may not burn at all, leaving the original forest structure and species composition intact (Perera and Buse 2014). Consequently, the composition of the residual vegetation and structural features such as live trees, snags, and downed logs fluctuates across a burn.

In turn, forest regeneration patterns vary, influenced by the presence or absence of residual vegetative reproductive structures such as coniferous seeds released from serotinous cones, underground suckers, or wind-blown seeds from fire skips and burn edges (Brassard and Chen 2006, Perera and Buse 2014). Residual snags and logs also affect regrowth since they provide substrate, shade, and physical protection for young seedlings (Brassard and Chen 2006). Finally, site-specific variations in soils, climate, and topography also affect regeneration patterns and, combined with varying residual vegetation compositions, result in a heterogeneous landscape within a single fire perimeter (Franklin and Dyrness 1973, Brand 1991, Turner et al. 1997, Bonnet et al. 2005, Irvine et al. 2009, Crotteau et al. 2013, Perera and Buse 2014).

3.1.1 Climate Change

With the onset of climate change, the cycle of burning and regeneration that has defined the boreal forest is changing. Summers in the boreal region are predicted to become warmer and drier, which will both lengthen and intensify the fire season (Westerling et al. 2006, Fauria and Johnson 2007, Soja et al. 2007, Balshi 2009, Littell et al. 2010). Larger and more severe fires are predicted to occur more frequently, which will increase the amount of forest in an open stand-initiation stage (Westerling et al. 2006, Fauria and Johnson 2007, Soja et al. 2007, Balshi 2009, Littell et al. 2010), (Appendix A describes stand development stages). Larger and more severe fires will also change the composition and spatial patterns of residual vegetation, potentially homogenizing the landscape within a fire perimeter (Cansler and McKenzie 2014). Warmer and drier summers could also change forest regeneration patterns following a fire by limiting the establishment and growth of plant species dependent on moist conditions (Little et al. 2010).

Because boreal animals have adapted to a landscape shaped by fire, a change in fire regime and regeneration patterns would likely affect the wildlife of boreal forests. Historically, fire has been an important ecological function that influences species diversity. As succession progresses, plant communities change in composition and structure, and animal communities shift in response to the changing habitat (Fox 1983, Fisher and Wilkinson 2005). For example, the snowshoe hare (*Lepus americanus*) is an important boreal prey species whose presence can be predicted based on a forest stand's developmental stage. Hares depend on high stem-density forests to provide browse and cover, a feature primarily found in young stands, and in old-growth forests where canopy gaps promote a multi-layered structure (Hodges 2000a, 2000b, Hodson et al. 2011). Unfortunately, although responses of animals to fire are documented for some small mammals and birds, substantial information gaps exist regarding responses of larger prey species and carnivores to fire (Fisher and Wilkinson 2005). This lack of information hinders both current conservation and management of boreal forest carnivores and the ability to adapt conservation strategies as fire regimes shift under climate change.

One such carnivore is the Canada lynx (*Lynx canadensis*), an iconic boreal forest species dependent on the snowshoe hare for prey and thus closely linked to forest structure. Studies of lynx in Alaska, Canada, and to a lesser extent in the sub-boreal regions of the contiguous US document general trends in lynx response to fire, but lack detailed information that could be used to improve lynx management and conservation (Koehler 1990, Staples 1995, Paragi et al. 1997). These studies describe lynx as selecting against recent burns in the open, stand initiation stage where shrubs and trees have not grown tall enough to provide cover and browse for snowshoe hares, especially during the winter when snow covers low understory structure (Hodson et al. 2011, von Kienast 2003, Koehler et al. 2008, Maletzke et al. 2008). Conversely, as forest regeneration progresses, burns in an early stand development stage are often composed of dense regenerating deciduous shrubs and conifer trees that provide quality snowshoe hare habitat and thus quality lynx habitat (Stephenson 1984, Paragi et al. 1997, Hodges 2000b, Mowat and Slough 2003). Stands regenerating post-fire that move into a late stand development stage, where a closed canopy inhibits understory growth and self-thinning eliminates branches in the understory, do not provide good snowshoe hare and lynx habitat (Koehler 1990, Paragi et al. 1997, Hodson et al. 2011). Forests in a late stand development stage may not provide understory conditions preferred by snowshoe hares and lynx until a disturbance resets forest succession by returning the area to the early stand development stage or until the forest matures into old-growth so that canopy gaps form, encouraging shrub growth and tree boughs provide understory cover (Maletzke et al. 2008, Squires et al. 2010, Hodson et al. 2011). However, beyond these general descriptions of lynx response to fire, little detail is known about how lynx respond to different burn severities, to the heterogeneity of regeneration in a burned area, or to the spatial configuration of a burned area. Answering these questions is paramount considering the prevalence of fire in lynx habitat and the increase in fire size, severity, and frequency predicted as a result of climate change.

3.1.2 Wildfires and Lynx in the Sub-Boreal Forests of Washington

Lynx in the contiguous US represent the southern range limit of their species. As with many species living at their range edge, southern lynx survive in suboptimal habitat as the boreal forest of Alaska and Canada transition into sub-boreal and then temperate forest types (Brown et al. 1996, Agee 2000, Buskirk et al. 2000b, McKelvey et al. 2000b). Furthermore, southern lynx habitat is more fragmented than habitat in the core of lynx range, interrupted by topography and a greater human influence (Buskirk et al. 2000b, Koehler et al. 2008). The relatively poor habitat conditions at the southern edge of lynx range do not support high lynx numbers; lynx in the contiguous US were listed as Federally Threatened in 2000 where they persist in Washington, Idaho, Wyoming, Montana, Colorado, Minnesota, and Maine (US Fish and Wildlife Service 2000, McKelvey et al. 2000b). As in most forest throughout the range of lynx range, disturbances play an important role in shaping southern lynx habitat, with wildfires dominating the western sub-boreal disturbance regime (Agee 2000). However, substantial information gaps exist regarding responses of southern lynx to fire despite their status as a Threatened species and the increase of fire impacts projected with climate change.

In an effort to elucidate how lynx in the south of their range respond to fire, this chapter examines lynx living in the North Cascades Mountains of Washington. Here, the only known breeding population of lynx in Washington exists among wildfires that have drastically altered their habitat since the early 1990s. Previous studies have estimated that snowshoe hare densities in the North Cascades are much lower than in the interior of their range in Canada and Alaska (Lewis et al. 2011), and that the current lynx habitat in Washington supports fewer than 87 individuals (Koehler et al. 2008).

The sub-boreal forest that snowshoe hares and lynx select in the North Cascades is limited to mid-elevations and is fragmented by rock, ice, and alpine meadows at higher elevations, and by ponderosa pine (*Pinus ponderosa*) and Douglas fir (*Pseudotsuga menziesii*) forest at lower elevations (Koehler et al. 2008, Lewis et al. 2011). Recent timber harvests, roads, and human development also fragment the lynx habitat.

Both the western and eastern slopes of the North Cascades sustain sub-boreal forest types, although the wetter, more heterogeneous forests of the western slope have not historically supported lynx (McKelvey et al. 2000a). The eastern-slope sub-boreal zone includes lodgepole pine (*Pinus contorta*) occupying the more gentle topography of the area (Franklin and Dyrness 1973). Lodgepole pine is an early successional species, often invading burn areas and sometimes persisting as the climax species if another seed source is not present (Agee 2000). Subalpine fir *(Abies lasiocarpa*) forests exist in moister, cooler areas of the sub-boreal zone and often include a large Engelmann spruce (*Picea engelmanii*) component. Engelmann spruce and subalpine fir ("spruce-fir" hereafter), often develop as a late successional community after a site has been occupied by lodgepole pine (Franklin and Dyrness 1973).

In general, fires in the sub-boreal forests of the eastern North Cascades slope are larger and more severe than on the western slope, facilitated by a drier climate and fewer fire barriers such as changes in topography and forest openings (Cansler and McKenzie 2014). Within the eastern-slope sub-boreal zone, the fire regime varies by forest type, with lodgepole pine forests burning somewhat more frequently than spruce-fir forests (Agee 1993, 2000).

Several fires have burned lynx habitat in the North Cascades in the last twenty years. In 1994, the Whiteface Fire burned 1,554 ha and the Thunder Mountain Fire burned 3,686 ha. In 2001, the Thirty-Mile Fire burned 2,465 ha and the Farewell Fire burned 32,278 ha. Most dramatically, the 2006 Tripod Burn grew to 70,644 ha, burning much of what was considered the most extensive and high-quality lynx habitat in Washington (Stinson 2001, Koehler et al. 2008).

Previous studies in the North Cascades describe core, hunting and resting lynx habitat as dense, young lodgepole pine stands (> 20 years old) in areas where lodgepole pine is the dominant forest type (Koehler 1990). However, much of this forest type burned in the Tripod

Fire. Where lodgepole pine is scarcer, lynx select multi-layered spruce-fire forests (Koehler et al. 2008). As in other areas of their range, lynx in the North Cascades generally avoid open habitats such as recent burns, clearcuts, and meadows, although anecdotal evidence suggests that lynx may be more willing to cross burns than other forest openings since remaining snags provide some cover, and that lynx sometimes cross burned areas to reach fire skips that support snowshoe hares (Walker 2005, Koehler et al. 2008).

Because no studies have examined how lynx respond to fires in Washington and only broad generalities exist to describe how lynx use burned areas across their range, my objectives in this chapter are to:

1. examine lynx use of burned areas using lynx location data collected in the 1994 Whiteface Burn and the 2006 Tripod Burn;
2. model how topography, climate, and land cover affect lynx use of burned areas;
3. model how burn severity and the spatial configuration of a burn affect lynx habitat use.

3.2 STUDY AREA

To characterize lynx use of burned areas, I examined the 1994 Whiteface Burn in the Black Pine Basin area, and the 2006 Tripod Burn, which nearly surrounds the 1994 Thunder Mountain Burn and is in the Loomis area (**Figure 3.1**; see also Chapter 2 for a description of the Black Pine Basin and Loomis areas). Both the Whiteface and Tripod Burn study areas are located on the Eastern slope of the North Cascade Mountains in Washington and fall within the Okanogan-Wenatchee Lynx Management Zone designated by the Washington State Lynx Recovery Plan (Stinson 2001).

The Whiteface Burn study area covers 1,554 ha and is located in the Okanogan-Wenatchee National Forest. The burn spans from 1 km north of Goat Creek, north to the Pasaytan Wilderness, east to Goat Peak, and west to Short Creek. Approximately 15 km east of the Whiteface Burn study area, the 70,644 ha Tripod Burn occupies territory within both the Loomis State Forest and the Okanogan-Wenatchee National Forest. This study examines only the western portion of the Tripod Burn, a 46,800 ha area that includes the Thunder Mountain Burn. The southern edge of the Tripod Burn study area falls 8 km north of Highway 20 and the northern edge of the study area falls 3 km south of the Canadian border. West to east, the study area spans from the North Twenty Mile Peak to near Skull and Crossbones Ridge.

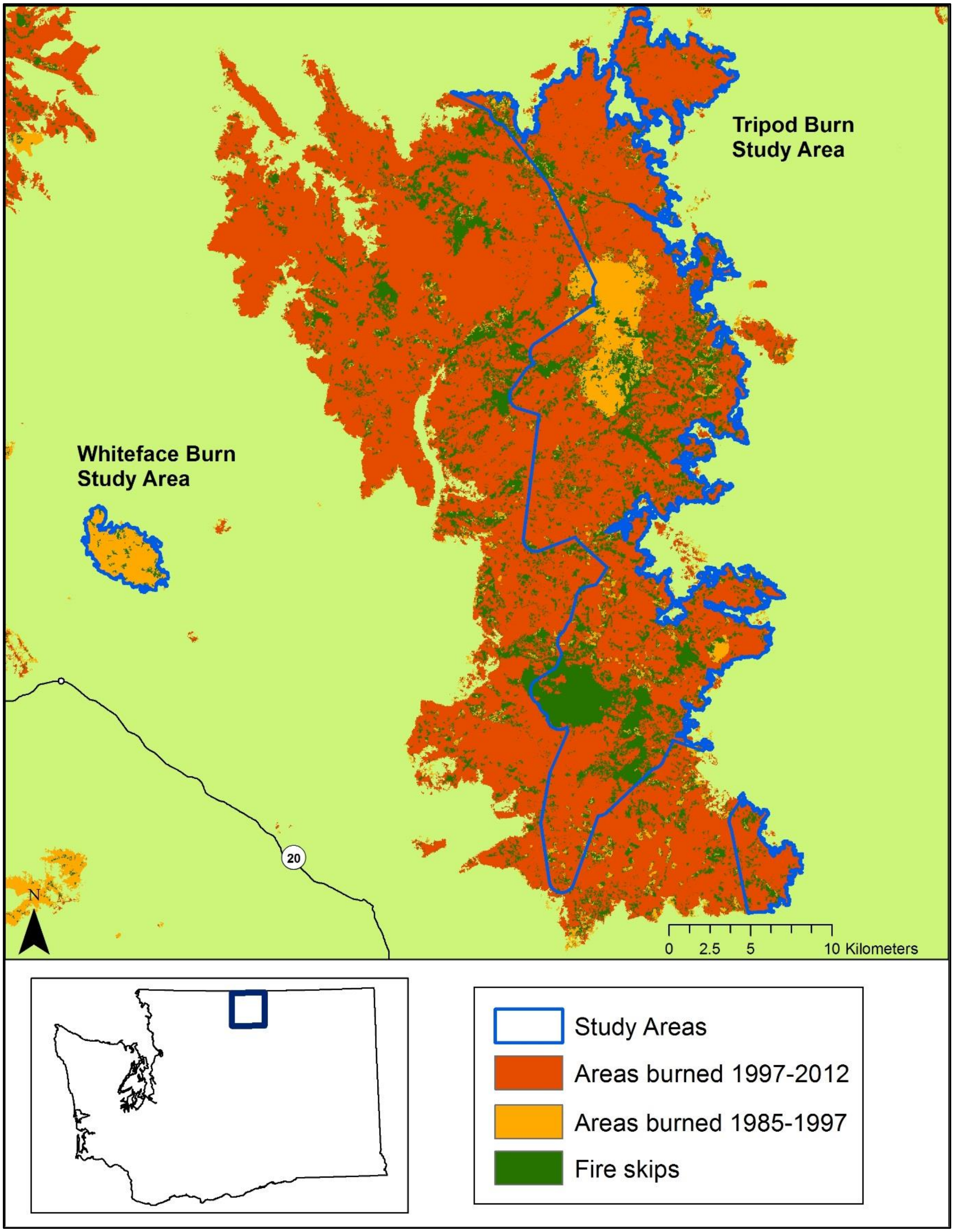

Tripod Burn
Study Area
Whiteface Burn
Study Area
20
N
0 2.5 5 10 Kilometers
Study Areas
Areas burned 1997-2012
Areas burned 1985-1997
Fire skips

Figure 3.1. The Whiteface and Tripod Burn study areas located on the eastern-slope of the North Cascades, Washington.

Cold, snowy winters and mild summers characterize the study areas, with average monthly temperatures in nearby Mazama, Washington (elevation: 664 m) ranging between -10°C and 23°C, with average annual snowfall of 305 cm (Western Regional Climate Center, http://www.wrcc.dri.edu/, accessed June 20, 2014).

As topography varies in the Whiteface and Tripod Burns, site temperature and moisture accumulation also varies. Site-specific climate in turn causes variation in forest types, ranging from sub-boreal forests in high-elevation areas and cool, mid-elevation pockets and aspects, to low-elevation dry forests (Lillybridge et al. 1995). The sub-boreal forest consists of Engelmann spruce-subalpine fir forest or lodgepole pine forests. On warmer mid-elevation sites, forests transitioning from sub-boreal types into a drier forest dominated by Douglas fir ("mixed forest" hereafter) exist while lower elevations are dominated by dry Douglas fir-ponderosa pine forests ("dry forest" hereafter) (Lillybridge et al. 1995).

The Whiteface Burn ranges from 1,280 m of elevation at its southern end to 2,222 m at the northern end, with an average elevation of 1,650 m and 80% of its area above 1,500 m. This variation in elevation supports a heterogeneous forest cover. Based on an examination of GIS land cover data, dry, mixed, and deciduous forest types cover 55% of the forested areas within the burn and largely exist at lower elevations. Sub-boreal forest types exist at higher elevations and comprise 45% of the regenerating and residual forest. Sub-boreal forest types dominated by lodgepole pine are rare in the Whiteface Burn and, of the sub-boreal forest stands, lodgepole pine forests comprise only 3% of the stands.

Based on field observations, my GIS land cover data underestimates the deciduous component of the burn, mapping deciduous forest mainly in riparian areas despite regenerating dry and mixed forest types being comprised largely of willow (*Salix scouleriana*) and alder

(*Alnus sinuata*) together with dry forest coniferous tree species. In the Whiteface Burn, 82% of the fire burned at a high severity (>50% canopy cover loss) while 10% burned at a low severity (<50% canopy cover loss) and 8% of the area within the perimeter of the burn was not burned at all (fire skips hereafter).

The Tripod Burn study area is higher in elevation than the Whiteface Burn, ranging from 855 m to 2,390 m with 93% of its area above 1,500 m. In contrast to the Whiteface Burn, the Tripod Burn study area has a large sub-boreal forest component with 88% of the regenerating and residual forest type in this category. The Tripod Burn study area also has more lodgepole pine forest, which comprises 35% of the forest within the regenerating and residual forest category.

In the Tripod Burn study area, 63% of the area burned at a high severity and 8% burned at a low severity. The Tripod fire nearly surrounded but did not re-burn the 1994 Thunder Mountain Burn, so 8% of the area within the Tripod Burn study area is classified as an old (1985-1997) burn. Fire skips in the Tripod Burn study area make up 21% of the burn and include a 1,850 ha island of forest that has not burned since the 1970 Forks Fire.

3.3 METHODS

Lynx were trapped and fitted with Global Positioning System (GPS) telemetry collars in the Okanagan-Wenatchee National Forest and the Loomis State Forest starting January 2007, just months after the Tripod fire, and finishing in April 2012. Trapping took place during the winter using box traps (Kolbe et al. 2003), and was a collaboration between the Washington Department of Fish and Wildlife, Washington Department of Natural Resources, U.S. Forest Service, U.S. Bureau of Land Management, and the U.S. Fish and Wildlife Service (John Rohrer, personal communication). The collars were programmed to record GPS locations every four hours for one year, except for one collar programmed to record GPS locations every six hours. For details on data filtering see Chapter 2.

3.3.1 Study Area Delineation for Modeling Available Burn Habitat

To delineate the Whiteface Burn study area, I used a raster dataset depicting wildfires in ArcGIS 10.1 (ESRI 2012) to define the perimeter of the Whiteface Burn. To outline the Tripod Burn study area, I used the raster dataset to define the eastern fire perimeter. However, because the Tripod Burn extends further west than any of the collared lynx ventured, I limited the western boundary by connecting sequential lynx locations with a straight line, and then buffering the lines by 766 m, the average straight-line distance traveled by a lynx in the four-hour period between GPS fix attempts. The outermost edge of the buffered lines was used to delineate the eastern extent of the Tripod Burn study area. To examine lynx habitat use in the Whiteface and Tripod Burn study areas, I used ArcGIS 10.1 (ESRI 2012) to generate random available locations within each study area equal to the number of used locations in each study area (Barbet-Massin et al. 2012).

3.3.2 Habitat Variables

I used GIS layers to represent the landscape characteristics that are important to lynx use of burned areas (**Table 3.1**). I used ArcGIS 10.1 (ESRI 2012) to derive continuous representations of each predictor variable using 30 m^2 pixels projected into the 1983 North American Datum Albers coordinate system. To capture habitat selection at different scales, I represented each land cover variable as a percentage within 3x3 and 27x27 pixel windows. I also represented canopy cover, topographic, and climate variables as the average value within these windows. A 3x3 window represents a small-scale area, as has a 90 m diameter. A 27x27 window represents a large-scale area and has an 810 m diameter. Appendix C provides detailed information on layer development.

Table 3.1. Habitat variables used in the Random Forest models of lynx habitat use in burned areas.

Variable Class	Variable	Layer Name	Measurement Type
Land Cover	Lodgepole pine	lp	Number of like pixels within a 3x3 or 27x27 window
	Spruce-fir	essf	
	Mixed forest	mixed	
	Dry forest	dry	
	Deciduous forest	decid	
	Ice or rock	rock_ice	
	Grassland	grass	
	Shrub land	shrub	
Disturbance	Old, high-severity fire	old_cut	Number of like pixels within a 3x3 or 27x27 window
	Old, low-severity fire	old_thin	
	New, high-severity fire	new_cut	
	New, low-severity	new_thin	
	Fire skips	fireskips	
Patch Metrics	Distance to edge of fire	distedge_fire	Meters
Topography	Slope	slope	Degrees averaged across a 3x3 or 27x27 window
	Distance to nearest draw	dist_draw	Meters
Climate	Compound Topographic Index	cti	Index, lower numbers indicate wetter areas. Index averaged across a 3x3 or 27x27 window
	Heat Load Index	hli	Index, lower numbers indicate warmer areas. Index averaged across a 3x3 or 27x27 window
	Growing season precipitation	gsp	Average total precipitation (mm) between April and September. Index averaged across a 3x3 or 27x27 window
Forest Structure	Canopy cover	can_cov	Average percent canopy cover in a 3x3 or 27x27 window

3.3.2.1 Land Cover

To characterize the Whiteface and Tripod Burn study areas, I categorized land cover into five forest types and three non-forest types. I include lodgepole pine forests and spruce-fir forests since they comprise the sub-boreal forest lynx select in the North Cascades (McKelvey et al. 2000c, Koehler et al. 2008, Maletzke et al. 2008). I also created a dry forest category since previous studies report lynx selecting against dry forests dominated by Douglas fir or ponderosa pine. Dry forests were prevalent in the Whiteface Burn study area and, to a lesser extent, in the Tripod Burn study area (Koehler et al. 2008, Maletzke et al. 2008). To capture forest stands transitioning between sub-boreal and dry forest types, I also included a mixed forest type. Finally, I included deciduous forests since these early successional communities can be prevalent in a regenerating burn. Non-forested areas of the burn study areas include grassy meadows, shrubby meadows, and barren areas such as rock outcrops or ice fields. I included land cover variables depicting each of these vegetation types.

My land cover data categorized 23% of the Whiteface Burn as "disturbed", meaning residual canopy cover was <10%. To assign "disturbed" areas with the most likely forest type regenerating in the area, I used the ArcGIS 10.1 tool, Nibble, to assign "disturbed" pixels a land cover type that was based on the land cover types of the surrounding pixels.

3.3.2.2 Burn Characteristics

Fire severity affects the residual dead or living vegetative cover left after the burn (Perera and Buse 2014). In high-severity burned areas, only blackened tree trunks remain while a low-severity burn consumes understory cover but trees survive. Regeneration patterns are affected by burn severity since residual trees provide propagules and shade for seedlings (Perera and Buse, 2014). As a result, lynx may use areas burned at a high or low severity differently in response to differing residual cover and forest development patterns. To capture the effect of burn severity, I included variables depicting old, low-severity burns (burn year 1994, canopy cover loss of 1-50%), and old, high-severity burns (burn year 1994, canopy cover loss of 51-100%) to represent the Whiteface Burn and the portion of the Thunder Mountain Burn within, but not re-burned by, the Tripod Fire. To represent the Tripod Burn I included variables to represent new, low-severity burns (burn year 2006, canopy cover loss of 1-50%) and new, high-severity burns (burn year 2006, canopy cover loss of 51-100%).

3.3.2.3 Patch Metrics

I examined how the spatial arrangement of burn pattern may influence lynx habitat selection by including a patch metric depicting the distance from each pixel within the burn to the nearest edge. In addition, I included a variable for grassy, shrubby, or rocky forest openings depicting the distance from each pixel within the forest opening to the nearest edge. In the Tripod Burn especially, forest openings such as meadows are interspersed throughout the burned forest. Because grassy, shrubby, or rocky areas often have less cover than burned areas, lynx may be less willing to use these openings (Koehler et al. 2008).

3.3.2.4 Topography

Because lynx select for areas of low slope in the North Cascades (McKelvey et al. 2000c, Koehler et al. 2008, Maletzke et al. 2008), I included slope as a landscape variable. I also included a variable depicting the distance to the nearest draw since lynx may use draws to travel (Stinson 2001).

3.3.2.5 Climate

Lynx may select burned areas with a cool, moist climate where forest recovery can occur faster (Buskirk et al. 2000b). Thus, I included a Heat Load Index variable depicting temperature based on aspect and slope (McCune and Keon 2002). I also included the Compound Topographic Index as a measure of wetness based on the amount of upstream contributing area and slope (Moore et al. 1993, Gessler et al. 1995). Similarly, I included a layer depicting the average precipitation accumulated during the growing season.

3.3.2.6 Forest Structure

The structure of residual fire skips and forest regrowth is likely an important factor in lynx habitat selection of burned areas since snowshoe hares select dense understory for cover and browsing (Hodges 2000b, Lewis et al. 2011). With no understory cover GIS layer available for the study areas, I used forest canopy cover to represent the general structure of a forest. Although canopy cover does not always correlate with understory cover, it may capture broad cover differences in a burned area.

3.3.3 Model Development

I developed habitat models for the Whiteface Burn and Tripod Burn using Random Forest (Brieman 2001) implemented in program R 3.1.2 (R development core 2014) with package rfUtilities (Liaw and Wiener 2002, Evans and Murphy 2014); (see Chapter 2 for an outline of the Random Forest procedure). For each burn study area I developed a model using both the large-scale and small-scale representations of each variable to determine the scale at which lynx select different habitat characteristics.

For each model I compared all used points within the burn to an equal number of random available points within the burn to insure unbiased sampling of each class (Evans and Cushman 2009). I assumed that autocorrelation and redundant data were minimal issues in the fire models because so few lynx points fell within the Whiteface and Tripod Burns, and because lynx could easily move out of a burned area or into a fire skip in the four hour period between GPS fixes so that habitats used at consecutive locations were not necessarily autocorrelated. Thus, I sub-sampled 80% of the data using the R program Spatial Intensity Weighted Subsample leaving 20% of the data for an independent validation.

To ease interpretation and improve model performance I screened for and removed multivariate redundant variables using a test developed by Murphy et al. (2010) prior to running each habitat model. Using only the most important variables for a Random Forest model also improves model interpretation and performance. I removed highly collinear variables identified by a Spearman rank test ($r > 0.8$) to further ease model interpretation. To identify the most parsimonious set of predictor variables for each burn model, I used a model selection procedure developed by Murphy et al. (2010). For each burn model, the procedure ran a Random Forest model using 4,000 bootstrap samples. The procedure then calculated a Model Improvement Ratio for each variable based on the variable's importance to the model. Variables were then grouped into prospective models by combining variables with Model Improvement Ratios above increasingly high thresholds (thresholds range from 0-1 in 0.1 increments). For each fire model I selected the model that minimized the out-of-bag error, the within-class error, and the number of variables. Using only the chosen set of predictor variables, I ran Random Forest a final time for each burn model.

To validate and assess the performance of each habitat model I used several statistics. I assessed model-fit using out-of-bag error by examining the percentage of out-of-bag locations incorrectly predicted by the Random Forest trees. I also performed an independent validation by back-predicting to the 20% data withheld from the sub-sample. I assessed the accuracy of these back-predictions, the proportion of used locations correctly predicted (sensitivity), and the proportion of available locations correctly predicted (specificity). I also assessed the area under the curve (AUC) of a Receiver Operator Characteristic, which measures how evenly the model predicts sensitivity and specificity, and the Kappa statistic which measures how much better the model predicted used and available points than expected by random chance (Murphy et al. 2010, Evans et al. 2011). Finally, to insure that each fire model explained significantly more variation in the data than expected by random chance, I assessed significance by randomizing the used and available data 1,000 times to create a null distribution of variance for comparison with each fire model. A fire model was considered significant if the variance explained by the model was significantly greater than the variance explained by the null distribution ($P < 0.05$; Murphy et al. 2010).

3.4 RESULTS

Data from 17 lynx were obtained. Three male and two female lynx were collared in the Black Pine Basin around the Whiteface Burn. Eleven male and one female lynx were collared in the Loomis State Forest near the Tripod Burn. In the Black Pine Basin, all five lynx spent time in the Whiteface Burn so that 11% (1,530 points) of the locations within the Black Pine Basin fell within the burn (**Figure 3.2**) (Appendix E provides a description of each lynx's within burn locations).

Within the Whiteface Burn study area, 48% of the locations were collected during the summer (May – October) and 52% were collected during the winter (November – April). In the Tripod Burn study area, 61% of the locations were collected during the summer and 39% were collected during the winter.

In the Loomis study area all but one lynx, whose home range was centered approximately 8 km from the closest edge of the Tripod Burn, spent time in the Tripod Burn. Six percent (1,578 points) of the lynx locations in the Loomis study area fell within the Tripod burn (**Figure 3.3**).

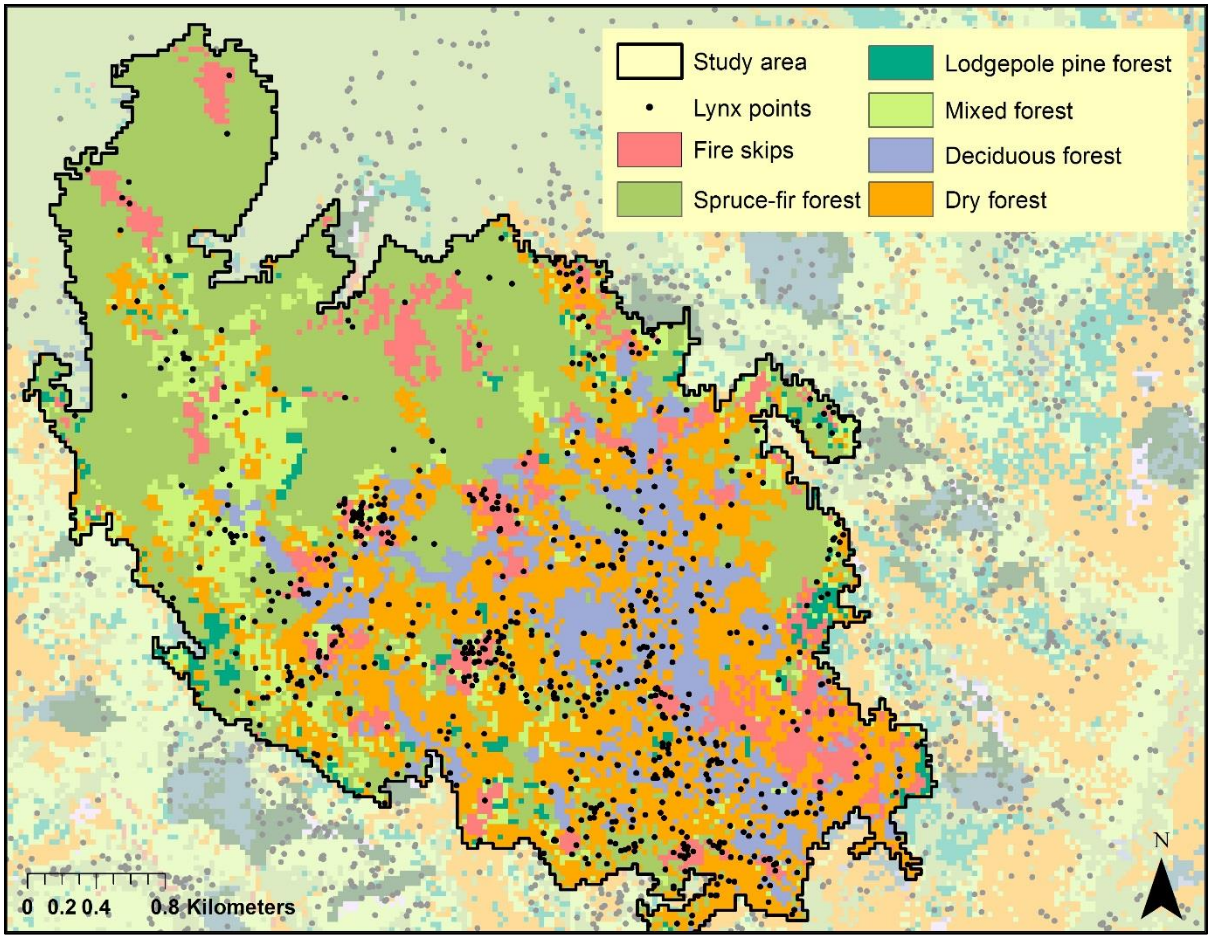


Figure 3.2. GPS lynx locations collected in the 1994, Whiteface Burn located on the eastern-slope of the North Cascade Mountains.

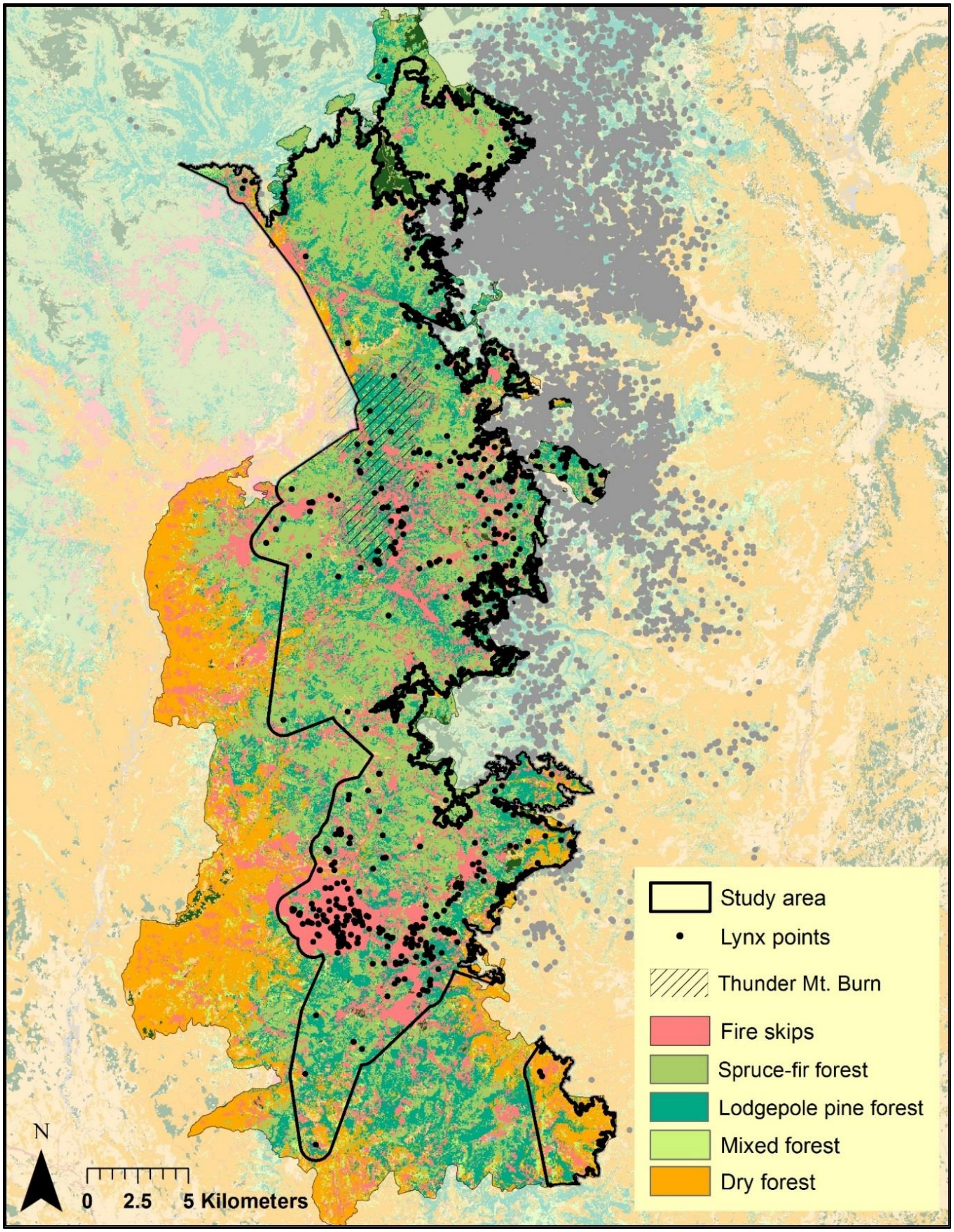

Study area
Lynx points
Thunder Mt. Burn
Fire skips
Spruce-fir forest
Lodgepole pine forest
Mixed forest
Dry forest
N
0 2.5 5 Kilometers

Figure 3.3. GPS lynx locations collected in the Tripod Burn located on the eastern-slope of the North Cascades Mountains. I truncated the western boundary of the Tripod study area to include only the area of the burn used by lynx, thus the western perimeter of the Tripod Burn extended further west than the study area.

3.4.1 Habitat Models

I tested distance to edge of the Whiteface Burn but because lynx used all areas of the burn, this variable did not help explain habitat use and so was not included in the model. For the Whiteface Burn Model, I excluded grass or shrub land cover types since field observations confirmed that such areas were not present in the burn. Consequently, I also did not include the variable depicting the distance to the edge of a grassy, shrubby, or rocky forest opening in the Whiteface Burn Model. No variables in the Whiteface Burn or Tripod Burn models were identified as collinear in the Spearman rank test, however the test for multivariate redundancy identified and removed growing season precipitation within a large- and small-scale area from the Whiteface Burn Model and growing season precipitation within a large-scale area from the Tripod Burn Model.

Both models performed well and model fit was high with error rates below 31%. Model validation revealed accuracy values above 70%. Both models were significant at $P < 0.05$ as compared to the null distribution created by randomizing the used and available points. Sensitivity and specificity values were high for the Tripod Burn Model and evenly distributed, indicating strong predictive power in both the use and available classes. The Kappa and AUC scores also indicate low cross-classification error, and AUC scores were similar to those of found by other models predicting coyote (*Canis latrans*) presence (McCue et al. 2013), and lynx presence (Simons-Legaard et al. 2013). Accuracy and AUC scores below 80% are expected from Random Forest models developed for highly mobile species and based on large radio telemetry datasets (Melanie Murphy, personal communication). For the Whiteface Burn Model, a higher sensitivity than specificity value indicated that the model predicted lynx points better than available points (**Table 3.2**).

Table 3.2. Model fit and validation statistics for the Tripod and Whiteface Burn Models. Accuracy (%) indicates the overall performance of the model when predicting the withheld, validation dataset. Sensitivity and specificity show the proportion of used locations correctly predicted and the proportion of available locations correctly predicted. Area under the curve of a Receiver Operator Characteristic (AUC) scores are a measure of how evenly the model predicts sensitivity and specificity. The Kappa (*k*) statistic is a measure of how much better the model predicted used and available points than expected by random chance. *P* values indicate significance of each model and out-of-bag error rates (%) show the mean misclassification rate of trees when predicting the out-of-bag data.

	Model Validation Statistics						Model Fit
Model	Accuracy (%)	Sensitivity	Specificity	*k*	AUC	*P* value	Out-of-bag error (%)
Tripod Burn	75.60	0.7457	0.7673	0.51	0.7560	$P < 0.001$	21.67
Whiteface Burn	70.92	0.7759	0.6684	0.42	0.7091	$P < 0.001$	30.96

3.4.2 General Model Results

The Tripod and Whiteface Burn Models were quite different in that top predictors of the Tripod Burn Model were nearly all variables describing burn severity or the distance from the edge of the burn. In contrast, retained habitat variables in the Whiteface Burn Model all described forest types and percent canopy cover, topography, and micro-climates and did not include any of the variables describing burn severity.

Lynx mostly selected variables at a large-scale although some small-scale depictions of a variable were included. Small-scale variables were always less important than their large-scale versions in the Tripod Burn Model. However, in the Whiteface Burn Model, heat load was more important at a small scale than at a large scale. Similarly, canopy cover within a small-scale area was important to lynx habitat selection within the Whiteface Burn while canopy cover at a large scale was not (**Figure 3.4**)

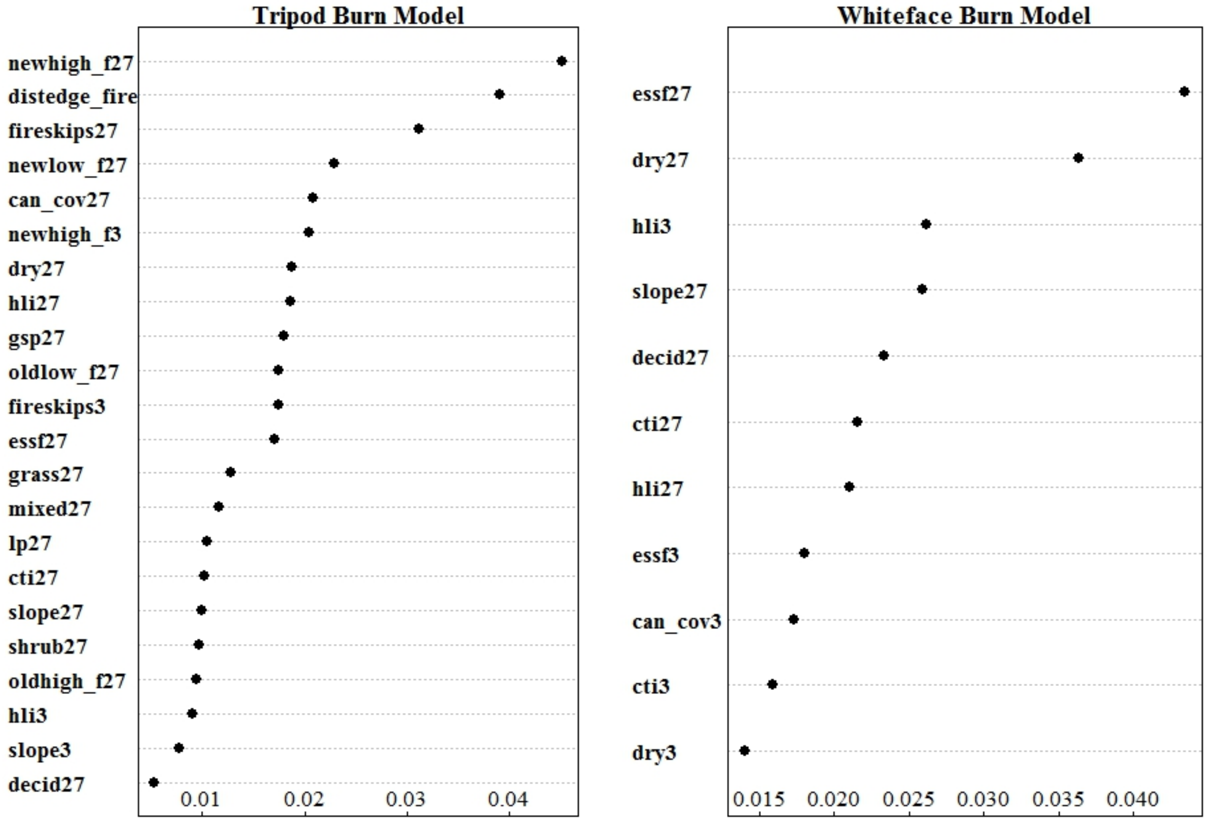


Figure 3.4. Importance plots for the Tripod and Whiteface Burn Models. Plots show the ranking of each habitat variable retained in the final Random Forest models. To determine the importance of each variable, the values of out-of-bag observations are randomly permuted, run down each tree, and predicted as used or available. The misclassification rate of the modified out-of-bag observations is subtracted from the misclassification rate of the unmodified out-of-bag observations and divided by the standard error. Numbers after the variable name identify it as being portrayed at a large scale (27x27 pixel area) or small scale (3x3 pixel area). Variables are explained in Table 3.1. Note different x-axes.

3.4.3 The Tripod Burn Model

Within the Tripod Burn perimeter, lynx selected areas near to residuals trees and fire skips. In addition, 79% of the lynx locations within the Tripod Burn were less than 1,000 m from the fire perimeter or in or near a fire skip. The most important variables in the model indicate that lynx avoided areas of new, high-severity burn at both large and small scales, and that lynx avoided venturing further than ~500 m from the burn perimeter. Lynx selected for large-scale areas with many fire skips. Within a small-scale area, lynx selected areas with 80% or more fire skip, indicating that lynx preferred to be very near or within a fire skip while using the Tripod Burn (**Figure 3.5**). Lynx also selected large-scale areas with low severity burn.

In congruence with lynx selection for fire skips and low severity burned areas, lynx selected for high canopy cover within a large-scale area when they were in the Tripod Burn (**Figure 3.6**).

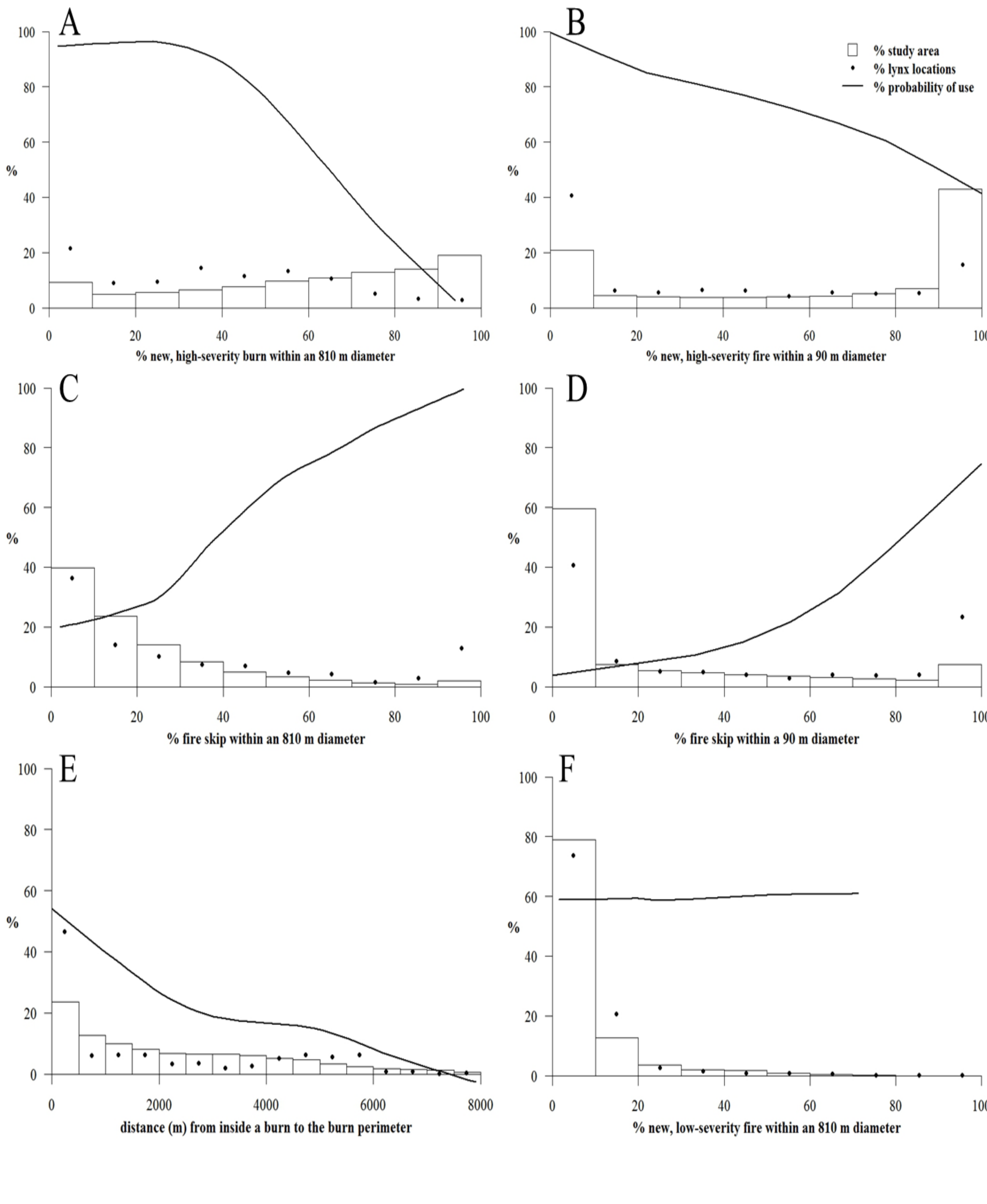

A
B
C
D
E
F
% study area
% lynx locations
% probability of use
%
% new, high-severity burn within an 810 m diameter
% new, high-severity fire within a 90 m diameter
% fire skip within an 810 m diameter
% fire skip within a 90 m diameter
distance (m) from inside a burn to the burn perimeter
% new, low-severity fire within an 810 m diameter

Figure 3.5. Lynx selection of burned areas in the Tripod Burn study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Histograms show the distribution of the focal habitat variable throughout the Tripod Burn study area. The dots represent the percentage of lynx points found within each histogram category of the focal habitat variable. Panels show lynx use of A) new, high-severity burn at a large scale; B) new, high-severity burn at a small scale; C) fire skips at a large scale; D) fires skips at a small scale; E) distance to the edge of the burn; and F) new, low-severity fire at a large scale.

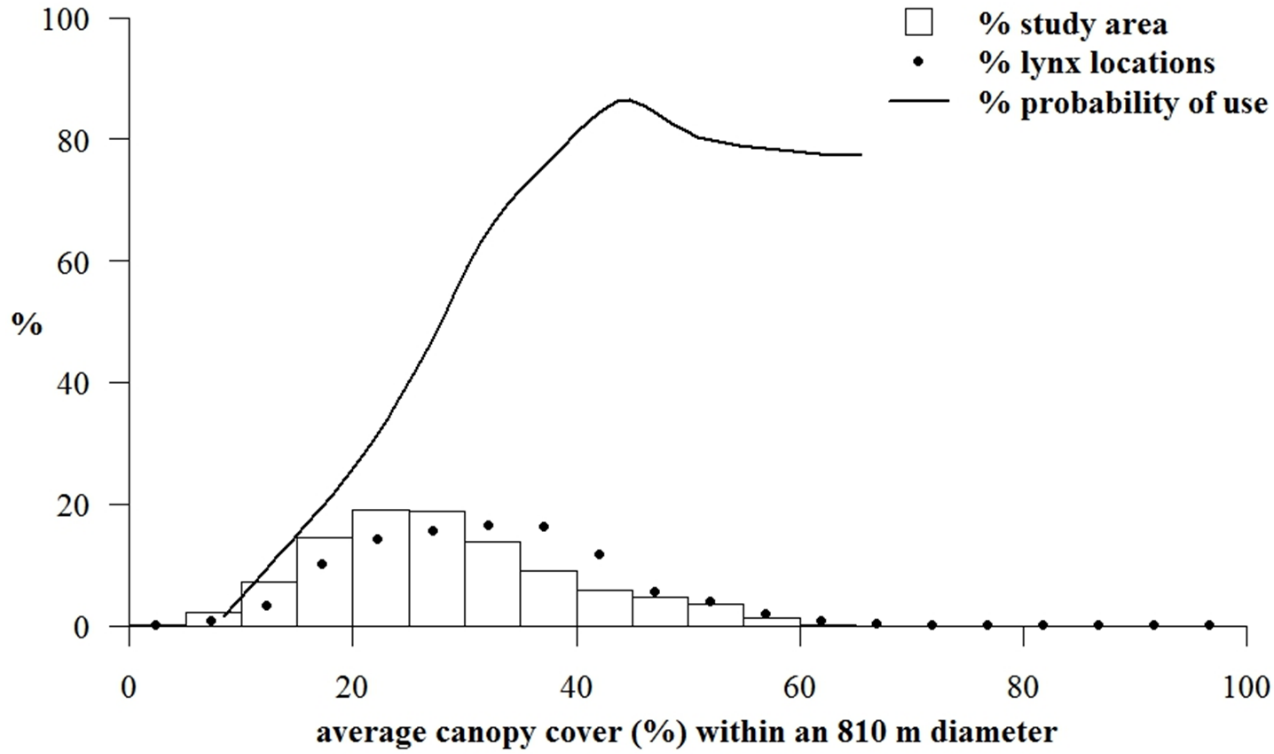


Figure 3.6. Lynx selection of canopy cover at a large scale in the Tripod Burn study area. Probability of use represents the effect of canopy cover on lynx habitat selection when the effect of all other habitat variables in the model are averaged.

Only one lynx used the 1994 Thunder Mountain Burn located within the Tripod Burn perimeter. Because the Thunder Burn was so seldom used, the Tripod Burn model predicted that lynx avoid old, burns, both high and low severity (**Figure 3.7**).

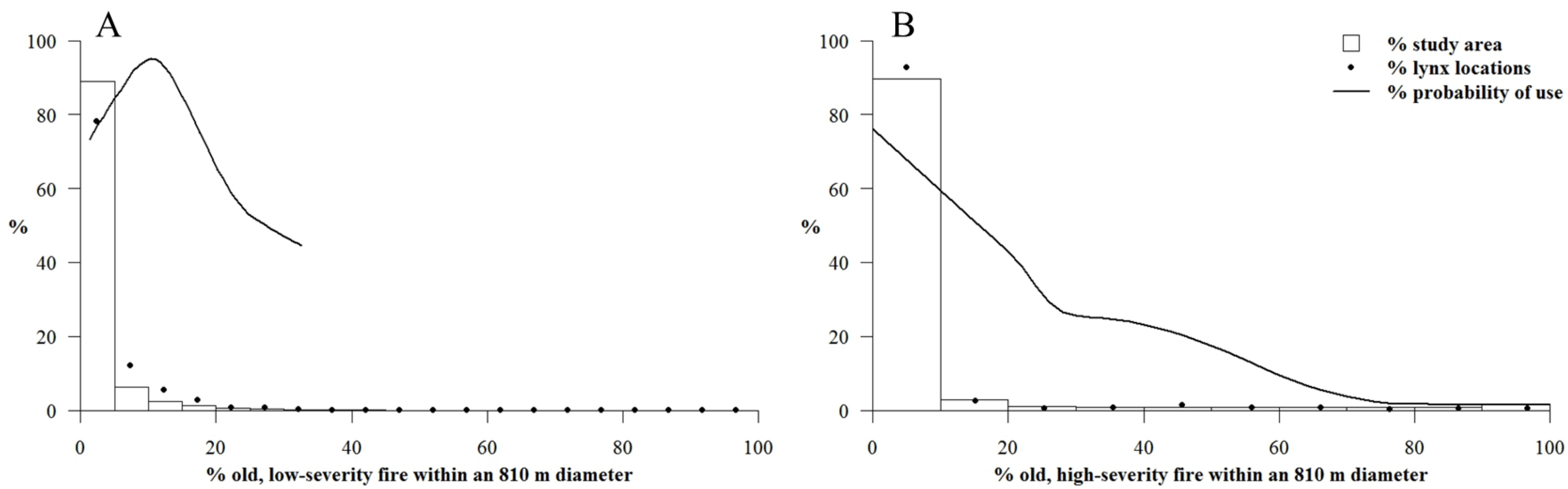


Figure 3.7. Lynx selection of old burned areas in the Tripod Burn study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) old, low-severity burn at a large scale; and B) old, high-severity burn at a large-scale.

Climate, topography, and forest type selection patterns were of less importance than selection explained by burn variables. Lynx selected for large- and small-scale areas with low to moderate slopes (**Figure 3.8**).

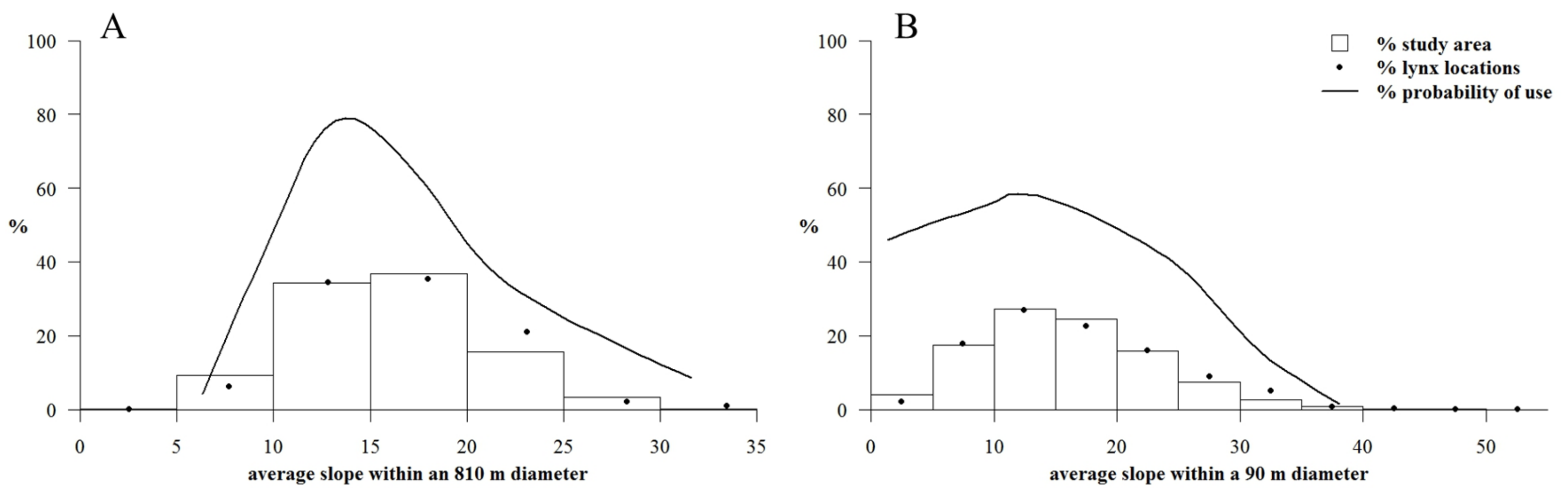


Figure 3.8. Lynx selection of slope in the Tripod Burn study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) slope at a large scale; and B) slope at a small scale.

Lynx selected for large- and small-scale areas with low heat loads, which are generally found on northeast-facing slopes. Lynx also selected for areas with average growing season precipitation above ~300 mm, but avoided areas receiving the greatest amounts of precipitation. The Cumulative Topographic Index also indicated that lynx avoided both the driest and wettest areas within a large-scale, and instead selected areas with moderate moisture accumulations (**Figure 3.9**).

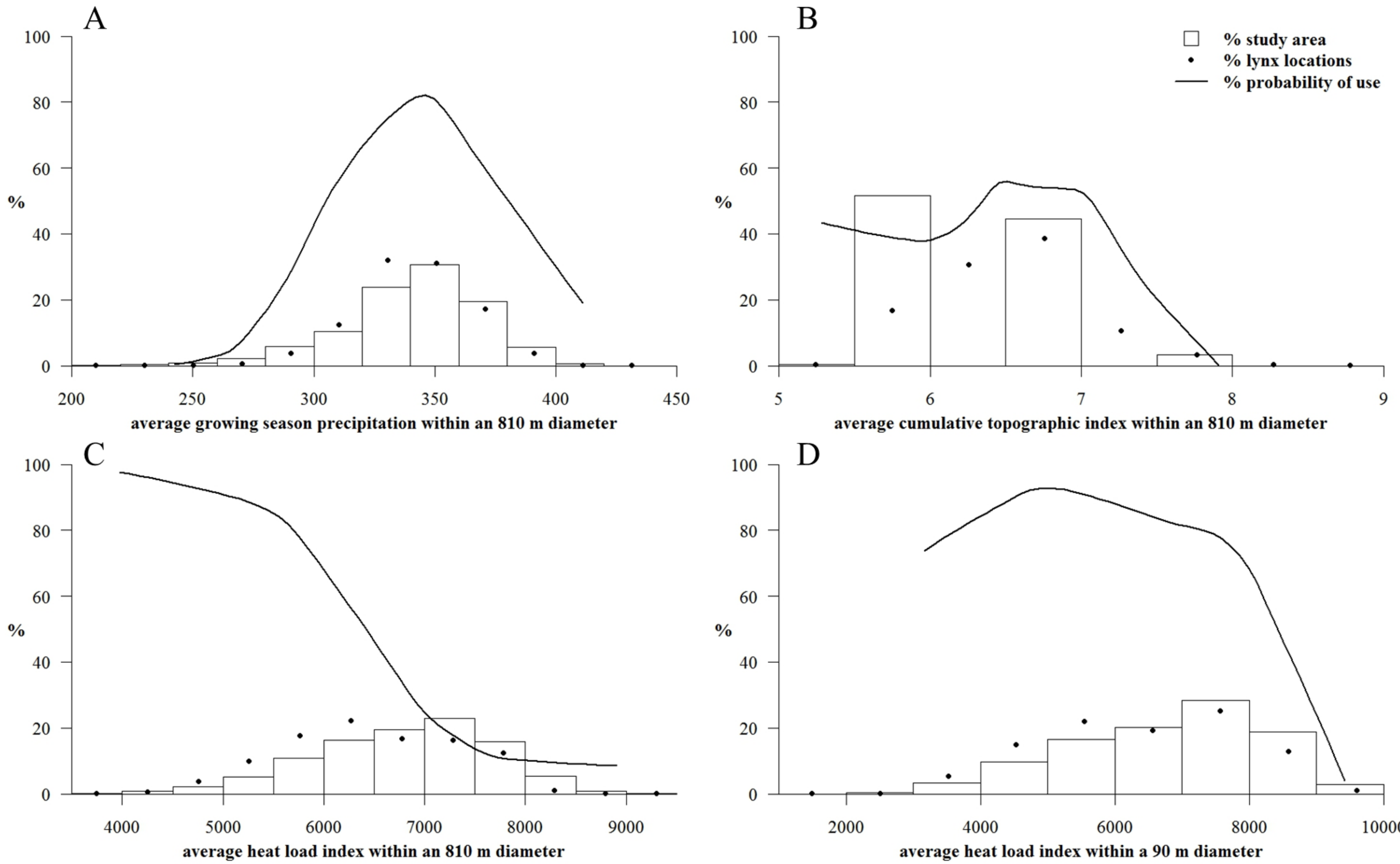
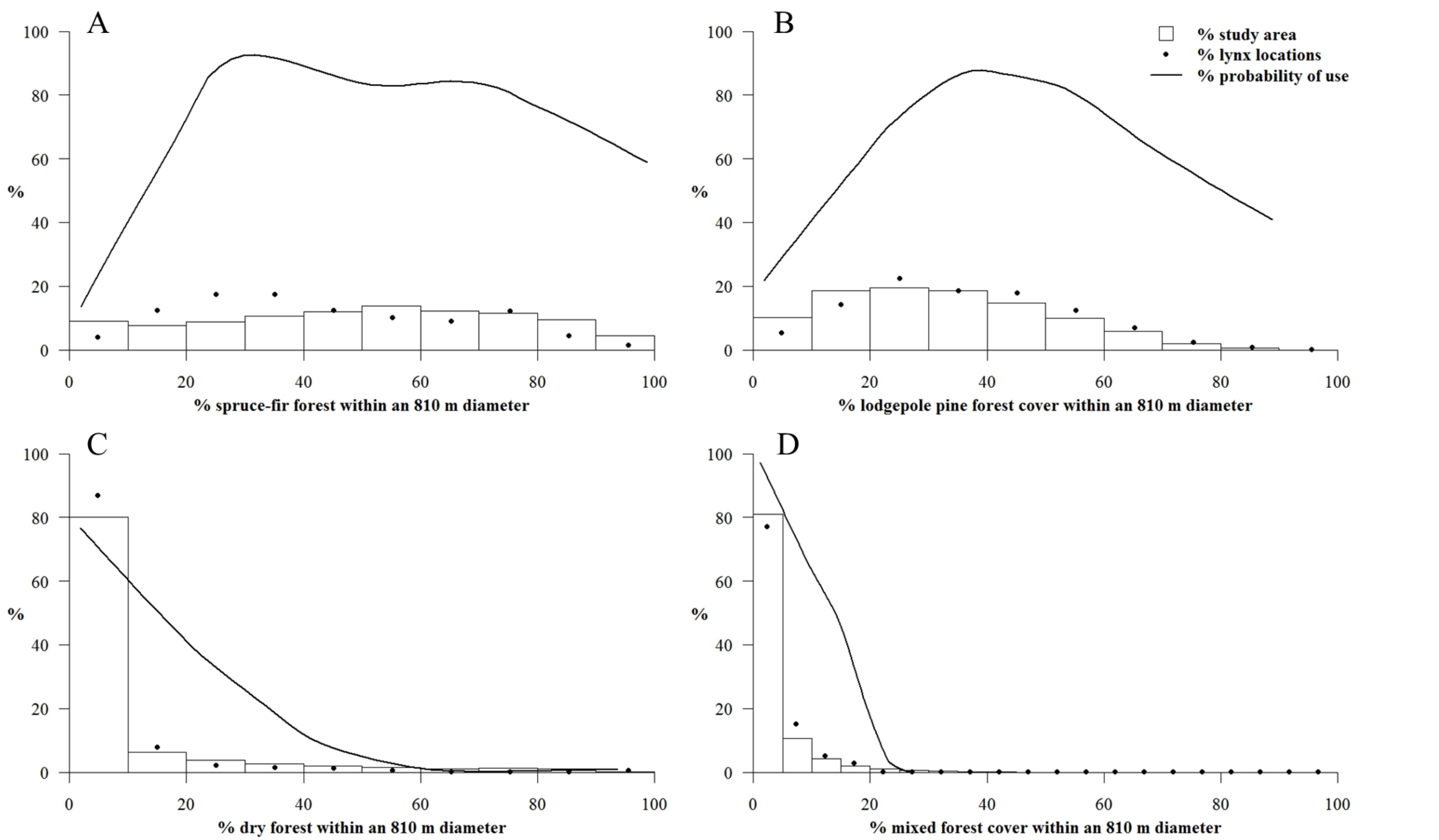

A
B
C
D
% study area
% lynx locations
% probability of use
%
average growing season precipitation within an 810 m diameter
average cumulative topographic index within an 810 m diameter
average heat load index within an 810 m diameter
average heat load index within a 90 m diameter

Figure 3.9. Lynx selection of climate in the Tripod Burn study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) average growing season precipitation at a large scale; B) average cumulative topographic index at a large scale; C) average heat load index at a large scale; and D) average heat load index at a small scale.

Within a large-scale area, lynx selected for spruce-fir and lodgepole pine forest, and avoided dry forests and increasing amounts of mixed forest. Although the results from the spruce-fir and lodgepole pine partial plots indicate a decrease in selection at the highest amounts of these forest covers, spruce-fir and lodgepole pine cover above 90% within a large-scale area is rare in the Tripod Burn, thus predictions at this level of cover are based on very little data (**Figure 3.10**).

Deciduous cover was the least important variable included in the model and explained only a very small portion of the data. The model indicates that lynx select against the very small amount of deciduous cover found in the Tripod Burn, although this result is based on little data.

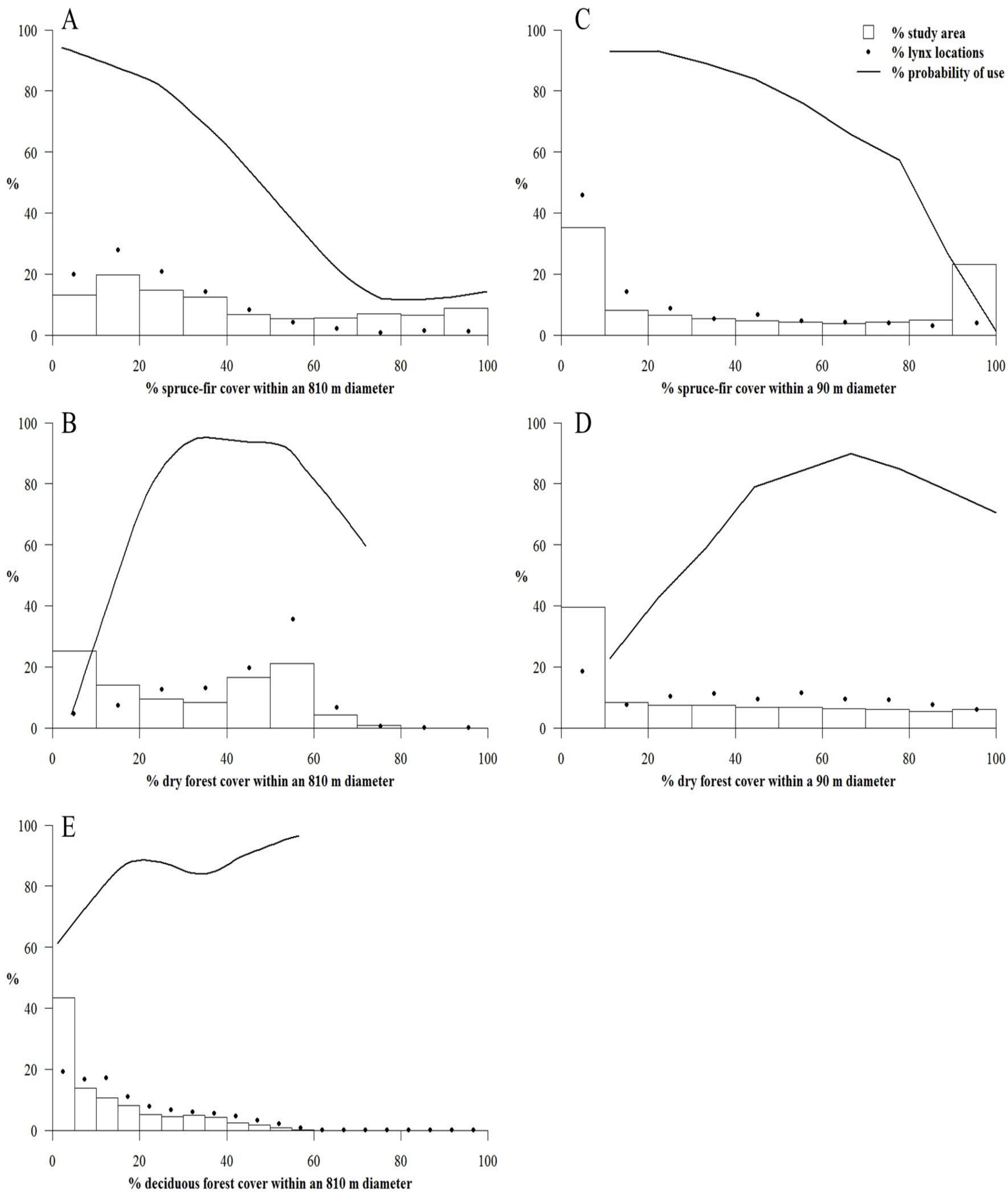


A
B
C
D
% study area
% lynx locations
% probability of use
%
% spruce-fir forest within an 810 m diameter
% lodgepole pine forest cover within an 810 m diameter
% dry forest within an 810 m diameter
% mixed forest cover within an 810 m diameter

Figure 3.10. Lynx selection of forest type in the Tripod Burn study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) spruce-fir forest at a large scale; B) lodgepole pine forest at a large scale; C) dry forest at a large scale; and D) mixed forest at a large scale.

3.4.4 The Whiteface Burn Model

Spruce-fir and dry forest cover within a large-scale area were the most important predictor variables in the Whiteface Burn Model. Lynx avoided increasing amounts of spruce-fir cover while selecting for increasing amounts of dry forest cover. Dry forest cover within a small-scale area was also selected by lynx, though its importance was less than that of dry forest at a large scale. Similarly, spruce-fir forest was also avoided within a small-scale area but was of less importance than at a large-scale. Finally, lynx selected for deciduous forests within a large-scale area (**Figure 3.11**).



A
B
C
D
E
% study area
% lynx locations
% probability of use
%
% spruce-fir cover within an 810 m diameter
% spruce-fir cover within a 90 m diameter
% dry forest cover within an 810 m diameter
% dry forest cover within a 90 m diameter
% deciduous forest cover within an 810 m diameter

Figure 3.11. Lynx selection of forest type in the Whiteface Burn study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) spruce-fir forest at a large scale; B) spruce-fir forest at a small scale; C) dry forest at a large scale; D) dry forest at a small scale; and E) deciduous forest at a large scale.

Lynx in the Whiteface Burn selected for low heat loads found on shallow, northeast-facing slopes. Lynx also selected for large- and small-scale areas with high moisture accumulations as depicted by the Compound Topographic Index, indicating lynx preference for moist draws (**Figure 3.12**).

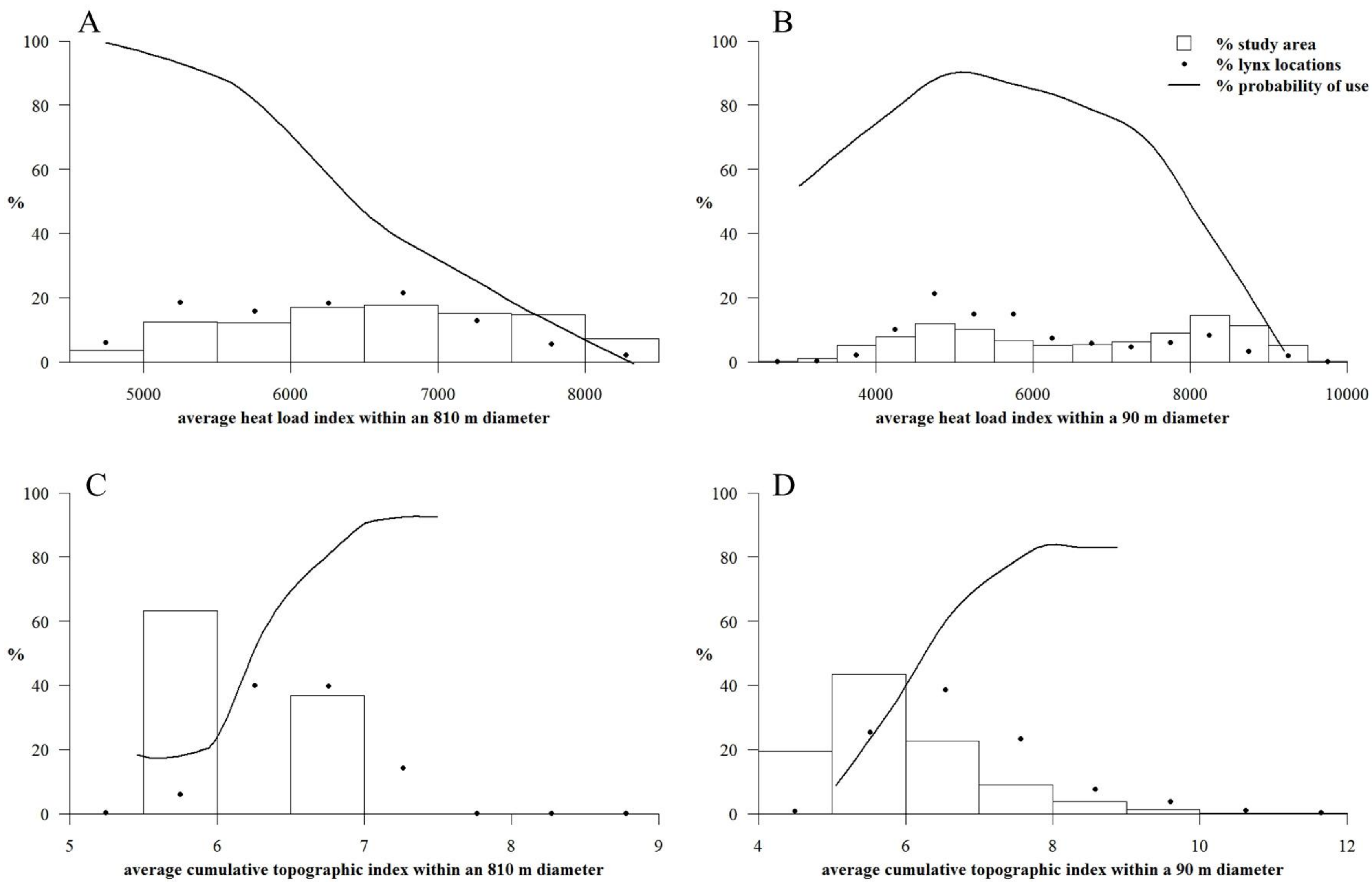

A
B
C
D
% study area
% lynx locations
% probability of use
%
average heat load index within an 810 m diameter
average heat load index within a 90 m diameter
average cumulative topographic index within an 810 m diameter
average cumulative topographic index within a 90 m diameter

Figure 3.12. Lynx selection of climate in the Whiteface Burn study area. Probability of use represents the effect of a focal habitat variable on lynx habitat selection when the effect of all other habitat variables in the model are averaged. Panels show lynx selection for A) average heat load at a large scale; B) average heat load at a small scale; C) average cumulative topographic index at a large scale; and D) average cumulative topographic index at a small scale.

Lynx selection for regenerating forest in the Whiteface Burn did not exclude their use of fire skips and residual trees within the burn. Lynx selected for higher amounts of canopy cover within a small-scale area, indicating that lynx selected areas within or very near residual trees found in fire skips or low-severity burned areas (**Figure 3.13**). Finally, slope within a large-scale area was also important to lynx habitat selection within the Whiteface Burn; lynx prefer shallow slopes (**Figure 3.14**).

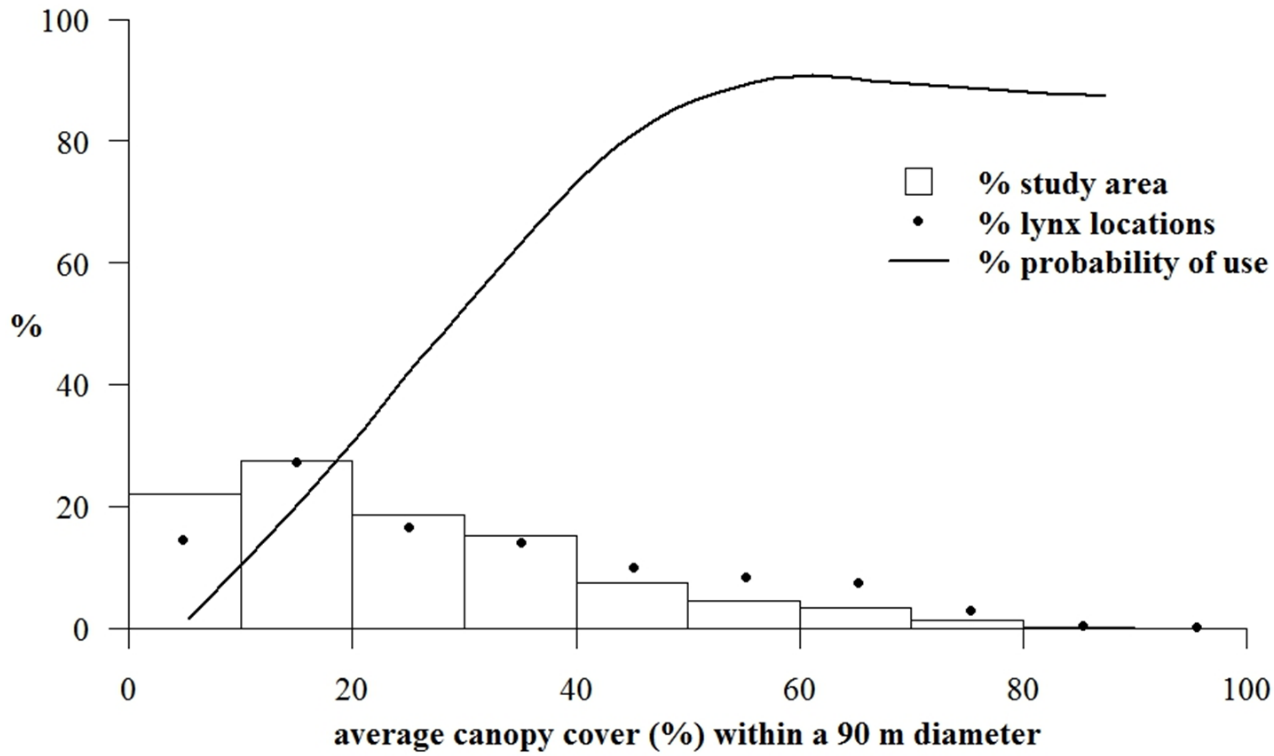


Figure 3.13. Lynx selection of canopy cover at a small scale in the Whiteface Burn study area. Probability of use represents the effect of canopy cover on lynx habitat selection when the effect of all other habitat variables in the model are averaged.

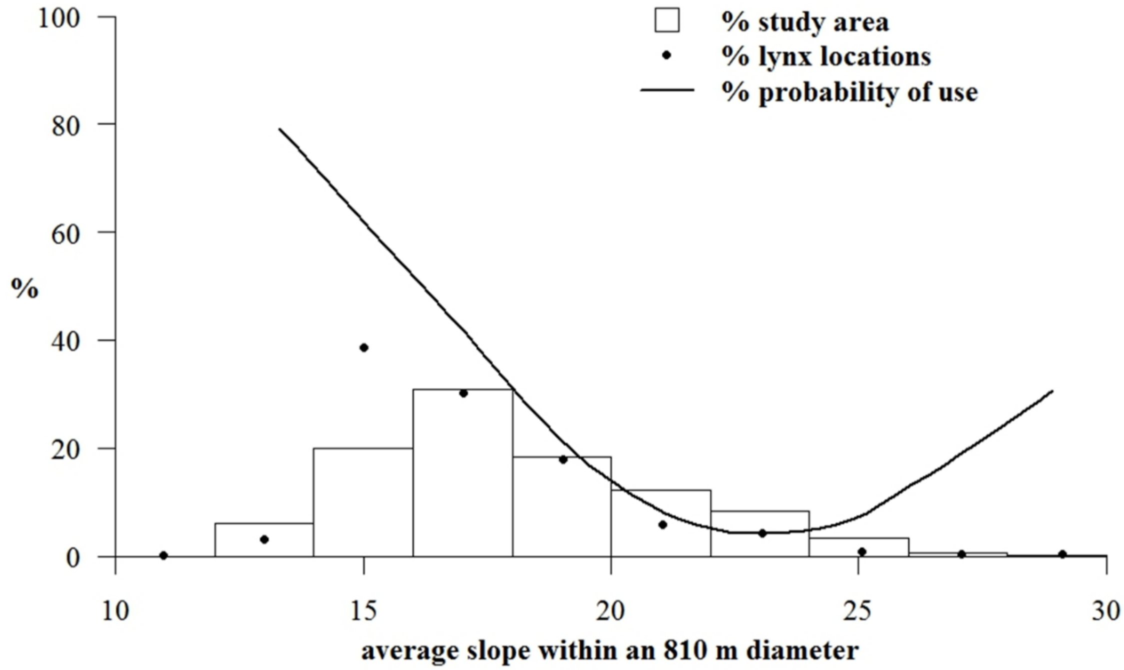


Figure 3.14. Lynx selection of slope at a small scale in the Whiteface Burn study area. Probability of use represents the effect of canopy cover on lynx habitat selection when the effect of all other habitat variables in the model are averaged.

3.5 DISCUSSION

Previous studies provide a generalized model describing lynx response to fire suggesting that lynx avoid new burns in the open, stand initiation stage and select older burns when a dense understory provides cover for snowshoe hares and lynx (Fox 1978, Paragi et al. 1997, Mowat and Slough 2003). My work expands upon this basic framework, as I used GPS collar data to examine at a fine scale how lynx use within-burn habitat heterogeneity. Most importantly, I found that residual cover left by low-severity burns and fire skips supported lynx use in new burns. In older burns, habitat quality varied according to micro-climate since cool, moister areas supported dense regeneration that provided habitats lynx selected regardless of forest type.

3.5.1 The Tripod Burn

My results support what other researchers have reported: the probability of lynx use is low in areas recently burned at a high severity (Paragi et al. 1997, Mowat and Slough 2003, Koehler 2008); (**Figure 3.15**). However, lynx were in fact able to use parts of the Tripod Burn immediately post-fire, making use of areas near to the burn perimeter and residual forest structure left by low-severity burns and fire skips. Specifically, within the Tripod Burn, lynx avoided open, severely burned areas, and selected for areas with residual live-tree cover. This finding corroborates an observation by Lewis et al. (2011) of lynx using fire skips in the Whiteface Burn a decade post-burn. The habitat functions provided by these fire skips varied as some fire skips I identified as travel habitat, while others, such as the 1,850 ha Forks fire skip, I identified as core habitat for lynx (Chapter 2). The spatial configuration of the burn also played into habitat selection, with lynx preferring to use areas near to the burn perimeter, which allowed them closer proximity to unburned forests and required less time crossing open, severely burned areas. However, the one lynx that regularly used the Forks fire skip demonstrated that if a fire skip provided a large patch of quality core habitat, venturing over 5 km from the perimeter was tolerable.

Figure 3.15. Open stand development in the 2006 Tripod Burn does not provide cover for core lynx habitat. The small sapling in the center of the photo is ~ 0.5 m tall. Photo taken by Bruce Akker in 2014.

The Tripod Burn Model indicated that lynx avoided the 1994 Thunder Mountain Burn located over 1 km within, but not re-burned by, the Tripod Burn. Given that regenerating burns such as the Whiteface Burn can provide high-quality core lynx habitat (Chapter 2, Paragi et al. 1997, Mowat and Slough 2003, Koehler 2008), this avoidance might seem confusing. However, several scenarios could explain this result:

1. Many lynx may not have known that regenerating habitat was available in the Thunder Mountain Burn, since most lynx did not venture further than 1 km into the Tripod Burn.

2. Lynx may have known that the Thunder Mountain Burn existed but were not willing to cross through the Tripod Burn to access it. However, one lynx living along the southern end of the Tripod Burn regularly crossed 5 km of the Tripod Burn to reach the large Forks fire skip.

3. Finally, perhaps regeneration of the Thunder Mountain Burn had not progressed enough at the time of data collection to entice lynx across the Tripod Burn (data were collected from 2007 – 2012, but only two lynx provided data in 2012).

Regardless of the reasons lynx avoided the Thunder Mountain Burn, my personal observations of this burn in 2014 (20 years post-burn), lead me to believe that much of the regenerating forest within the burn is composed primarily of thick lodgepole pine that has reached the early stand development stage that snowshoe hares and lynx select (**Figure 3.16**). Indeed, Koehler (1990) found that lynx in the Loomis area selected for 20-year-old lodgepole pine stands. Whether lynx currently cross the Tripod Burn to reach the Thunder Mountain Burn is unknown.

Figure 3.16. Regenerating lodgepole pine in the 1994 Thunder Mountain Burn is dense and tall (2 m reference pole). Photo taken by C. Vanbianchi in 2014.

Climate variables, topography, and forest type were less important than burn variables for lynx selection in the Tripod Burn, but were included in the model and, perhaps, explained lynx selection within fire skips, low severity burn areas, and areas near to the edge. As when selecting for core habitats, lynx in the Tripod Burn avoided dry forests and selected sub-boreal forest (Chapter 2, Koehler et al. 2008, Maletzke et al. 2008). Growing season precipitation roughly determines the forest type of an area, and the range of precipitation lynx selected also indicated that lynx avoided dry forests, selected wetter sub-boreal forests, and avoided the highest mountain tops where growing season precipitation is high but trees are sparse and slopes are steep (Franklin and Dyrness 1973). Furthermore, lynx selected for low heat loads, which, along with growing season precipitation, influence forest structure. Cool, moist areas may support the thick understory cover that snowshoe hares and lynx select (Aubry et al. 2000, Hodges 2000b). Cool, moist areas also assist in forest regeneration and may support understory growth in low-severity burns and regeneration in high-severity burns (Franklin and Dyrness 1973, Lillybridge et al. 1995, Casady et al. 2010, Crotteau 2013) that, although not tall and thick enough to create desirable lynx habitat in the Tripod Burn, may create habitat that is more tolerable to travel through.

Lynx in the Tripod Burn selected for low slopes. The Tripod Burn Model partial plot for average slope within a large-scale area indicates that lynx avoided areas with the lowest slopes, which were primarily found in an area further than 1,000 m inside the burn perimeter and there were no large fire skips to lure lynx across this swath of burn.

3.5.2 The Whiteface Burn

Older burns, such as the 1994 Whiteface Burn, often have regenerated enough within a decade or two to provide habitat for snowshoe hares and lynx (Fox 1978, Paragi et al. 1997, Mowat and Slough 2003). Indeed, results from the Black Pine Basin Core Habitat model revealed that much of the Whiteface Burn provided high quality core lynx habitat (Chapter 2). However, within the Whiteface Burn habitat quality varied and not all areas supported core lynx habitat. In contrast to the Tripod Burn Model, the Whiteface Burn Model indicated that habitat selection in the Whiteface Burn was not centered on selecting areas where low-severity burn or fire skips retained forest structure. The nearly 20-year-old 1994 Whiteface Burn was old enough that even areas burned at a high severity had regenerated into core lynx habitat so that selection centered on climate and forest regeneration conditions that promoted thicker cover.

Lynx in the Whiteface Burn favored areas where cool and moist growing conditions supported thick understory cover. Interestingly, selection for thick understory resulted in selection of forest types opposite to those selected in my Core Habitat Models (Chapter 2); lynx selected for dry forests and against spruce-fir forests. A field examination of the Whiteface Burn explained this interesting switch in lynx-selected forest type. At the northern end of the Whiteface Burn, sub-boreal climate conditions support the regeneration of spruce-fir forests while at the southern, lower-elevation end of the Whiteface Burn, dry forest regeneration is common. Spruce-fir regeneration at the northern end of the burn is short and sparse, perhaps due to a cooler, shorter growing season. Coupled with an apparently limited lodgepole pine seed source to initiate stands of characteristically dense lodgepole pine regeneration, sub-boreal forest regeneration in the Whiteface Burn provides little cover for snowshoe hares and lynx, thus explaining lynx avoidance of this forest type (**Figure 3.17**).

At the southern end of the burn and especially in draws, large amounts of willow and alder are mixed with Douglas fir and ponderosa pine trees in the regenerating dry forests. The densely growing deciduous species provide thick understory cover for snowshoe hare and lynx, which matches findings by Mowat and Slough (2003) that lynx and snowshoe hares in the Yukon selected dense willow patches. Although the partial plot depicting lynx use of dry forest indicates that lynx use declines at the highest amounts of cover, this decline in use applied only in a small portion of the burn where dry forest cover exceeded > 60%. Here, a fire skip and low-severity burns left a stand of mature dry forest with an open understory (**Figure 3.18**).

By selecting the dry forests lynx usually avoid (Chapter 2, Maletzke et al. 2008), lynx in the Whiteface Burn demonstrated an ability to adjust their behavior to take advantage of favorable understory conditions. Selection for regenerating dry forests also demonstrates the importance of thick understory structure over forest type for lynx habitat, confirming prior research (Mowat and Slough 2003).

Figure 3.17. Typical spruce-fir regeneration in the 1994 Whiteface Burn. Poor growing conditions support only sparse forest regeneration that is not yet suitable core lynx habitat. The white pole is 2 m tall. Photo taken by C. Vanbianchi in 2014.

Figure 3.18. Typical stand of dense regenerating dry forest intermixed with willow and alder trees in the 1994 Whiteface Burn. Favorable growing conditions support dense understory growth providing core lynx habitat. The white pole is 2 m tall. Photo taken by C. Vanbianchi in 2014.

3.5.3 Wildfires Versus Timber Harvest as Disturbance Regimes Affecting Lynx

Areas disturbed by wildfires are not uniform. Instead, wildfires create a diversity of habitat conditions that depend upon burn severity and micro-climates that influence forest regeneration rates and patterns. In turn, lynx respond to burned areas with habitat selection patterns that are more nuanced than previously described patterns for lynx in harvested areas (Simons-Legaard et al. 2013). Lynx in my study responded to spatial patterns and residual forest structure left by low-severity burns and fire skips in new burns. In old burns, lynx responded positively to areas where micro-climates encourage dense understory cover, regardless of forest type. The heterogeneous habitats created by wildfires are in contrast to disturbed habitats created by timber harvest which, even when designed to emulate a fire disturbance, create more uniform patterns of disturbance with less edge area and fewer standing live trees left after harvest (McRae et al. 2001). Regeneration patterns between burned areas and harvested areas also differ since residual trees and coarse woody debris left post-fire can seed and protect young seedlings (Brassard and Chen 2006). Furthermore, cycles of harvest are often shorter than burn cycles and occur over smaller areas (McRae et al. 2001). Lynx and snowshoe hares avoid harvest conditions that eliminate understory cover, such as thins and new clearcuts, but are benefitted by old clearcuts that promote thick forest regeneration (Squires et al. 2010, Simons-Legaard et al. 2013). In contrast to this relatively simple and more predictable response, the heterogeneous habitat created by burns provide lynx with more varied habitats to suit their survival needs than areas disturbed by timber harvest, especially in new burns where fire skips and low-severity burns create cover for lynx.

3.5.4 Climate Change

Within-burn heterogeneity allows lynx to make the most of recently-burned areas, perhaps making fire a more beneficial disturbance regime than traditional timber harvest. However, as climate change progresses and summers in the boreal region become dryer and warmer, the wildfire season is predicted to become longer and more severe (Westerling et al. 2006, Soja et al. 2007, Fauria and Johnson 2007, Balshi 2009, Littell et al. 2010), with more frequent fires burning larger areas at higher severity. Not only will this regime shift cause more lynx habitat to revert to the open, stand-initiation stage snowshoe hares and lynx avoid, higher severity burns will homogenize the area within a burn perimeter so that the residual trees and fire skips lynx select are less abundant (Cansler and McKenzie 2014). In addition to reducing the residual cover found within a new burn, climate change could also degrade regenerating lynx habitat in old burns since warmer and drier summers would hinder the regeneration of dense forest stands (Littell et al. 2010).

Landscapes in lynx range will continue to be fragmented and homogenized by timber harvest and by more frequent and severe fires under climate change. To help mitigate for timber harvest and increased burning, managing forest disturbances to maximize residual cover could help to both facilitate lynx use in new disturbances and improve growing conditions in regenerating forests, thus providing cover for snowshoe hares and lynx. For example, designing timber harvest units with high edge-to-area ratios, standing live trees, and islands of un-cut trees would better emulate the features of wildfires that support lynx use, retaining some cover for lynx in new clearcuts. Managers could also prescribe burns and craft timber harvest units that would act as fire breaks to decrease the spread and intensity of increasingly catastrophic fires under climate change, thus preserving the historical, heterogeneous burn patterns that provide cover for lynx.

Wildfires in the boreal and sub-boreal forests are natural and important disturbances central to their ecology. My results provide some of the first detailed information describing lynx-fire ecology and clearly demonstrate the importance of within-burn heterogeneity to lynx habitat. Understanding the features of burned areas that support both lynx use in new burns and regeneration of understory cover in old burns will help managers predict how lynx will respond to climate change and to prepare and mitigate for its effects on lynx habitat.

CHAPTER 4
LYNX HABITAT CONNECTIVITY IN THE NORTH CASCADE MOUNTAINS, WASHINGTON

4.1 LITERATURE REVIEW AND OBJECTIVES

Healthy ecosystem function relies in large part on movement: rivers flow to seas, fires spread through forests, mammals travel to find food, fish migrate from oceans to streams to spawn, and seeds disperse across the landscape. These movements in nature occur at different spatial and temporal scales (Crooks and Sanjayan 2006). For example, a bird may move daily across a home range to reach food sources, while a mammal may migrate yearly across a landscape to reach its breeding grounds. Importantly, as humans increasingly alter the planet, the movements of wildlife and other ecosystem processes are inhibited by dams, development, deforestation, roads, and a variety of other human-induced barriers. Habitat loss and fragmentation have become top factors in species declines around the world (Wilcove et al. 1998, Brooks et al. 2002, Ewers and Didham 2006). Connectivity conservation has emerged as a popular strategy for mitigating the effects of fragmentation so that movements in nature may persist (Crooks and Sanjayan 2006, Ewers and Didham 2006).

4.1.1 Connectivity Conservation

Habitat fragmentation and the associated loss of connectivity can have many negative consequences for individual animals and for populations of animals. Habitat fragmentation can impede animals dispersing to a new home range and obstruct the movement of individuals seeking mates or resources such as food and water (Wilcox and Murphy 1985, Fischer and Lindenmayer 2007). Fragmentation can also separate populations so that they become genetically isolated and in danger of inbreeding depression (Frankham 2006). The persistence of metapopulations, which are made up of several small, separate groups, relies on the dispersal of individuals between occupied habitat patches. Increased fragmentation within a metapopulation can prevent the recolonization of isolated habitat patches (Hanski 1998). Similarly, some populations operate in a source-sink dynamic where areas of low habitat quality result in population “sinks” where a birth rate is lower than the death rate, while in the source areas, high quality habitat results in birth rates higher than the death rate. Surplus individuals from the source population disperse into the less-populated sink areas, thus rescuing sink populations from decline and extinction (Pulliam 1988). In these cases, habitat fragmentation can impede movements between source and sink populations so that sink populations no longer receive the number of immigrants necessary to sustain their populations. Finally, as climate change and other human impacts cause habitat degradation and loss, populations may need to shift their ranges to escape poor habitat, relying on connected landscapes to facilitate these movements (Parmesan 2006, Chen et al. 2011, Lenoir and Svenning 2015).

How well habitats within landscapes facilitate wildlife movements varies by species (Crooks and Sanjayan 2006). For example, a river may disconnect habitat patches for a hare but pose no barrier to a bird. Scale can also affect whether a landscape is connected or not, since different types of movement occur over different scales (Ims 1995, Taylor et al. 2006). For example, a population occupying discrete habitat patches within a mountain range may be interconnected, yet at a broader scale may be disconnected from populations in neighboring mountain ranges. Thus, conservationists should assess the connectivity of a landscape for individual species at scales relevant to the particular species of interest (Pither and Taylor 1998, Taylor et al. 2006).

Further, connectivity can be viewed from either a structural or functional perspective. Structural connectivity is based on a simple binary description of a fragmented landscape in which islands of habitat are surrounded by a uniformly inhospitable matrix (Wiens 2006). Islands of habitat that are connected by corridors of habitat acting as bridges across the matrix are considered structurally connected (Tischendorf and Fahrig 2000). However, this definition of connectivity fails to consider that, in most cases, the matrix is not an entirely hostile environment (Chetkiewicz et al. 2006, Prugh et al. 2008). Landscapes are complex and are best described functionally as continuous spectrums of habitat quality rather than as habitat and non-habitat (Chetkiewicz et al. 2006).

Functional connectivity takes into consideration an animal's behavioral response to the spectrum of habitat quality available, recognizing that presumed non-habitat may actually be used as travel habitat (Tischendorf and Fahrig 2000). Thus, a landscape that appears to be structurally unconnected may in fact be connected if linkages of matrix habitats suitable for traveling exist. Similarly, a landscape that appears to be structurally connected may be functionally unconnected if, for example, the corridor is too narrow to buffer an animal from surrounding inhospitable habitats, or if the corridor is longer than the animal's maximum dispersal distance (With 1997, Tischendorf and Fahrig 2000, Taylor et al. 2006, Beier et al. 2008). Functional connectivity's realistic incorporation of animal behavior and habitat use makes this definition of connectivity a more fruitful approach for conservation (Tischendorf and Fahrig 2000, Chetkiewicz et al. 2006).

4.1.2 Connectivity Modeling

Although modeling functional connectivity linkages may produce more accurate results than identifying structural connectivity corridors, identifying functional connectivity linkages involves considerable time and resources. In contrast to simply consulting

Geographic Information System (GIS) spatial data of land cover to identify structural connectivity corridors, identifying functional connectivity linkages requires researchers to have a deeper understanding of the focal species' behavioral response to landscape features. Modelers first select landscape features believed to influence the movements of the focal species such as forest structure, topography, land cover, or human disturbances (Beier et al. 2008). The selected landscape features are assigned numerical values reflecting their resistance to movement for the focal animal (Beier et al. 2008). High resistance values indicate that a landscape feature is either highly avoided, or results in a loss of fitness or a low survival rate for animals passing through the landscape feature (Zeller et al. 2012). Although using empirical methods is preferred, expert opinion and literature review are often used to assign resistance values simply because of our limited understanding of the movement ecology of many species (Chetkiewicz et al. 2006). Resource selection models, such as Resource Selection Functions or Random Forest models, offer researchers empirical methods of assigning resistance values to landscape features by comparing the habitat features at used animal locations to the habitat features at non-used or available locations (Chetkiewicz and Boyce 2009, Chapter 2).

Resource selection models are often based on locations collected from animals in their home range. These locations are then pooled across different activities such as hunting, resting, or traveling, so that the model reveals a generalized pattern of habitat selection for an animal in its home range. But because animals often select different habitats for different activities (Roever et al. 2014), summing habitat selection across these varying functions and habitats becomes problematic for connectivity modeling. Specifically, animals may use the best habitats for common daily activities such as foraging or resting ("core" habitat hereafter), but tolerate additional habitats for traveling (and especially dispersing) (Roever et al. 2014). Failing to recognize that an animal uses a wider range of habitats for traveling than for core habitats could result in underestimating connectivity. In addition, if different habitats are selected for daily activities and for traveling, generalized selection for habitat may be averaged so that strong selection for or against any one habitat is not detected (Roever et al. 2014). Or, if an animal rarely travels between patches of habitat used for common daily activities, selection of important but rarely-used travel habitats could go undetected (Roever et al. 2014). Finally, the shape and direction of the habitat selection curve may depend on the behavioral state of the animal (Roever et al. 2014). For these reasons, habitat models that differentiate between habitats used for common activities such as foraging or resting and those used for traveling may provide more accurate resistance values for modeling functional habitat linkages.

Once modelers assign resistance values to each landscape feature, a resistance surface is created by assigning each pixel in a Geographic Information System (GIS) a resistance value corresponding to the landscape features at each pixel's location (Chetkiewicz and Boyce 2009, McRae and Kavanagh 2011). Concentrations of high quality habitat (e. g., areas with low resistance to movement), often called "Habitat Concentration Areas" (HCA) (WWHCWG 2010), are identified on the resistance surface, which is then used to model connectivity and identify habitat linkages between Habitat Concentration Areas (Chetkiewicz and Boyce 2009). Least cost path analysis is most often used to model connectivity and identifies the pathway between two source patches with the smallest cumulative resistance (Beier et al. 2008).

Because least cost path analysis will always identify a least cost path, modelers must evaluate each identified path to gauge functional connectivity between source patches (Beier et al. 2008). One requirement for functional connectivity modeling is that a least cost path must not be longer than an animal's maximum dispersal distance. In addition, least cost pathways are only one pixel wide, and modelers must ensure that the pathway is embedded in enough suitable habitat to buffer a traveling animal from surrounding unsuitable matrix habitats (Beier et al. 2008).

By obtaining animal location data to model travel habitat selection, basing a resistance surface off the habitat model, and then selecting only high-quality least cost paths, functional connectivity linkages can be identified. Once such potential linkages are identified, they can be prioritized for connectivity conservation.

4.1.3 Lynx in a Fragmented Landscape

Canada lynx (*Lynx canadensis*) in the contiguous US are in the southern edge of lynx range. Lynx were federally listed as Threatened in 2000 (US Fish and Wildlife Service 2000). Typical of a population living in its range periphery, lynx in the contiguous US survive in lower-quality, fragmented habitats (Brown et al. 1996, Buskirk et al. 2000b, McKelvey et al. 2000b). The relatively continuous tracts of boreal forest that lynx select in the core of their range in Canada and Alaska become fragmented as they transition into southern forest types (Agee 2000). In the western US, the sub-boreal forests lynx select are limited to high elevations, such that topography further fragments lynx habitat (Agee 2000). In addition, human disturbances such as roads, development, and timber harvest fragment lynx habitat in the US (Buskirk et al. 2000b, Koehler et al. 2008). Climate change is already shrinking sub-boreal forest range northward and upward in elevation (Soja et al. 2007, Fisichelli et al. 2014), and may affect peripheral lynx populations sooner than those in a range core (Anderson et al. 2009). In addition, climate change is projected to increase the frequency, size, and intensity of wildfires, further fragmenting lynx habitat (Fauria and Johnson 2007, Soja et al. 2007, Balshi 2009, Littell et al. 2010).

Lynx in the contiguous US often must cross fragmented landscapes to reach suitable patches of core, hunting and resting habitat within their home ranges. Southern lynx also travel long distances across landscapes to find mates, to disperse into new territories, and to explore (Aubry et al. 2000, Squires and Laurion 2000, Squires and Oakleaf 2005). Furthermore, lynx populations in the US consist of fewer individuals than populations in the range core, and genetic diversity contributed by immigrating lynx from Canada may be important to reduce inbreeding in southern lynx populations (Schwartz et al. 2002). Immigrating lynx from Canada may also be important to sustaining southern lynx populations (McKelvey et al. 2000b, Murray et al. 2008).

4.1.4 Lynx Core Habitat and Travel Habitat

Lynx are specialized predators of the snowshoe hare (*Lepus americanus*), and lynx habitat selection has been closely tied to snowshoe hare abundance (Koehler 1990, Aubry et al. 2000, Murray et al. 2008). For core hunting, resting, and denning habitat, lynx in the US select sub-boreal forests with dense understory cover, which provides forage and cover for snowshoe hares. This forest structure is often found in either young regenerating forest stands or in old-growth forests where canopy gaps allow understory vegetation to grow and low-reaching branches provide additional horizontal structure (Aubry et al. 2000, Buskirk et al. 2000b, Hodges 2000b, Koehler et al. 2008, Maletzke et al. 2008, Squires et al. 2010). Lynx generally avoid forest openings such as meadows, shrubby areas, and recent disturbances that do not provide adequate cover for snowshoe hares (Koehler 1990, Koehler et al. 2008, Maletzke et al. 2008).

However, lynx in the contiguous US do travel through low-quality habitats, such as open mature forests and thinned forests (Koehler 1990), shrub-steppe (Squires and Laurion 2000), and dry forests or recently-burned areas (Walker 2005, Chapter 2). These observations suggest that lynx use a wider range of habitats for traveling than for core habitats. These observations also indicate that to model functional connectivity for lynx effectively, resistance values should be based on resource selection models that specifically examine habitat use of lynx during their travels.

4.1.5 Lynx in the North Cascades Mountains, Washington

Lynx in the North Cascades of Washington comprise the only breeding population of lynx in the state (Stinson 2001). Lynx habitat in Washington is naturally fragmented by topography and forest openings such as meadows, rocky or icy areas, and shrubby areas (Koehler et al. 2008). Human-caused disturbances such as timber harvest, agriculture, roads, and developments also fragment the landscape (Stinson 2001). In addition, wildfires frequently burn forests in the North Cascades. In 2006, the Tripod Fire burned most of what was considered the best lynx habitat in Washington (Agee 2000, Stinson 2001, Koehler et al. 2008). The combination of natural and human induced disturbances create a complex mosaic of habitat for lynx in the North Cascades.

Although four studies have examined lynx habitat connectivity in Washington, none modeled lynx habitat connectivity across the North Cascades at a meso-scale (**Table 4.1**)

Table 4.1. Existing habitat connectivity models for lynx in Washington. Singleton et al. (2002) modeled connectivity in the North Cascades before the 2006 Tripod Burn disturbed the landscape.

	Model Area	Resistance surface based on:	Scale of model
Singleton et al. (2002)	NW US and SW BC	Expert opinion and literature review	Regional connectivity. HCAs = 459 – 7,138 km^2 [a]
WWHCWG (2010)	NW US and SW BC	Expert opinion and literature review	Regional connectivity. HCAs = 596 – 5,916 km^2 [a]
Begley and Long (2009)	Stevens Pass area, North Cascades	Expert opinion and literature review	Local connectivity mapped by a resistance raster using 30 m^2 pixel size[b]
Gaines et al. (in press)	NE Washington	Expert opinion and literature review	Local connectivity mapped by a resistance raster using 30 m^2 pixel size[b]
This Chapter	Eastern slope of the North Cascades	GPS lynx location data	Landscape connectivity. HCAs = 10 – 1,272 km^2 [a]

[a] The range of Habitat Concentration Areas sizes used to model connectivity between.
[b] Connectivity was not mapped between Habitat Concentration Areas, a resistance surface was used for fine scale analysis of low and high resistance areas to compare management alternatives.

In this chapter, I develop a functional connectivity model for lynx in the North Cascades with the goal of highlighting both areas of current connectivity and areas where movement for lynx is restricted. My work is based on separate core and travel habitat models constructed using 20,564 GPS locations from 17 lynx.

4.2 STUDY AREA

I modeled lynx habitat connectivity throughout the North Cascade Mountains of northcentral Washington. My study area includes 20,260 km^2 from the British Columbia-Washington border southward to 10 km south of Highway 2, and from 25 km west of the Cascade crest to 15 km east of Highway 97 (**Figure 4.1**). The North Cascades study area includes all of the Okanogan Lynx Management Zones designated by the Washington

Department of Fish and Wildlife (Stinson 2001). Seventy-eight percent of the study area is public land with private property mostly concentrated in low elevation areas such as the Okanogan and Methow Valleys; developed private properties comprise 4% of the study area.

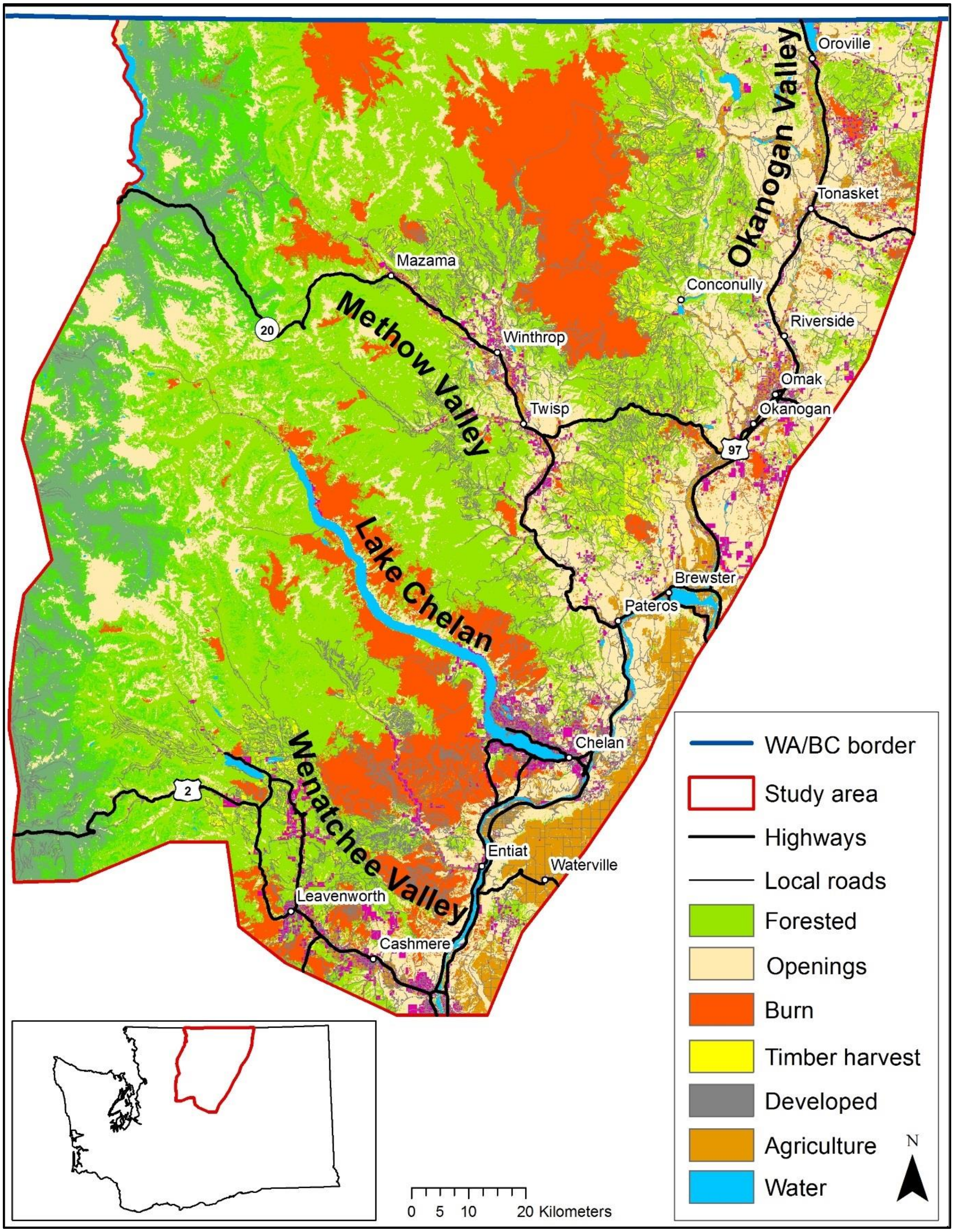


Figure 4.1. The North Cascades study area.

A majority of the study area is mountainous, with elevations ranging from 188 m to 3,214 m, and 60% of the area above 1,000 m. Climate varies with elevation throughout the study area. Average monthly temperatures in Mazama (elevation 664 m) range from -10°C to 23°C with an average annual snowfall of 305 cm. Further east, average monthly temperatures in Omak (elevation 257 m) range from -5.5°C to 32°C with an average annual snowfall of 37 cm (Western Regional Climate Center, http://www.wrcc.dri.edu/, accessed June 20, 2014).

The land cover also varies with elevation. Forests grow at higher elevations and on north-facing slopes at lower elevations. Open shrub lands dominate low elevation areas and south-facing slopes. Although the study area is 50% forested, only 14% of the study area is comprised of the sub-boreal forests lynx select. Open areas cover 30% of the study area. Disturbances (since 1985) caused by wildfires or timber harvest cover 16% of the study area. The largest disturbance was the 70,644 ha Tripod Fire, which burned much of Washington's lynx habitat in 2006 (Agee 2000, Stinson 2001, Koehler et al. 2008).

Nearly 22,000 km of roads exist on the study area, ranging from closed forest roads to major highways. Highway 97 runs north-south along the eastern edge of the study area and both Highway 20 (closed during winter from Mazama to the western slope of the Cascades) and Highway 2 run east-west and bisect the study area. Even in the most remote areas of the study area, the furthest straight-line distance from a road is only 17 km.

4.3 METHODS

To model functional connectivity for lynx throughout the North Cascades, I used the results of my Overall Core Habitat model and my Travel Habitat Model developed in Chapter 2. These models identified the habitat variables important for defining core and travel habitat for lynx in the Black Pine Basin and Loomis areas of the North Cascades and were based on location data obtained from lynx trapped and fitted with Global Positioning System (GPS) telemetry collars in the Okanagan-Wenatchee National Forest and the Loomis State Forest from 2006 to 2012. Trapping took place during the winter using box traps (Kolbe et al. 2003), as a collaboration between the Washington Department of Fish and Wildlife, Washington Department of Natural Resources, U.S. Forest Service, U.S. Bureau of Land Management, and the U.S. Fish and Wildlife Service (John Rohrer, personal communication). I developed the habitat models using Random Forest (Brieman 2001, Cutler et al. 2007) implemented in program R version 3.2.1 (R development core 2014) using package rfUtilities (Evans and Cushman 2009, Evans et al. 2011, Evans and Murphy 2014) to compare the habitat variables present at used lynx GPS locations and random available locations (Chapter 2). Habitat variables were depicted with raster data layers I developed in ArcGIS 10.1 (ESRI 2012). I created continuous representations of each habitat variable using 30 m^2 pixels projected into the 1983 North American Datum Albers coordinate system (Appendix C describes data layer development).

4.3.1 Identification of Habitat Concentration Areas

To model connectivity in the North Cascades I first needed to identify concentrated areas of core lynx habitat, or, Habitat Concentration Areas (Singleton et al. 2002, WWHCWG 2010). For this step, I created a habitat quality raster by extrapolating the results of my Overall Core Habitat Model (Chapter 2) across the North Cascades study area. This raster depicted the probability of lynx use for each pixel, which I equated with underlying habitat quality. These values were scaled from 1 (poor habitat) to 10 (good habitat). Seventeen variables were selected by the Overall Core Habitat Model as important predictors of lynx core habitat selection (**Table 4.2**). Lynx selected areas with sub-boreal forests dominated by lodgepole pine (*Pinus contorta*) or Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) ("spruce-fir" hereafter), while dry forests, characterized by Douglas fir (*Pseudotsuga menziesii*) and ponderosa pine (*Pinus ponderosa*), were selected against. Lynx also selected forests transitioning between sub-boreal types and dry forests dominated by Douglas fir and intermixed with sub-boreal species ("mixed forest" hereafter). Grasslands, shrub-steppe, old thins, areas recently burned at high severity, and areas within a burn perimeter were avoided by lynx, as were steep slopes and areas with sparse canopy cover. Climate variables were also important to lynx habitat selection. Lynx selected for areas with greater moisture accumulations as depicted by the Compound Topographic Index, a measure of moisture accumulation based on slope and upslope area. Lynx selected for cooler, moister slopes as depicted by the Heat Load Index, which incorporates both aspect and slope. Finally, lynx selected areas with greater amounts of growing season precipitation.

Table 4.2. Habitat variables important to lynx core habitat selection according to the Overall Core Habitat Model (Chapter 2). Variables depicted within a 3x3 pixel window (90 m diameter) represent habitat selection at a small-scale, while variables depicted within a 27x27 pixel window (810 m diameter) represent habitat selection at a large-scale. Only the scale lynx selected in the Overall Core Habitat Model is presented for each variable.

Variable Class	Variable	Measurement Type
Land Cover	Lodgepole pine Spruce-fir Mixed forest Dry forest Grassland Shrub land	Number of like pixels within a 27x27 window
Disturbance	Old, thinned forest	Number of like pixels within a 27x27 window
	New, high-severity burn	Number of like pixels within 3x3 and 27x27 windows
Patch Metrics	Distance to edge of burn	Meters from a pixel within a burn to the nearest edge of the burn
Topography	Slope	Degrees averaged across 3x3 and 27x27 windows
Climate	Compound Topographic Index	Index, lower numbers indicate wetter areas. Index averaged across a 27x27 window
	Heat Load Index	Index, lower numbers indicate warmer areas. Index averaged across a 27x27 window
	Growing season precipitation	Average total precipitation (mm) between April and September. Index averaged across a 27x27 window
Forest Structure	Canopy cover	Average percent canopy cover in 3x3 and 27x27 windows

Next, I added six landscape variables that are hypothesized to impact core habitat for lynx, but that were not present in the areas the radio-collared lynx used, and hence, were not included in the Random Forest models. Values for these variables were based on expert opinion (mine and five other experts familiar with lynx and the region). These experts were consulted in February 2015. A value of 0 represented no impact on lynx habitat, 10 represented a major negative impact, and negative numbers represented a positive impact on lynx habitat (**Table 4.3**). To adjust the habitat quality raster I subtracted the average of these assigned values from affected pixels. For example, in areas within 50 m of road, the habitat value in the habitat quality raster was lowered by 4.

Table 4.3. Landscape variables used in the connectivity modeling that were developed from expert opinion from 6 people. These variables were not included in the habitat modeling in Chapter 2, but were present and thought to be important to lynx in the more extensive landscape used for connectivity modeling. A value of 0 represents no impact, 10 represents a major negative impact, and negative numbers represent a positive impact on lynx habitat.

Habitat variable	Assigned average value	Range of estimated habitat values
Distance to developed area (m)[b]		
0	8	5 – 10
0 - 50	6	2 – 9
50 - 100	3	0 – 5
100 - 250	1	0 – 2
250 - 500	0	0 – 1
500 - 1,000	0	0
>1,000	0	0
Distance to road (m)[c]		
0	7	2 – 10
0 - 50	4	0 – 6
50 - 100	2	0 – 3
100 - 250	0	0 – 2
250 - 500	0	0 – 1
500 - 1,000	0	0
>1,000	0	0
West-side sub-boreal forest[a,d]		
Present	2	-5 – 4
Not present	0	0
West-side wet forest[a,e]		
Present	6	1 – 10
Not present	0	0
Agriculture[a]		
Present	7	4 – 10
Not present	0	0
Water[f]		
Present	6	4 – 8
Not present	0	0

[a] Represented as present or not present within a 30 x 30 m pixel.
[b] Tax parcels with residential or commercial development.
[c] Highways only. Local roads are not believed to negatively impact lynx habitat according to literature and expert opinion.
[d] A sub-boreal forest type primarily found west of the Cascade crest and wetter than sub-boreal forests east of the crest.
[e] Wet forest primarily found west of the Cascade crest, below the west-side sub-boreal forest zone.
[f] Large lakes and rivers.

During the next step of identifying Habitat Concentration Areas within the North Cascades, I used the R program package adehabitatHR (Calenge 2006) to estimate home ranges (95% minimum convex polygons) for each radio-collared lynx that localized in the Black Pine Basin or Loomis areas and provided at least six months of data (See Chapter 2). Excluding Male 339, who did not have a well-localized home range, the average home range size was 88 km^2 (**Table 4.4**).

Table 4.4. Minimum Convex Polygon (MCP) home range estimates for lynx using GPS location data collected in the North Cascades. The average habitat value per pixel was calculated within each lynx' home range, excluding lynx 336 since a large portion of his home range fell beyond the limit of the habitat quality raster. Lower numbers indicate poorer average habitat.

Lynx ID	95% MCP home range in km^2	Average habitat value per pixel	Standard deviation
Male 339	674	5.0	2.7
Male 327	231	3.8	1.9
Male 311	127	5.9	2.1
Male 338	116	7.6	2.3
Male 346	98	7.4	1.8
Male 347	78	7.4	2.0
Male 309	75	8.0	1.8
Male 329	73	6.0	1.8
Male 336	36	Not calculated	
Male 308	36	8.9	1.1
Male 348	19	7.9	1.9
Female 340	131	6.1	1.9
Female 330	67	6.8	1.5
Female 349	61	8.6	1.4

I then used each home range polygon and the adjusted habitat quality raster to calculate the average habitat value within each lynx home range. Male 336 was excluded from this analysis since his home range straddled the Washington/British Columbia border and was thus partly outside my study area and beyond the limit of my habitat quality raster.

To complete the final step of identifying Habitat Concentration Areas within the North Cascades, I used the ArcGIS tool Core Mapper (Shirk and McRae 2013) to perform a moving window analysis across my habitat quality raster. For this analysis, I used an 88 km^2 neighborhood, which was the average home range size of the GPS-collared lynx. For each pixel on the landscape, the moving window analysis identified the average habitat value of pixels in the 88 km^2 window surrounding the focal pixel. I then used the tool to extract all pixels with an average neighborhood value greater than 3.8, the lowest average habitat value used by any of the GPS-collared lynx. I chose to use the lowest average habitat value because it resulted in an ample distribution of Habitat Concentration Areas that allowed me to model habitat linkages between them.

Core Mapper identified 15 Habitat Concentration Areas. I discarded 2 of the Habitat Concentration Areas because of their small size (< 1 km^2), and another because it was located along the eastern edge of the study area, across the Okanogan Valley and outside of the North Cascades Mountains. I also split the largest area in two to increase the number and distribution of linkages modeled between that area and an adjacent Habitat Concentration Area. While the division of the large Habitat Concentration Area was arbitrary, I believe it resulted in a more realistic depiction of linkages since more than one linkage is likely for such a large area.

4.3.2 Creating the Resistance Surface

To create a resistance surface for modeling habitat linkages, I applied the results of my Travel Habitat Model (Chapter 2), which identified the habitats lynx select while traveling through the matrix. I extrapolated the results of the Travel Habitat Model throughout the North Cascades and scaled the raster so that a value of 1 represented areas of no resistance to movement, and 10 represented areas of high resistance to movement. The Travel Habitat Model identified 20 variables that predict how lynx select habitat while traveling through matrix areas. Although lynx select travel habitats similar to those they select in core areas, in most cases lynx used a wider range of habitat conditions for travel habitats compared to core habitats (**Table 4.5**).

Table 4.5. Habitat variables identified by the Travel Habitat Model (Chapter 2) as being important to lynx. Variables depicted within a 3x3 pixel window (90 m diameter) represent habitat selection at a small scale while variables depicted within a 27x27 pixel window (810 m diameter) represent habitat selection at a large scale. Only the scale lynx selected in the Travel Habitat Model is presented for each variable.

Variable Class	Variable	Measurement Type
Land Cover	Lodgepole pine	Number of like pixels within a 27x27 window
	Spruce-fir	Number of like pixels within 3x3 and 27x27 windows
	Mixed forest Deciduous forest Dry forest Grassland Shrub land	Number of like pixels within a 27x27 window
Disturbance	Old, thinned forest New clearcut New, high-severity burn	Number of like pixels within a 27x27 window
Patch Metrics	Distance to edge of burn	Meters from a pixel within a burn to the nearest edge of the burn
Topography	Slope	Degrees averaged across 3x3 and 27x27 windows
Climate	Compound Topographic Index	Index, lower numbers indicate wetter areas. Index averaged across 3x3 and 27x27 windows
	Heat Load Index	Index, lower numbers indicate warmer areas. Index averaged across a 27x27 window
	Growing season precipitation	Average total precipitation (mm) between April and September. Index averaged across a 27x27 window
Forest Structure	Canopy cover	Average percent canopy cover in 3x3 and 27x27 windows

As with the habitat quality raster, I also adjusted the resistance surface created by the travel habitat raster by incorporating important habitat variables missing from the Travel Habitat Model but present within the greater North Cascades landscape. I adjusted the resistance surface using the average value assigned by myself and five other lynx biologists to each missing variable with a value of 0 having no effect on the resistance of travel habitat, 10 significantly increasing resistance, and negative numbers decreasing resistance. None of the missing variables were believed to pose absolute barriers to lynx movement. I adjusted the resistance surface by adding the average of these values to the resistance surface. For example, the resistance of areas within 50 m of a road was increased by 1, indicating that areas near roads would have only a minor impact on lynx movements (**Table 4.6**).

Table 4.6. Landscape variables used in the connectivity modeling that were developed from expert opinion from 6 people. These variables were not included in the Travel Habitat Model developed in Chapter 2, but were present and thought to be important to lynx in the more extensive landscape used for connectivity modeling. A value of 0 represents no increase in resistance, 10 represents a major increase in resistance, and negative numbers represent a decrease in resistance to lynx movement.

Habitat variable	Assigned average value	Range of estimated habitat values
Distance to developed area (m)[b]		
0	4	2 – 8
0 - 50	2	0 – 5
50 - 100	1	0 – 2
100 - 250	0	0
250 - 500	0	0
500 - 1,000	0	0
>1,000	0	0
Distance to road (m)[c]		
0	3	2 – 5
0 - 50	1	0 – 3
50 - 100	0	0 – 1
100 - 250	0	0
250 - 500	0	0
500 - 1,000	0	0
>1,000	0	0
West-side sub-boreal forest[a,d]		
Present	-1	-3 – 0
Not present	0	0
West-side wet forest[a,e]		
Present	1	0 – 3
Not present	0	0
Agriculture[a]		
Present	5	0 – 8
Not present	0	0
Water[f]		
Present	4	0 – 7
Not present	0	0

a Represented as present or not present within a 30 x 30 m pixel.
b Tax parcels with residential or commercial development.
c Highways only. Local roads are not believed to negatively impact lynx habitat according to literature and expert opinion.
d A sub-boreal forest type primarily found west of the Cascade crest and wetter than sub-boreal forests east of the crest.
e Wet forest primarily found west of the Cascade crest, below the west-side sub-boreal forest zone.
f Large lakes and rivers

4.3.3 Modeling Connectivity

I used Linkage Mapper 1.0 (McRae and Kavanagh 2011) in ArcGIS to identify Least Cost Paths over my resistance surface and linking my Habitat Concentrations Areas, thus modeling connectivity for lynx across the North Cascades. First, I used the tool to perform a cost-weighted analysis by calculating the cost of moving from any pixel on the landscape to a selected Habitat Concentration Area, the cost of a pixel being its resistance value times the diameter of the pixel. This step produced an individual cost-weighted distance raster for each Habitat Concentration Area.

I also used Linkage Mapper to determine which Habitat Concentration Areas were adjacent to each other in terms of Euclidean distance and cost-weighted distance. Each individual cost-weighted distance raster was then combined with those of adjacent Habitat Concentration Areas by *retaining the lowest value* for each pixel. By combining individual cost-weighted distance rasters in this way, I produced a map displaying the weighted cost that would be accrued traveling from each pixel on the landscape to the *nearest* Habitat Concentration Area (McRae and Kavanagh 2011)

I then used Linkage Mapper to calculate the pixel-wide Least Cost Path (the path along which the lowest cost-weighted value is accumulated) between each adjacent Habitat Concentration Area (**Figure 4.5**). Linkages were then mapped between Habitat Concentration Areas by *adding together* the pixel values of individual cost-weighted distance rasters produced in earlier steps. Mapping linkages highlighted areas where the lowest costs accumulated. Primary linkages are those that contain the Least Cost Paths. I also modeled secondary linkages, representing linkages that also accrue low weighted-costs (McRae and Kavanagh 2011). The value of the Least Cost Path was then subtracted from its surrounding linkage so that each primary linkage contained a Least Cost Path valued at zero with the surrounding pixels showing the increasingly costly routes. For each least cost path, I used Linkage Mapper to calculate several statistics to assist evaluating each path's quality and thus contribution to connectivity. These statistics explained the Euclidian distance between adjacent Habitat Concentration Areas, the cost-weighted distance of each Least Cost Path, and the un-weighted length of each Least Cost Path. I also calculated the cost-weight accumulated along each path normalized by the Euclidian distance. The accumulated cost-weight along each path was normalized by the un-weighted length of the path, providing the average resistance a lynx would face while traveling along each Least Cost Path. Ratios closer to 1 represent higher quality paths (WWHCWG 2010).

4.4 RESULTS

The final habitat quality raster for lynx in the North Cascade had values that ranged from -20.1 to 10.9 with a mean value of 2.2 and a standard deviation of 3.3 (**Figure 4.2**). The final resistance surface values ranged from 1 to 21.9 with a mean value of 8.2 and a standard deviation of 2.5 (**Figure 4.3**).

I identified 12 Habitat Concentration Areas ranging in size from 10 km^2 to 1,459 km^2 (**Table 4.7**, **Figure 4.2**). Although the majority of each Habitat Concentration Area lies within the Okanogan Lynx Management Zone designated by the Washington State Lynx Recovery Plan (Stinson 2001), the southernmost Habitat Concentration Area (area 11) lies south of Highway 2 and completely outside of the Lynx Management Zone. Habitat Concentration Areas 5, 8, and 10 are all smaller than the smallest home range identified for lynx in this study (**Table 4.4**). Nonetheless these small Habitat Concentration Areas can provide valuable patches of core habitat for lynx passing through the area.

Table 4.7. Habitat Concentration Areas identified for lynx in the North Cascades. Lower values indicate poorer average habitat quality. Bold fonts represent areas smaller than the smallest home rage estimated for lynx in this study. Habitat Concentration Area 11 was not surveyed for lynx since it lies outside of the Okanogan Lynx Management Zone.

Habitat Concentration Area	Area (km^2)	Average habitat value	Standard deviation of habitat value	Most recent official documentation of lynx in the surrounding area
1	599	5.9	2.4	2012
2	1,459	4.6	1.7	2012
3	1,272	4.5	1.5	2012
4	60	4.5	1.4	2012
5	**16**	**4.0**	**1.1**	**2012**
6	24	4.1	1.2	2012[a]
7	926	4.6	1.5	1991
8	**17**	**3.9**	**0.8**	**2012**[b]
9	64	4.5	1.0	1991[c]
10	**10**	**3.9**	**1.0**	**1991[c]**
11	126	4.6	1.6	**Not surveyed**
12	30	4.5	0.7	**1991[c]**

[a] Date refers to the same lynx documentations reported for the nearby Habitat Concentration Areas 5 and 7 and does not necessarily indicate that a lynx was present in area 6.
[b] Date refers to the same lynx documentation reported for the nearby Habitat Concentration Area 3 and does not necessarily indicate that a lynx was present in area 8.
[c] Date refers to the same lynx documentation reported for the nearby Habitat Concentration Area 7 and does not necessarily indicate that a lynx was present in areas 10 and 12.


2a
1
2b
Okanogan Valley
Methow Valley
4
5
6
3
Lake Chelan
8
7
9
10
11
Wenatchee Valley
12
Water
Study area
Habitat Concentration Areas
No recent lynx documentation
Removed Habitat Concentration Area
High : 10.9
Low : -20.1
0 5 10 20 Kilometers
N

Figure 4.2. Habitat Concentration Areas identified within the North Cascades study area. The red Habitat Concentration Area was removed because it was outside of the North Cascade Mountains. The two Habitat Concentration Areas removed for being < 1 km^2 are too small to see in this map. No lynx have been documented south of Lake Chelan since 1992 although lynx were documented near Habitat Concentration Areas 7, 9, and 12 in 1973, 1989, and 1991.

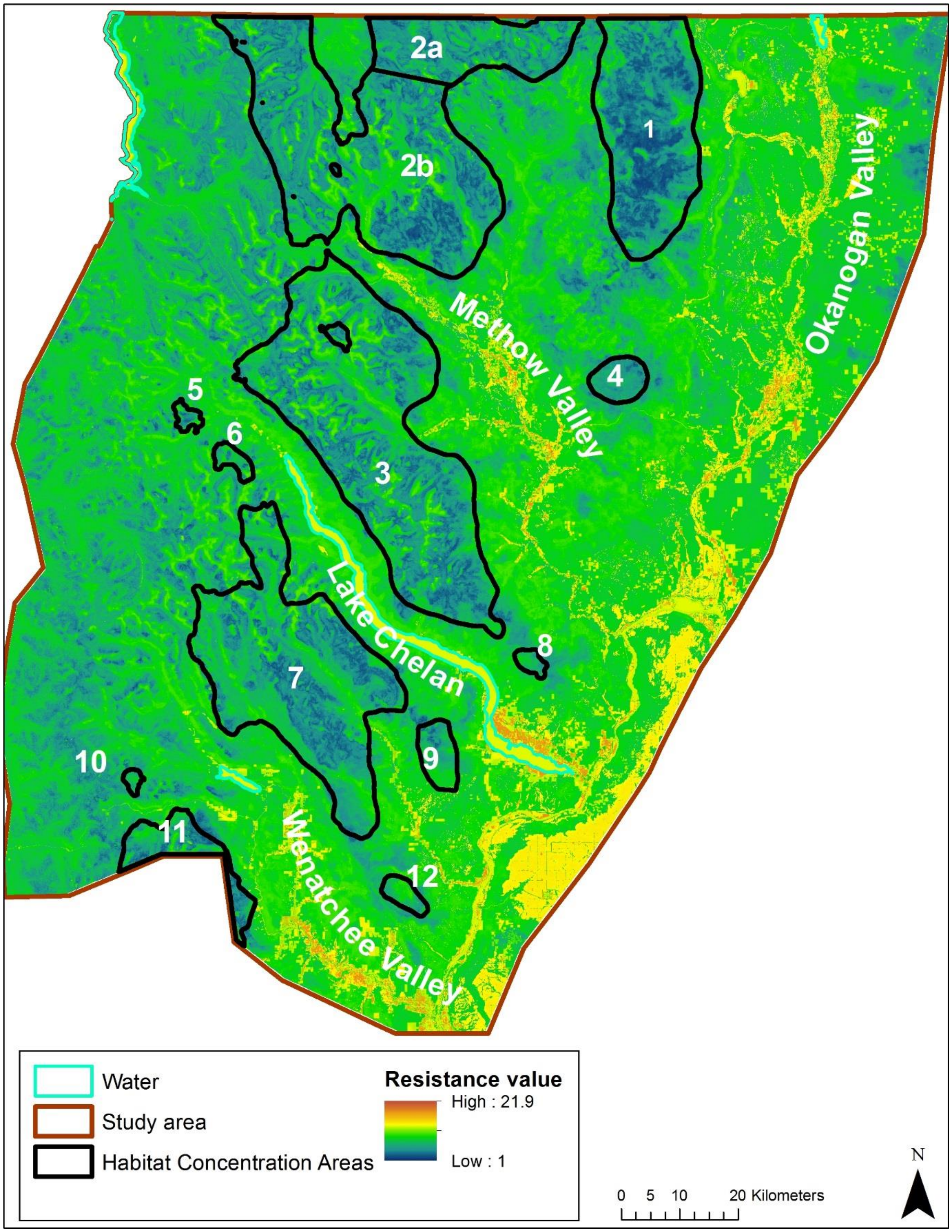


Figure 4.3. Resistance surface displaying the resistance to lynx movement within the North Cascades.

The cost-weighted distance map (**Figure 4.4**) highlights that cost is low for lynx moving in the sub-boreal and mixed forest zone but that cost quickly accumulates to the east of the mountains towards the low-elevation Okanogan Valley and west of the crest where west-side sub-boreal forests dominate. Weighted cost also increases in the Methow and Wenatchee Valleys and around Lake Chelan. Within high-elevation forested areas, burns such as the 2003 Farewell Fire and the 2006 Tatoosh and Tripod Fires increase resistance, but fire skips and regenerating forest communities lower the resistance to movement through these areas.

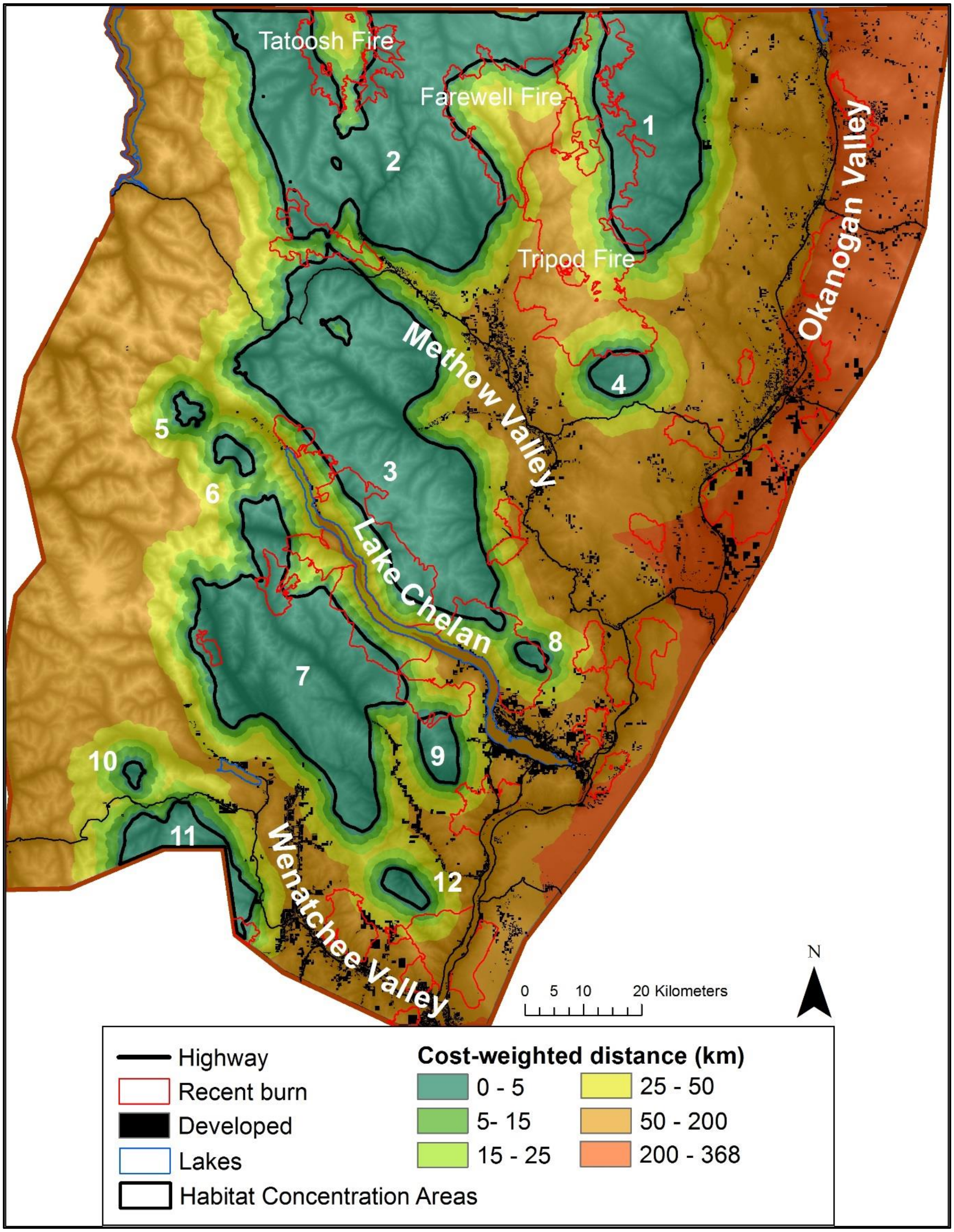
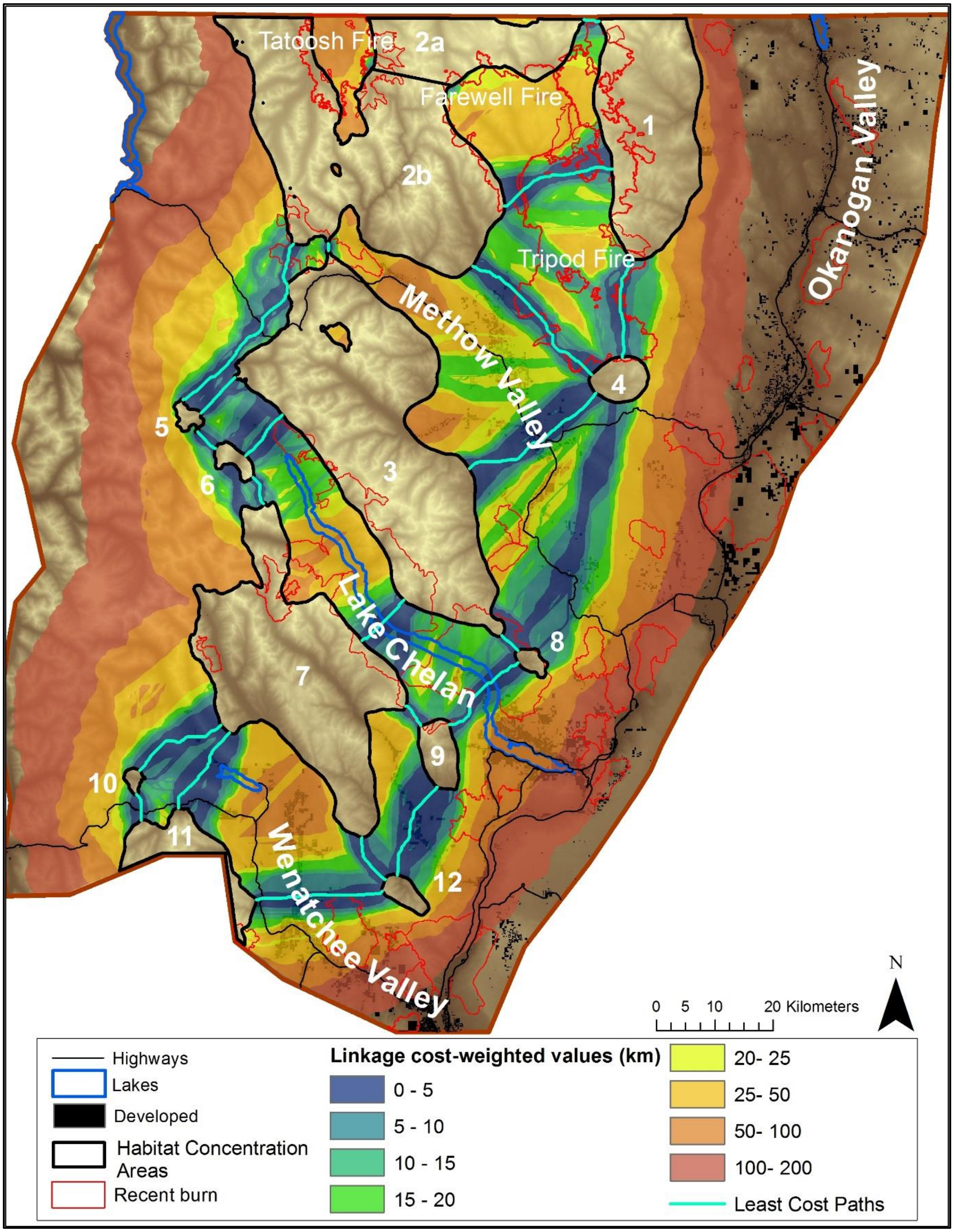


Figure 4.4. Cost-weighted distance map symbolizing the difficulty for lynx of moving from any pixel to the nearest Habitat Concentration Area. Recent burns occurred between 1995 and 2012.



Tatoosh Fire
2a
Farewell Fire
1
2b
Tripod Fire
Okanogan Valley
Methow Valley
4
5
3
6
Lake Chelan
8
7
9
10
11
Wenatchee Valley
12
N
0 5 10 20 Kilometers
Highways
Lakes
Developed
Habitat Concentration Areas
Recent burn
Linkage cost-weighted values (km)
0 - 5
5 - 10
10 - 15
15 - 20
20- 25
25- 50
50- 100
100- 200
Least Cost Paths

Figure 4.5. Linkages for lynx in the North Cascades. Least Cost Paths indicate primary linkages between adjacent Habitat Concentration Areas. Secondary linkages provide alternate, low-cost paths and can be valuable for connectivity conservation. Colors in primary linkages are relative to the Least Cost Path *within* each primary linkage so that cooler colors represent the lowest resistance of a linkage to move through while warmer colors represent increasing resistance. Thus, primary linkage colors are not scaled so that comparisons can be made between them and this map does not indicate which of the primary linkages present lower costs than others.

In some cases, more than one linkage between adjacent Habitat Concentration Areas was identified. To assist with identifying the primary linkage, Linkage Mapper also modeled the Least Cost Path between each pair of adjacent Habitat Concentration Areas, and identified 21 Least Cost Paths connecting the Habitat Concentration Areas into a single network (**Figure 4.5**). Each of the 21 Least Cost Path's un-weighted and weighted lengths were shorter than 367 km, which was the longest dispersal distance made by radio-collared lynx in my study. (**Table 4.8**, **Figure 4.6**). Cost weighted distances ranged from 10 - 215 km and weighted cost/path length ratios ranged from 4.8 - 9.3 (**Table 4.8**).

Table 4.8. Linkage statistics for evaluating the quality of each Least Cost Path for lynx in the North Cascades. Cost-weighted distances and weighted-cost/path-length ratios in bold typeface indicate the four paths with the lowest connectivity values for lynx.

Least Cost Path	Cost-weighted distance (km)	Euclidian distance (km)	Least Cost Path length (km)	Weighted cost divided by Euclidian distance	Weighted cost divided by path length
2b-3	10	1	1	8.8	8.3
1-2a	14	3	3	5.3	4.8
7-9	17	4	5	4.5	3.8
6-7	25	4	5	6.0	4.8
3-8	28	4	4	7.5	7.3
5-6	29	4	4	7.1	6.7
10-11	36	4	5	8.2	7.7
7-12	56	8	9	7.4	6.3
3-5	67	8	8	8.2	8.0
3-6	73	9	10	8.0	7.4
3-7	83	10	10	8.4	8.1
1-4	111	17	18	6.7	6.1
7-11	123	15	17	8.3	7.4
1-2b	127	18	21	7.0	5.9
7-10	126	16	18	8.0	7.1
8-9	**134**	**15**	**17**	**8.7**	**7.7**
9-12	**146**	**16**	**18**	**8.9**	**8.2**
4-2b	203	27	30	7.4	6.9
2b-5	208	33	37	6.4	5.6
11-12	**208**	**22**	**22**	**9.6**	**9.3**
3-4	**215**	**25**	**27**	**8.6**	**7.9**

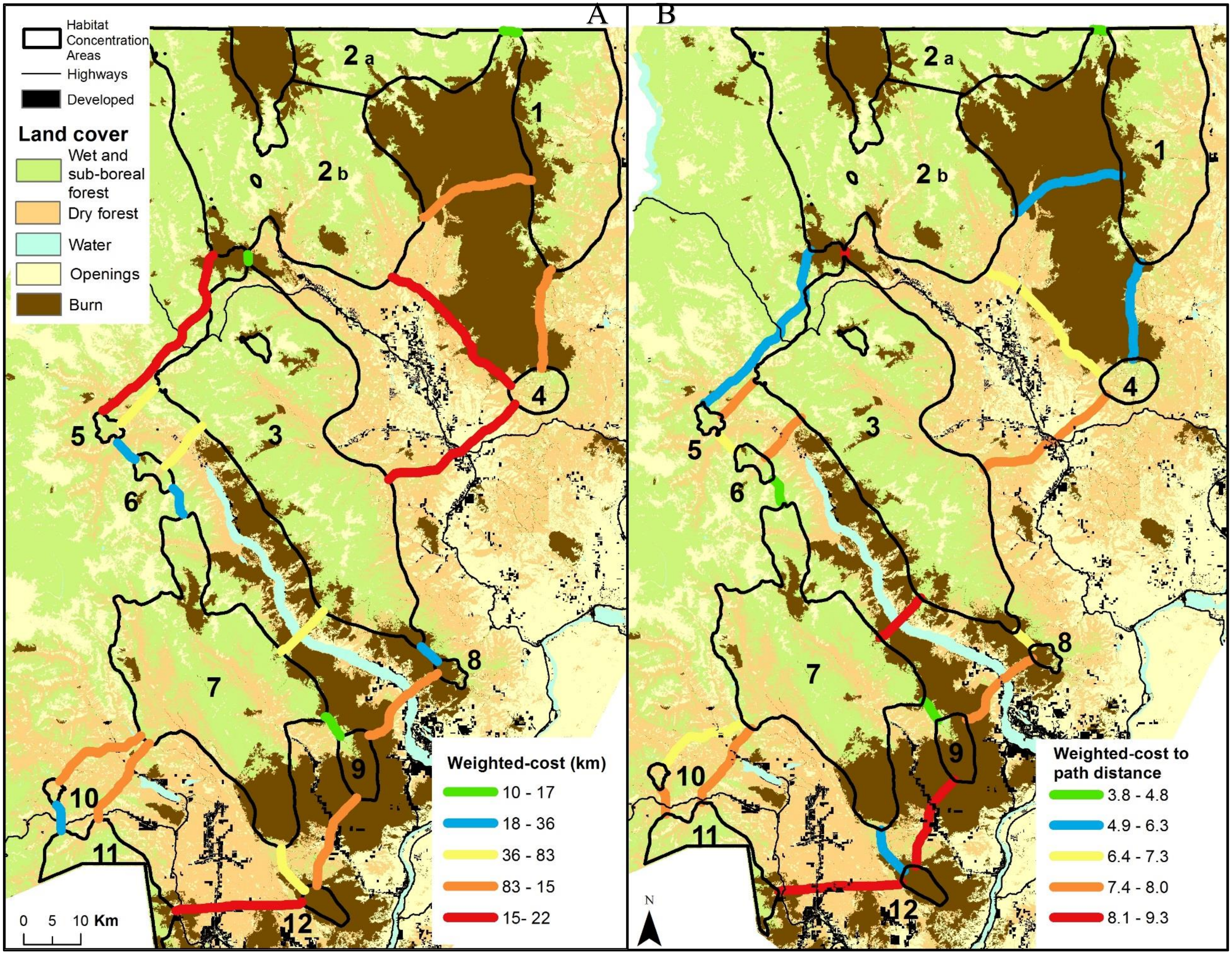

A
B
Habitat Concentration Areas
Highways
Developed
Land cover
Wet and sub-boreal forest
Dry forest
Water
Openings
Burn
2 a
2 b
1
3
4
5
6
7
8
9
10
11
12
Weighted-cost (km)
10 - 17
18 - 36
36 - 83
83 - 15
15- 22
0 5 10 Km
Weighted-cost to path distance
3.8 - 4.8
4.9 - 6.3
6.4 - 7.3
7.4 - 8.0
8.1 - 9.3
N

Figure 4.6. Least Cost Paths connecting Habitat Concentration Areas in the North Cascades. The total weighted-cost of each Least Cost Path (Map A) represents the accumulated resistance value of each path. The weighted-cost to path distance of each Least Cost Paths (Map B) represents the accumulated resistance divided by the total un-weighted distance of each path.

4.5 DISCUSSION

Lynx regularly travel long distances and through a variety of habitats generally not selected as core hunting, denning, and resting habitat (Mowat et al. 2000, Squires and Laurion 2000). Indeed, some of the GPS-collared lynx in this study went on exploratory movements outside of their home ranges or dispersed into British Columbia, traversing high peaks above tree line and recently-burned areas. These lynx also crossed valley bottoms with farm land and human development, open sage or grass lands, and over several highways (Appendix F). Despite an ability to travel through a variety of habitats within the matrix, my models show that for lynx, the contrast between core habitat and travel habitat has important implications in terms of how connected a landscape is. Core lynx habitat is forested (Koehler 2008, Squires 2010) and lynx prefer to travel through matrix areas with some sort of forest cover (Chapter 2). Higher contrast matrix such as open sage-steppe, and human dominated areas are less desirable to traveling lynx (Chapter 2). By creating a connectivity model for lynx in the North Cascades, my results show where in the North Cascades this highly mobile species may find habitat conditions most suitable for traveling.

4.5.1 Habitat Concentration Areas

Twelve Habitat Concentration Areas were identified in my model. Although the areas south of Lake Chelan (6, 7 and 9 – 12) are not currently known to support resident lynx and their most recent lynx documentation was in 1991 (Stinson 2001, Robert Naney, personal communication), these Habitat Concentration Areas are within the historical range of lynx and could conceivably be occupied in the future, especially during peak snowshoe hare-lynx cycles when lynx numbers are high and populations can expand (Schwartz et al. 2002). It is also important to note that the modeled Habitat Concentration Areas do not represent all lynx habitat in the North Cascades. The primary purpose for identifying Habitat Concentration Areas was to map only the best lynx habitat, constraining the definition of core habitat enough that space remained to model linkages between the Habitat Concentration Areas (WWHCWG 2010). Thus, core lynx habitat of lower but suitable value exists outside of the Habitat Concentration Areas.

Habitat Concentration areas 5, 8, and 10 were all less than 19 km^2, which is the smallest home range size identified for a lynx in this study (**Table 4.4**). While these small Habitat Concentration Areas may not be large enough to support a lynx, they can act as "stepping stones" (Dickson et al. 2013) for lynx to hunt in while passing through the area. Alternatively, since these small Habitat Concentration Areas are surrounded by lower quality but still core habitat, they may indeed indicate broader areas capable of supporting lynx.

4.5.2 Cost-Weighted Distance Map

The cost-weighted map is perhaps the most informative and important product of my connectivity analysis (**Figure 4.4**) (WWHCWG 2010). Although it does not specifically highlight linkages, the cost-weighted map contains linkage information since the linkage map is simply the sum of individual, adjacent cost-weighted maps (WWHCWG 2010). In addition, this map portrays the full range of areas a travelling lynx may use and allows users to compare the qualities of different linkage areas. Finally, the cost-weighted distance map highlights broad areas of low resistance and broad areas of high weighted-cost where connectivity is low or in need of restoration.

The cost-weighted map illustrates four main areas were resistance to lynx movement is high (**Figure 4.4**). At the southern end of the study area, the Wenatchee Valley separates Habitat Concentration Areas 7 and 12 from areas 10 and 11. In the center of the study area, the low-elevation Lake Chelan area increases resistance between Habitat Concentration Areas 3 and 5 – 7, 9 and 12. At the northern end of the study area, the Tripod Burn creates resistance to lynx moving between Habitat Concentration Areas 1 and 4 and areas 1 and 2, and the Methow Valley separates areas 2 and 3. Areas of high resistance between the northerly Habitat Concentration Areas are perhaps the most pertinent to current lynx conservation and management since Habitat Concentration Areas 1 – 4 are the heart of Washington lynx range and support a known population of lynx. Taking a closer look at the cost-weighted map of this area (**Figure 4.7**) reveals where connectivity through the Tripod Burn and the Methow Valley is highest: The northern end of the Tripod Burn supports high connectivity between Habitat Concentration Areas 1 and 2, and a direct north-south route between areas 1 and 4 presents the least weighted-cost. To connect Habitat Concentration Areas 2 and 3, northwest of Mazama and through the Needles Fire presents the least resistance, although connectivity is also high between Mazama and halfway to Winthrop near an area called Big Valley Ranch (**Figure 4.7**). Finally, connectivity is high along the western edges of Habitat Concentration Areas 2 and 3.

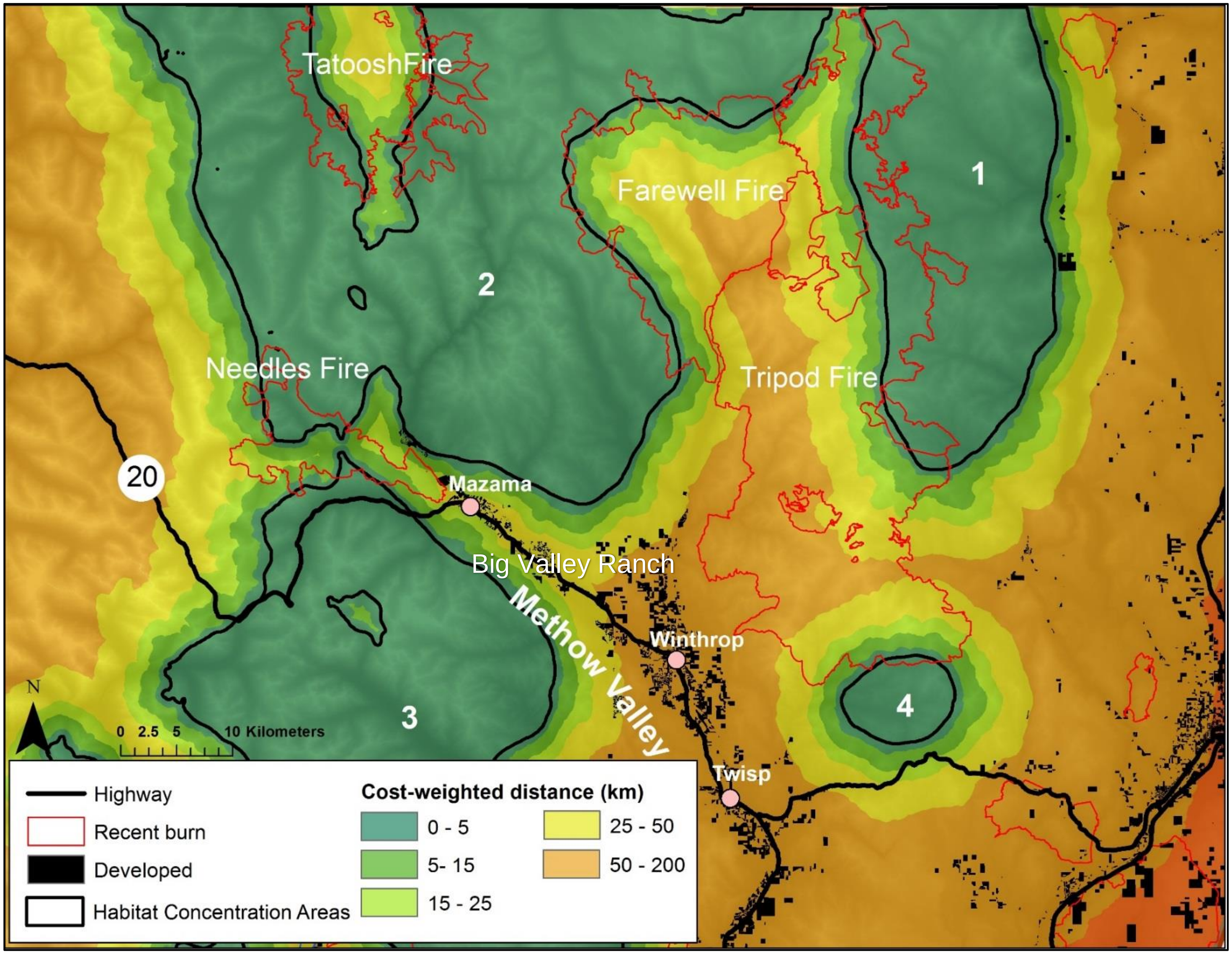


Figure 4.7. Close-up depiction of the cost-weighted distance map for Habitat Concentration Areas 1, 2, 3, and 4. Cooler colors represent lower accumulations of weighted cost.

4.5.3 Linkage Map

After examining the cost-weighted map, the linkage map can help to highlight where primary linkages (those that contain a Least Cost Path) and secondary linkages exist between adjacent Habitat Concentration Areas. Several linkages clearly emerge at the northern end of the study area (**Figure 4.8**): The northern end of the Tripod Burn supports the primary linkage between Habitat Concentration Areas 1 and 2b, and the north-south route between areas 1 and 4 supports a primary linkage. Similarly, the primary linkage between Habitat Concentration Areas 2 and 3 is just northwest of Mazama, and a primary linkage to area 5 runs north-south along the western edge of Habitat Concentration Areas 2 and 3.

Least Cost Paths themselves are only one-pixel-wide pathways and are therefore sensitive to errors in the underlying GIS layers used to create the resistance surface. Least Cost Paths themselves should not be interpreted or used as an exact map of a pathway. Instead, focusing on the alternative routes clustered around the Least Cost Path indicates the broader, more realistic area of low resistance linkage.

In addition to highlighting where primary linkages exist between adjacent Habitat Concentration Areas, the linkage map also includes secondary linkages that may not have been obvious from an examination of the cost-distance map. For example, between Habitat Concentration Areas 1 and 2, several secondary linkages cross the Tripod Burn. Although secondary linkages may not be the Least Cost Path, they may provide important alternate routes for lynx and should be incorporated into conservation efforts since they can increase landscape connectivity and provide insurance against fragmentation should human impacts or fire alter a primary linkage. Mapped secondary linkages are scaled relative to the surrounding landscape and can be compared between.

One disadvantage of the linkage map compared to the cost-weighted map is that the linkage map can give the false impression that suitable habitat for traveling is limited to the best primary and secondary linkage areas. For example, the Mazama and Big Valley Ranch areas are identified by the cost-weighted map as having fairly high connectivity between Habitat Concentration Areas 2 and 3. However, in the linkage map, this same area is portrayed as having low connectivity because it is scaled relative to the Least Cost Path connecting Habitat Concentration Areas 2 and 3. Indeed, one lynx radio-collared for this study (male 312) crossed the Methow Valley near Mazama, demonstrating that in addition to modeled linkages, low resistance areas identified by the cost-weighted map are important to connectivity (**Figure 4.9**).

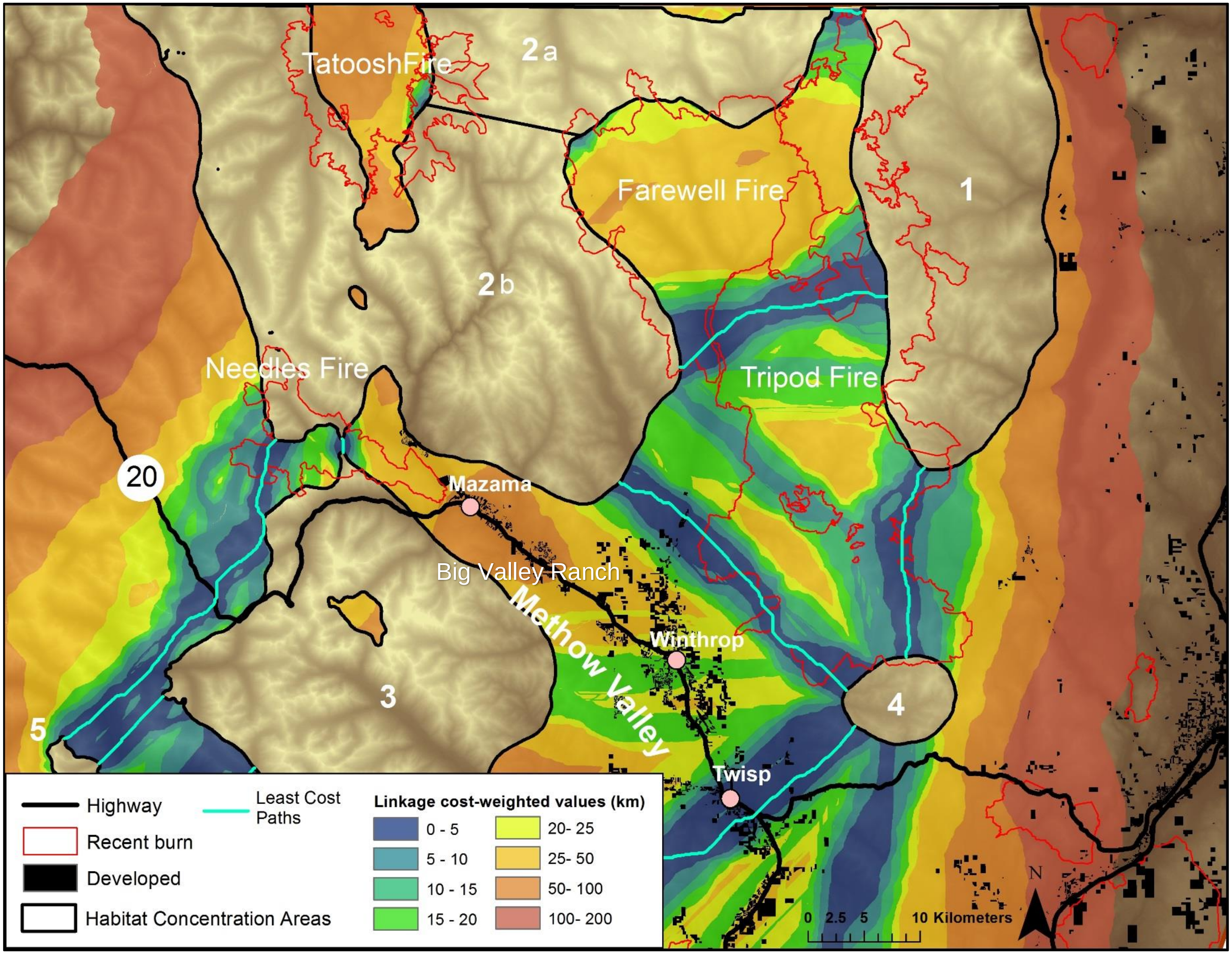

TatooshFire
2a
Farewell Fire
1
2b
Needles Fire
Tripod Fire
20
Mazama
Big Valley Ranch
Methow Valley
Winthrop
3
4
5
Twisp
Highway
Least Cost Paths
Recent burn
Developed
Habitat Concentration Areas
Linkage cost-weighted values (km)
0 - 5
5 - 10
10 - 15
15 - 20
20- 25
25- 50
50- 100
100- 200
0 2.5 5 10 Kilometers
N

Figure 4.8. Close-up depiction of the linkages connecting Habitat Concentration Areas 1, 2, 3, 4 and 5. The linkage map is scaled so that the Least Cost Path in a linkage equals zero with the alternative routes increasing in resistance as they emanate outward from the Least Cost Path. Thus, cool colors present the lowest resistance *within that linkage* to lynx movement while warmer colors in the linkage present higher resistance to movement. Because of this scaling, primary linkages cannot be compared to each other based on their color. Secondary linkages are scaled relative to the surrounding landscape and can be compared to each other based on their color.

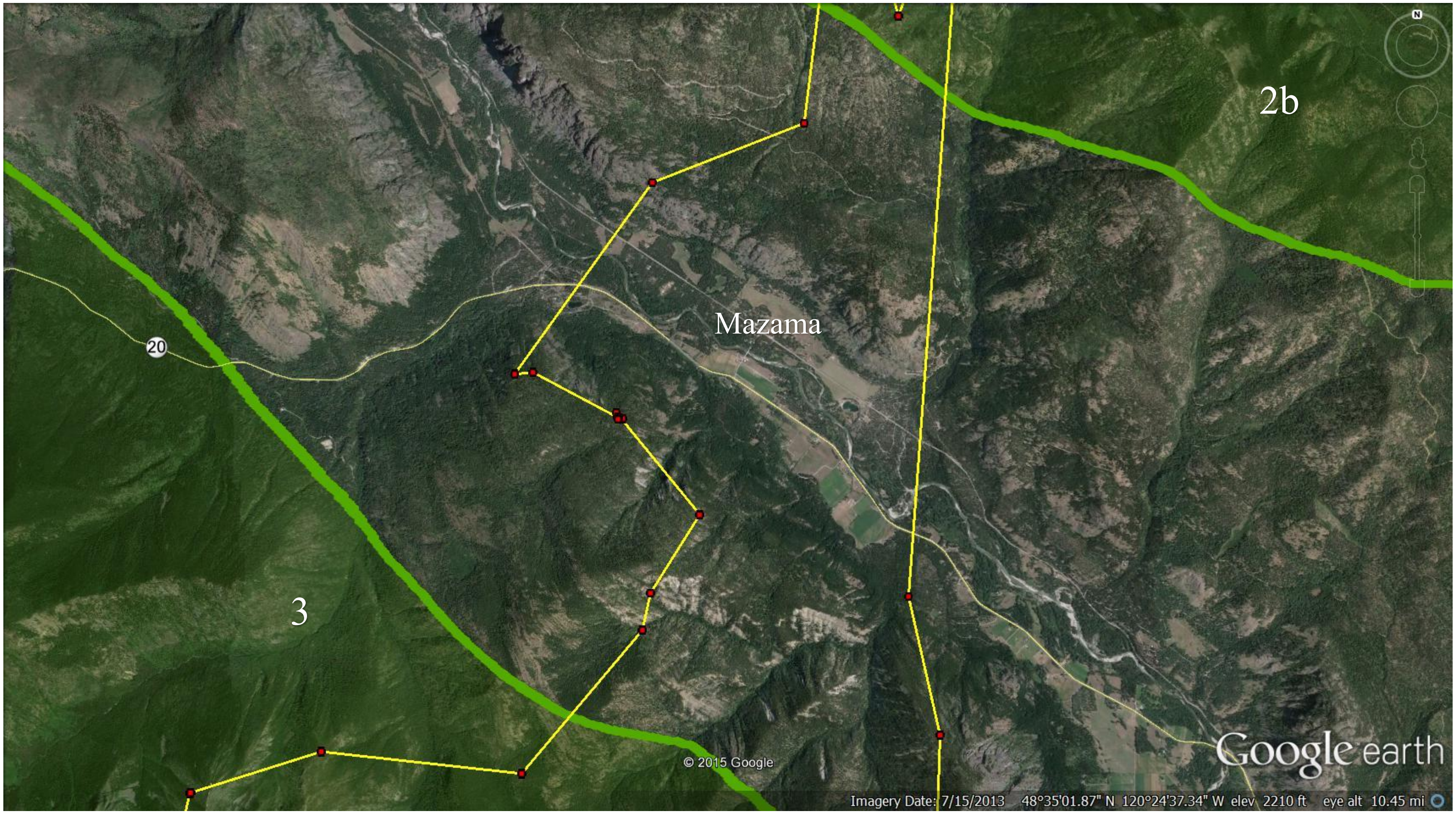


Figure 4.9. Male 312's movement pathway across the Methow Valley overlaid onto a Google Earth image (Google Earth 2013). Green areas delineate Habitat Concentration Areas 2b and 3. The yellow line is the straight line distance between 312's GPS locations, represented by red dots. This figure exemplifies a situation where a suitable linkage exists, although it was not identified in my model as the Least Cost Path between areas 2b and 3.

4.5.4 Evaluating Linkages

Once linkages are identified by the cost-weighted and linkage maps, these areas must be evaluated since their presence does not guarantee that they are suitable for lynx to travel through, only that they are paths of least resistance between Habitat Concentration Areas. For example, the linkage connecting Habitat Concentration Areas 3 and 4 may be the best available route between those areas, but a simple examination of the linkage overlaid on satellite imagery shows that this route is a poor linkage since it passes through developed and open areas of the Methow Valley, a dangerous and unattractive prospect for a lynx (**Figure 4.10**). Conversely, the linkages connecting areas 2b and 4 and areas 1 and 4 are more suitable since they traverse forested areas away from human development (**Figure 4.10**).

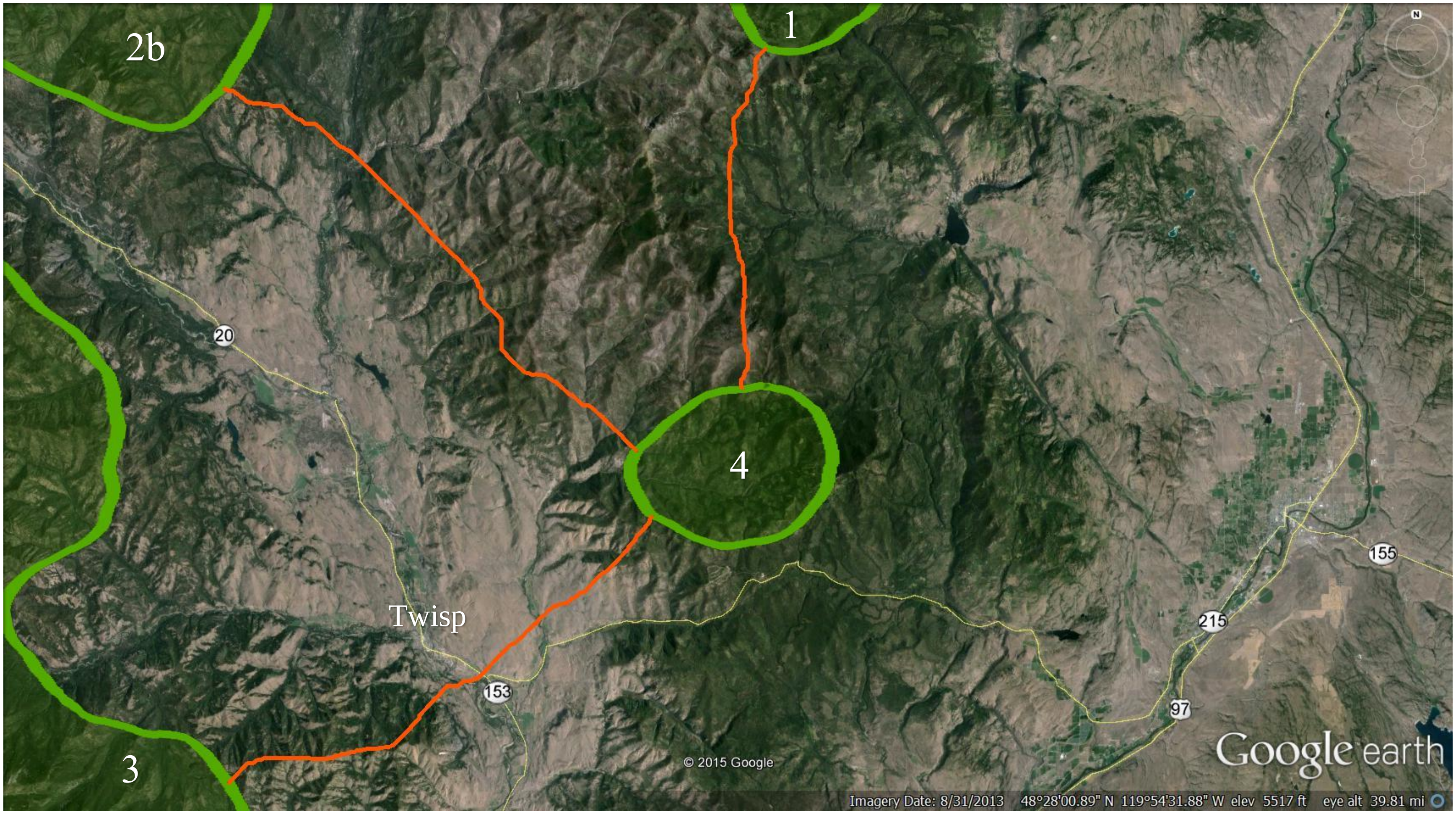


Figure 4.10. Least Cost Paths and Habitat Concentration Areas overlaid onto a Google Earth image (Google Earth 2013). The green areas delineate Habitat Concentration Areas and the orange lines are the Least Cost Paths between them. The Least Cost Path connecting area 4 to area 3 crosses the Methow Valley and presents lynx with developed areas and open, low quality matrix habitat. In contrast, the Least Cost Paths connecting area 4 to area 1, and area 4 to area 2b present lynx with higher quality, forested habitat.

Metrics of Least Cost Path quality such as the path length, the weighted-cost distance of each path, and the ratio of weighted-cost to actual path distance, can also help assess and compare the quality of primary linkages. All of my modeled linkages were shorter than 367 km, which is the longest dispersal path traveled by a radio-collared lynx in my study (**Table 4.8**). Several paths stand out as connecting Habitat Concentration Areas with current or past records of lynx and as having either low accumulations of resistance (cost-weighted distance) or low cost-weight to path length ratios. The Least Cost Path between Habitat Concentration Areas 2b and 3 represents a high quality linkage and connects these currently occupied areas. In addition, the Least Cost Paths between Habitat Concentration Area 2 (a and b) and 1 represent high quality linkages across the Tripod Burn, as do the Least Cost Path between Habitat Concentration Areas 2b and 4, and areas 1 and 4. Least Cost Paths from Habitat Concentration Areas 2b and 3 to areas 5 and 6 also represent high quality linkages and connect currently known lynx populations to Habitat Concentration Areas south of Lake Chelan were lynx are not currently known to live but have been documented in the past (**Table 4.8**, **Figure 4.6**).

Conversely, four paths stand out as having both high accumulations of resistance (cost-weighted distance) and high cost-weight to path length ratios. These paths cross through low-elevation landscapes with dry forest, burned or other non-forested openings, or residential development, and connect Habitat Concentration Areas 3-4, 8-9, 9-12, and 11-12 (**Table 4.8**, **Figure 4.6**).

4.5.5 Model Interpretation

My work highlights areas where the easiest paths for a traveling lynx exist according to my model. However, these are not the only possible linkages on the real landscape. Linkage modeling is constrained by the number and placement of Habitat Concentration Areas and only linkages between these areas are identified. In addition, a dispersing or exploring animal often does not have prior knowledge of the landscape and is therefore unlikely to precisely follow a mapped linkage. Traveling outside a linkage may be especially common for lynx since they are tolerant of many habitats and are therefore not constrained to using only the best habitats.

To create my connectivity model, I used the best available GIS layers, current to approximately 2012. However, GIS based connectivity models are sensitive to the age, quality, and scale of the underlying GIS layers. Human development and natural impacts such as fire will continue to change lynx habitat connectivity within the North Cascades ecoregion.

Finally, the meso-landscape scale at which I modeled linkages does not imply that important linkages do not exist within smaller areas, simply that my models were not created at that resolution. Modeling linkages at a large scale is an area for further study that could build upon and complement the work done in this study.

4.5.6 Implications for Lynx Management and Conservation

Lynx in the North Cascades must move across the landscape to disperse, explore, find mates, and escape habitat degradation after a disturbance such as a forest fire. These movements allow lynx to access patchy resources and for gene mixing amongst this small population. However, the North Cascades is fragmented by recent forest fires, and human developments and open areas in valley bottoms (Chapter 2, Koehler et al. 2008).

New burns reduce forest cover and thus reduce connectivity for lynx. Residual forest structures, especially in fire skips, provide valuable cover for lynx crossing recent burns and help alleviate the contrast between core habitats and new burns. Salvage logging, which removes cover from new burns, reduces connectivity for lynx across burns. For this reason, managers should retain residual structure post-burn, which will not only provide cover for lynx, but will also promote growing conditions for regenerating vegetation, allowing burned areas to recover more quickly (Brassard and Chen 2006).

Linkages across forested areas of the North Cascades, although periodically degraded by new fires, support connectivity for lynx. However, open, human-populated valley bottoms present higher resistance matrix for lynx. Linkages across valley bottoms are also more vulnerable since expanding human developments degrade connectivity. Areas of connectivity identified in my models across open and developed valley bottoms provide direction for conducting field-based assessments and validation of linkages so that managers can prioritize and conserve these vulnerable linkages.

Because the Habitat Concentration Areas north of Lake Chelan support the only known lynx in Washington, preserving connectivity amongst them is of particular importance. The Methow Valley currently presents high resistance to lynx movement between the Habitat Concentration Areas north of Lake Chelan, however my cost-weighted map demonstrates that the area between Mazama and the Big Valley Ranch provides connectivity for lynx across the Methow Valley (**Figure 4.11**). To ensure that this area of connectivity continues to facilitate traveling lynx, forest cover will need to be maintained.

Highway 20, which runs up the Methow Valley and across Habitat Concentration Area 3, is not depicted as presenting lynx with a high cost of movement in my connectivity model since it is a two-lane highway and is closed during the snowy months between Newhalem (on the west side of the crest) and six miles west of Mazama. However, lynx have commonly been killed by vehicles in other areas of their range (Devineau et al. 2010) and there is risk for lynx of vehicle collision, especially in likely connectivity areas of the Methow Valley between Mazama and Big Valley Ranch. Signs indicating wildlife crossing could help mitigate the risk of road kills along this stretch of highway (**Figure 4.11**).

In a landscape continually impacted by a growing human presence and increasing wildfires, identifying and conserving areas that facilitate lynx movement will help to ensure that dispersing lynx reach new home ranges, find mates, escape degraded habitats, and exchange genes. My study is the first model of meso-scale connectivity in the North Cascades to be built using animal GPS data and, importantly, incorporates lynx response to burned areas, an aspect of lynx habitat use that has previously received little attention. My model provides an overview of core lynx habitat and where important linkages may exist, lending land managers a guide for focusing future work that validates and prioritizes lynx habitat linkages in the North Cascades.

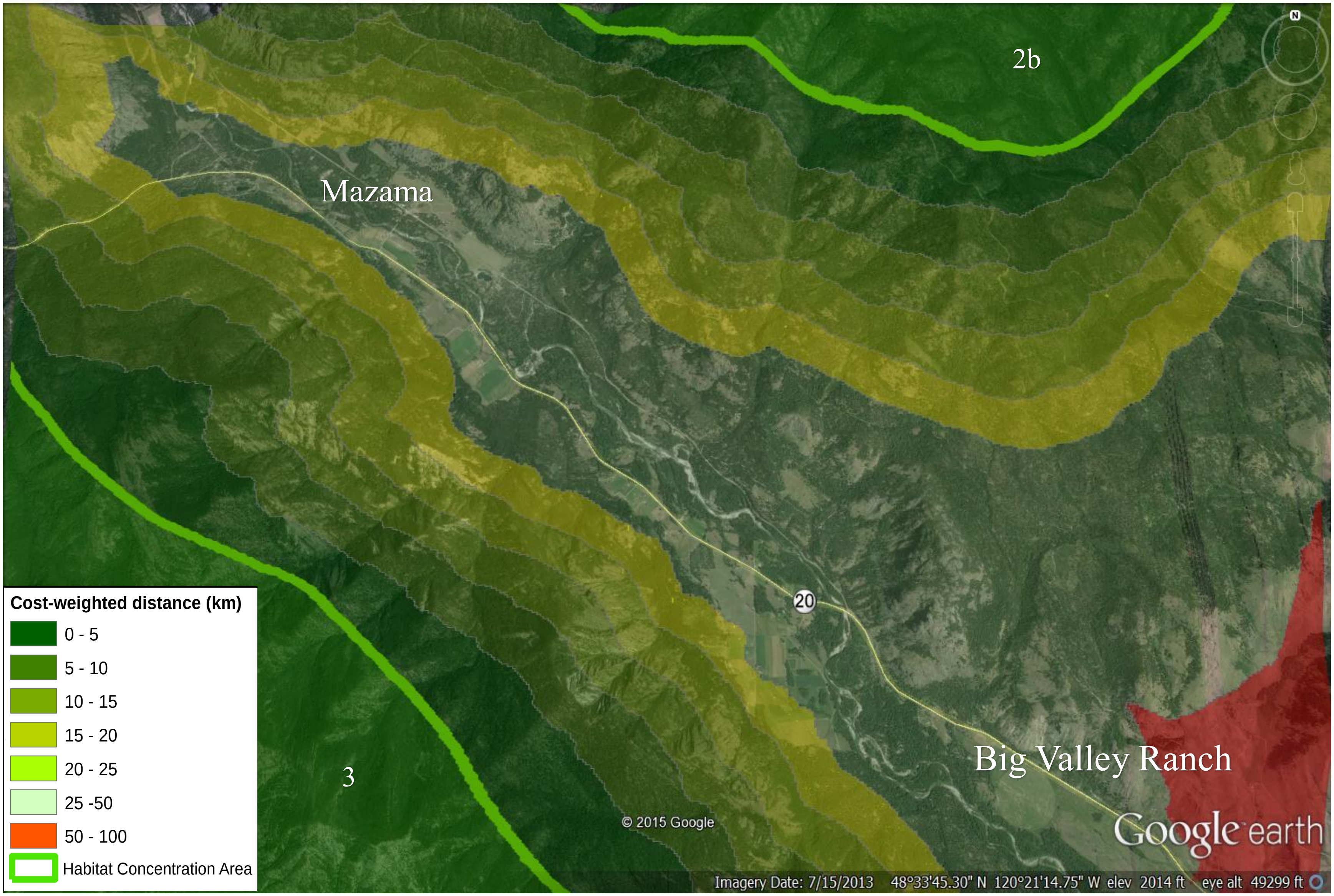

2b
Mazama
20
3
Big Valley Ranch
© 2015 Google
Google earth
Imagery Date: 7/15/2013 48°33'45.30" N 120°21'14.75" W elev 2014 ft eye alt 49299 ft
Cost-weighted distance (km)
0 - 5
5 - 10
10 - 15
15 - 20
20 - 25
25 -50
50 - 100
Habitat Concentration Area

Figure 4.11. Forested areas between Mazama and Big Valley Ranch support connectivity for lynx crossing the Methow Valley. Cost-weighted distance values expanding outward from Habitat Concentration Areas 2b and 3 are overlaid onto a Google Earth image (Google Earth 2013).

CHAPTER 5
CONCLUSIONS

5.1 OVERVIEW

Lynx (*Lynx canadensis*) in the North Cascade Mountains of Washington comprise one of the few remaining populations living at their southern range boundary in the contiguous US (McKelvey et al. 2000b). Lynx at the southern limit of their range survive in patchy habitat, fragmented by topography, unsuitable land cover types, human disturbances, and natural disturbances such as wildfires (Buskirk et al. 2000b, McKelvey et al. 2000b). Comparatively poor habitat and greater human impact on the landscape have resulted in southern lynx populations that are smaller and more vulnerable than those in the range core of Canada and Alaska, where relatively contiguous expanses of boreal forest occur. Indeed, lynx in the contiguous US were listed as Threatened in 2000 (US Fish and Wildlife Service 2000, McKelvey et al. 2000b). Compounding the current fragmentation of southern lynx habitat, climate change is projected to increase the size, frequency, and intensity of wildfires (Westerling et al. 2006, Fauria and Johnson 2007, Soja et al. 2007, Balshi 2009, Littell et al. 2010). An altered forest fire regime could increase the amount of forest in the open stand-initiation stage lynx and snowshoe hares avoid, jeopardizing the future of southern lynx. (Westerling et al. 2006, Fauria and Johnson 2007, Soja et al. 2007, Balshi 2009, Littell et al. 2010).

Given the unique and tenuous habitat conditions southern lynx face, a detailed understanding of how they respond to fire and to fragmented habitat is important for managing and conserving southern lynx. In addition, identifying and protecting areas that support connectivity between habitat patches can reduce the negative effects of habitat fragmentation. The information presented in this thesis details lynx habitat use in the North Cascades, and includes a detailed analysis of lynx response to burned areas. My work thus fills important knowledge gaps regarding habitat use in a heterogeneous landscape comprised of various forests habitats, natural disturbances, forest openings, and human-induced impacts. My work also includes a connectivity model for lynx in the North Cascades that provides maps of linkages between important lynx habitat patches.

5.2 HABITAT SELECTION

In general, southern lynx select sub-boreal forest with dense understory cover and they avoid open areas. Within this broad framework, the tree species that comprise sub-boreal forests vary, as do the disturbance histories that create the dense understories characteristic of many habitats that lynx select. Indeed, I found that in the North Cascades there was some variation in lynx habitat selection between the Black Pine Basin and Loomis study areas.

In the Black Pine Basin study area, spruce (*Picea engelmannii*)-fir (*Abies lasiocarpa*) forests are common, as are mixed forests comprised of typical sub-boreal species and the dry forest species, Douglas fir (*Pseudotsuga menziesii*). Lynx in this area took advantage of the local abundance of these forest types and selected them as core habitat. However, lodgepole pine (*Pinus contorta*) forests are rare in the Black Pine Basin study area, and lynx did not select them. This result contrasts with studies elsewhere where lodgepole is much more common and lynx select this forest cover in those landscapes (Aubry et al. 2000). Conversely, in the Loomis study area, lodgepole pine forests are common and lynx selected them in addition to spruce-fir forests. Mixed forests are less common on the Loomis study area and did not significantly contribute to core lynx habitat. These results confirm prior work that lynx in the North Cascades use both lodgepole pine and spruce-fir forests as core habitat (Koehler 1990, Koehler et al. 2008, Maletzke et al. 2008). In addition, I documented lynx habitat selection to include mixed forest types where they are abundant. My results also point to somewhat more flexible habitat selection patterns than might be assumed for a species often considered a habitat specialist (Peers et al. 2012).

Because core, sub-boreal forest habitats are fragmented in the North Cascades, lynx must travel through matrix (areas between core habitats) to reach patches of resources. I created a specific Travel Habitat Model to discover what landscape conditions facilitate lynx movement through the matrix. This Travel Habitat Model revealed details of lynx habitat selection that a generalized model of habitat selection for lynx could not have, since animals often select different habitats for different activities (Roever et al. 2014). For example, lynx use the best sub-boreal forest habitats as core habitat for activities such as hunting and resting, but as my results revealed, they use additional habitats for traveling. Specifically, the results of my Travel Habitat Model indicate that although lynx will use open areas such as new burns and steep slopes when traveling, lynx preferred to travel through areas of the matrix with habitats more similar to those they selected in core habitats, namely features that provided cover. Recognizing that lynx tolerate a wider range of habitats for traveling than for core habitats allowed me to better define travel habitat for lynx in the North Cascades. This result is particularly important because it provides managers with information needed to retain landscape features that facilitate the movement of lynx and provide for habitat connectivity between high quality areas.

The boreal forest is characterized in large part by dramatic and frequent wildfires that create a heterogeneous mosaic of successional stages (Agee 2000, Perera and Buse 2014). Wildfires burn millions of hectares every year in the boreal forest (Perera and Buse 2014), and thus play an important role in shaping lynx habitat. However, prior to my research few studies specifically examined lynx response to burned areas, and the dominant model explained only that lynx do not use new burns and that lynx select young regenerating forests in old burns. My fire models paint a more nuanced picture of lynx response to burns. For example, lynx in my study did generally avoid the 2006 Tripod Burn (1-6 years old at the time of this study) when selecting core habitat, however, they also made use of residual live-tree cover in low-severity burn areas and in fire skips. Indeed, a particularly large fire skip supported core lynx habitat that one lynx incorporated into his home range. My results highlight the importance of residual live-tree cover, especially fire skips, for providing lynx with travel habitat and for patches of core hunting habitat.

Within the 1994 Whiteface Burn (nearly 20 years old at the time of study), lynx selected young, regenerating forests. However, the type of forest lynx selected was surprising; lynx selected dry forests, a forest type usually avoided by lynx when selecting core habitats. A field examination of the Whiteface Burn explained this unexpected habitat selection by lynx. Dry forest regeneration in the Whiteface Burn was heavily intermixed with deciduous tree species, especially in moister areas, which provided a dense understory. On the other hand, spruce-fir regeneration in the Whiteface Burn was short and sparse, providing little understory cover. This contrast illustrates two important points: understory cover may be a more important factor in lynx habitat selection than forest type, and moist microclimates conducive to abundant plant growth provide lynx habitat in old burns while microclimates that are not conducive to plant growth create poor habitat. By creating habitat models that specifically examine habitat use within old and new burns, my results expand and refine our understanding of lynx habitat selection following wildfires. My results are noteworthy in documenting the conditions that enable some of the earliest re-use of burned areas on record for lynx.

5.3 HABITAT CONNECTIVITY

Combating the effects of habitat fragmentation is an important element to successful conservation of southern lynx. Habitat fragmentation can impede animals dispersing to a new home range or seeking mates and resources (Wilcox and Murphy 1985, Fischer and Lindenmayer 2007). Inbreeding depression can result if fragmentation separates populations so that they become genetically isolated (Frankham 2006). Increased fragmentation can also prevent the repopulation of isolated habitat patches within a metapopulation (Hanski 1998), and inhibit the rescue of sink populations from decline and extinction (Pulliam 1988).

Connectivity conservation has emerged as a popular strategy for mitigating the effects of fragmentation (Crooks and Sanjayan 2006, Ewers and Didham 2006), and can help conserve southern lynx facing habitat fragmentation. This tool is most meaningful when based on location or movement data used to parameterize habitat models that explicitly define the habitats a species uses to travel. I modeled habitat connectivity for lynx in the North Cascades based on travel habitat selection derived from radio-collar location data. The assessment highlighted areas of low connectivity for lynx, which primarily exist in low elevation, open, and developed valley bottoms, and where new fires burned at high severity over large tracts of forest. The maps also indicate where within the areas of low connectivity the best habitat linkages exist. Because the only known population of North Cascades lynx resides in the northernmost portion of my North Cascades study area, connectivity maps of this area are of immediate importance to land managers. My maps indicate that the Tripod Burn and the southern portion of the Methow Valley present high resistance to lynx movement. In contrast, my maps also indicate that residual stands of trees and fire skips in the Tripod Burn support linkages, and that forest cover near Mazama and the Big Valley Ranch areas of the Methow Valley provide connectivity for lynx.

5.4 MANAGEMENT IMPLICATIONS

Although forest fires cause a temporary loss of core lynx habitat, managers should not consider new burns as unusable by lynx. Residual trees should be protected, especially fire skips, and salvage logging should be discouraged since standing dead trees promote growing conditions for regenerating vegetation, allowing burned areas to recover more quickly (Brassard and Chen 2006). As time since fire increases, burned areas with cool and moist microclimates may recover quickly and provide the best lynx habitat. These areas are important for lynx conservation.

When designing timber harvest activities in lynx habitat, managers should strive to mimic the characteristics of natural disturbances, such as burns, that lynx use. To mimic burns, managers should leave islands of uncut forest that emulate fire skips, retain some standing trees to provide cover for lynx traveling to forest islands or across cuts, and design harvest units with a high edge-to-area ratio. Practices that encourage tree regeneration post-harvest would help to return harvested areas to core lynx habitat more quickly.

In addition, managers could design harvest units and prescribe burns to act as fire breaks. Fire breaks would decrease the spread and intensity of fires and help to retain residual trees and fire skips, thus combating the homogenizing effect climate change may have on future landscapes.

Most human development in the North Cascades occurs in low-elevation valley bottoms and not in sub-boreal core lynx habitat. However, lynx depend on travel habitat through valley bottoms to move between core areas, necessitating the conservation or restoration of these cross-valley linkages. Developments that decrease forest cover should be minimized within linkages and traffic signs indicating wildlife crossing may help mitigate the risk of road kills.

As the effects of climate change mount and wildfires increase in size, frequency, and number, southern lynx habitat will suffer. It is important that we protect the full breadth of core lynx habitats from human disturbances so as not to compound losses due to increasing fire disturbances. In addition to a temporary loss of core habitat, more frequent fires will increase fragmentation, thus heightening the importance of habitat linkages to preserve connectivity. Finally, lynx movements will increase with more frequent burning since immediately post-fire, displaced lynx must find new home ranges.

My conclusion that lynx habitat selection is flexible and adaptable to current levels of fragmentation provides hope for the future of southern lynx. However, as the effects of human population growth and climate change accelerate and areas of high-quality lynx habitat are increasingly fragmented and degraded, it is paramount that we manage the complete array of core and travel lynx habitats. Only then will lynx at the southern range edge continue to make the most of their fragmented and heterogeneous landscapes.

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APPENDICES

APPENDIX A: Stand Succession Terminology

The terminology used to describe the forest conditions post-disturbance that lynx select or avoid varies throughout the literature. Here, I detail the terminology I use to describe the post-disturbance forest conditions applicable to lynx and snowshoe hare habitat.

Forest Structure: the structure of a forest characterized by its physical attributes such as tree density, number of layers, height, average diameter at breast height, or canopy cover (Hall et al. 1995).

Stand Development: The different stages of forest structure a stand undergoes with time since a disturbance. Stand development is not synonymous with the succession of seral stages, which describes the changing patterns of plant species with time since disturbance (Hall et al. 1995)

Lynx and snowshoe hares are more dependent on forest structure than on forest species composition (Koehler 1990, Hodges et al. 2000b). For this reason, I will primarily refer to the changes a forest goes through post-disturbance in terms of stand development. I have created four stages of stand development based on categories created by Oliver and Larsen (1990) but modified to capture important characteristics of lynx and snowshoe hare habitat.

1. **Open Stand Initiation**: This stage is based on the Stand-Initiation category described by Oliver and Larsen (1990). While Oliver and Larsen include both the earliest stages of regeneration where seedlings are very small and later when seedlings develop into taller trees, I will divide their category in two. The open stand initiation stage describes only the earliest regeneration of a forest when seedlings and

shrubs are not thick or tall enough to provide adequate cover for snowshoe hares, especially during the snowy months, and is thus poor lynx habitat. von Kienast (2003) and Koehler et al. (2008) both observed lynx avoiding this stage where it was present on burns ten or less years-old.

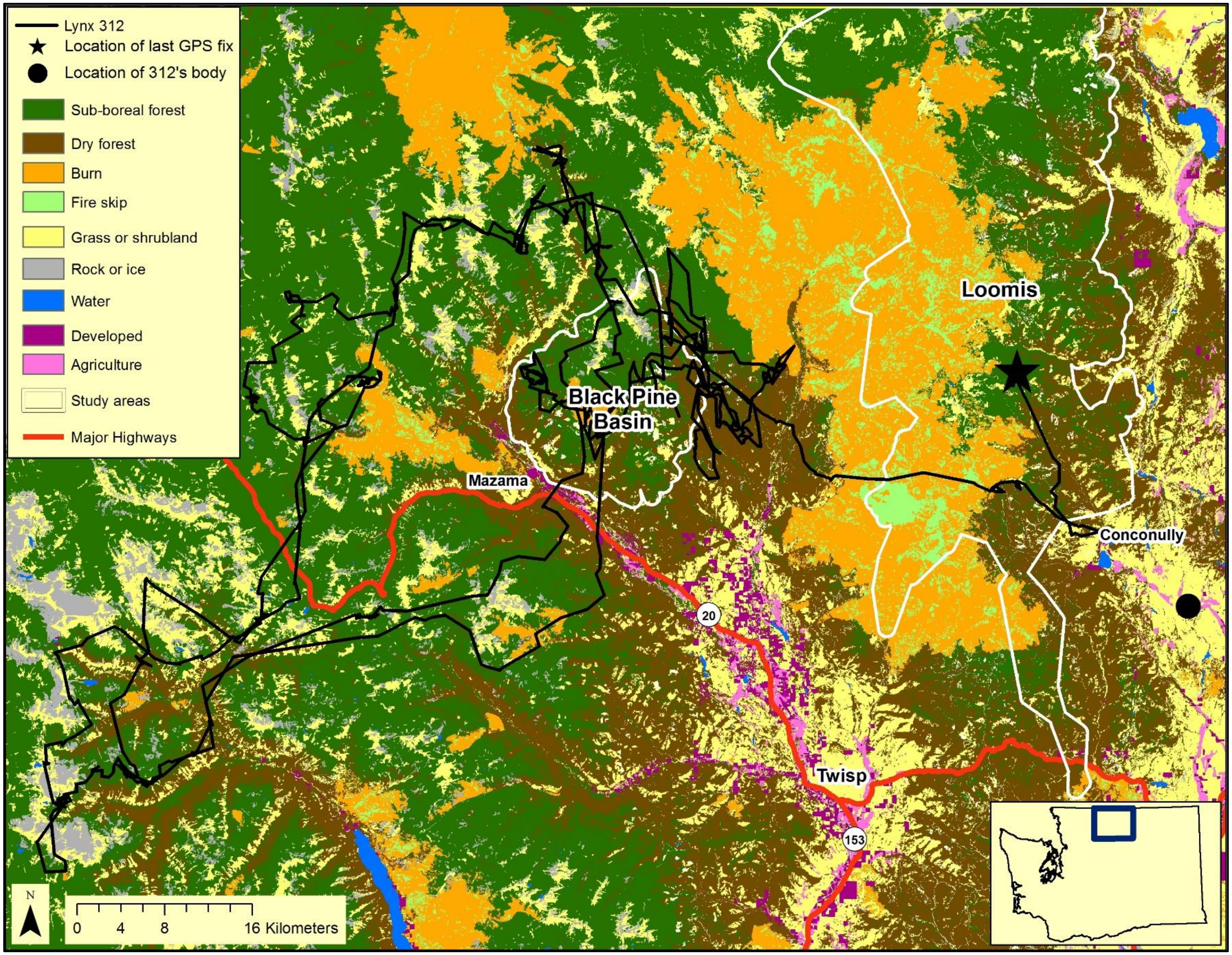
2. **Early Stand Development**: This stage describes the more advanced end of Oliver and Larsen's (1990) Stand-Initiation category. I describe the early stand development stage as any forest stand that has regenerated to the point where trees and shrubs are tall and dense enough to provide cover and brows for snowshoe hares year-round, and thus hunting habitat for lynx. The plant species creating this stage in the North Cascades are often a mix of deciduous and coniferous trees on moister sites or lodgepole pine (*Pinus contorta*) trees on drier sites. Koehler et al. (1990) described lynx and snowshoe hares selecting this stand development stage where it was present on 20 year-old lodgepole pine sites.

3. **Late Stand Development**: This stage is based on Oliver and Larsen's (1990) Stem Exclusion stage. I describe this stage as having a very open understory. Competition causes the trees to self-thin and lower branches to thin. A closed canopy prevents shade-intolerant species from growing in the understory. With an absence of cover and brows in the understory, snowshoe hares and lynx avoid this stand development stage. Koehler (1990) found snowshoe hares and lynx avoid forest stands in this development stage found in lodgepole pine stands over 43 years old.

4. **Old-growth**: To create the old-growth category, I combined Oliver and Larsen's (1990) Understory Re-Initiation and Old-Growth stages. I describe this forest structure as having developed a multi-layered structure. Canopy gaps allow

understory trees and shrubs to grow, while long branches reach the ground and contribute to the understory cover. Forest stands that reach this stage provide the cover and brows snowshoe hares and thus lynx select. Koehler et al. (2008) found lynx selected for multi-layered Engelmann spruce- (*Picea engelmannii*) subalpine fir (*Abies lasiocarpa*) forests in the North Cascades, although a stand age was not reported.

APPENDIX B: Male 312's Movement Path



Lynx 312
Location of last GPS fix
Location of 312's body
Sub-boreal forest
Dry forest
Burn
Fire skip
Grass or shrubland
Rock or ice
Water
Developed
Agriculture
Study areas
Major Highways
Loomis
Black Pine Basin
Mazama
Conconully
20
Twisp
153
N
0 4 8 16 Kilometers

Figure B.1. Male 312's movement pathway in the North Cascades. Male 312's GPS collar died and thus stopped collecting locations while he was within the Loomis study area. His body was found outside of the Loomis study area near Conconully, Washington.

APPENDIX C:GIS Layer Information

C.1 Roads

Layer: TIGER/Line Shapefile, 2012, State, Washington, Primary and Secondary Roads State-based Shapefile
Source: U.S. Department of Commerce, U.S. Census Bureau, Geography Division.
Format: Vector digital data.
Date of Publication: 2012.
Source Scale: Unavailable.
Web Link: http://www2.census.gov/geo/tiger/TIGER2012/PRISECROADS/tl_2012_53_prisecroads.zip

I converted the TIGER Line shapefile into a 30 m raster and assigned each pixel in the raster a value indicating its distance (measured in meters) to the nearest road. I then categorized each pixel as within 0, 50, 100, 250, 500, or 1,000 meters from the nearest road, or > 1,000 meters from the nearest road.

C.2 Human Development

Layer: Landuse10.
Source: Washington Department of Ecology Geographic Information System (GIS) Technical Services.
Format: Vector digital data.
Date of Publication: 10/01/2010. Updated as needed.
Source Scale: Unavailable.
Web Link: http://www.ecy.wa.gov/services/gis/data/data.htm

The Landuse10 layer depicts tax parcel land use as defined by Department of Revenue two digit land use codes or by the Ecology GIS staff. I used the attribute DESCR to eliminate any relatively undeveloped lands including agricultural lands, roads and railroads, designated forest land, mining activities, utilities, parks, and timberland (12,835 parcels eliminated). The remaining parcels (13,516) mostly had buildings on them. I then converted this polygon layer to a raster and assigned each pixel in the layer a value of distance (measured in meters) to the nearest developed area.

C.3 Disturbance

Layer: LandTrendr.
Source: Laboratory for Applications of Remote Sensing in Ecology, Oregon State University, and the Pacific Northwest Research Station.
Format: Raster data.
Pixel Size: 30 meters.
Date of Publication: In the process of being updated as of 2011. Unpublished.
Source Scale: Unavailable.
Web link: http://landtrendr.forestry.oregonstate.edu/

Layer: S_R06.FireHistoryPL
Source: Data Resource Management/Fire and Aviation, Pacific Northwest Region, US Forest Service.
Format: Vector digital data.
Date of Publication: 06/24/2009. Updated annually.
Source Scale: 1: 24000
Web Link: http://www.fs.fed.us/r6/data-library/gis/okanogan/index.shtml

Layer: baselayer.BL_VECTOR.US_HIST_FIRE_PERIMTRS_DD83_NEW
Source: Geospatial Multi-Agency Coordination Group.
Format: Vector digital data.
Date of Publication: Unknown. Last updated in 2011.
Source Scale: Unavailable.
Web Link: http://www.geomac.gov/

Layer: Wa_historical_fires_1973_2012
Source: Washington Department of Natural Resources, USDA Forest Service, and the Bureau of Land Management.
Format: Vector digital data.
Date of Publication: Unknown. Last updated 2013.
Source Scale: Unavailable.
Web Link: Unavailable.

Layer: FACTS.
Source: Forest Service, U.S. Department of Agriculture.
Format: Vector digital data.
Date of Publication: 2009, updated regularly.
Source Scale: Unavailable.
Web Link: Unavailable.

Layer: FP_GIS_FPA_ (Forest Practice Application)
Source: Washington Department of Natural Resources, Forest Practices Division.
Format: Vector digital data.
Date of Publication: Unpublished.
Source Scale: 1: 1000
Web Link: http://fortress.wa.gov/dnr/app1/dataweb/dmmatrix.html

Layer: ROPA.TS_FMA_ALL_SV (Sold_completed_harvest).
Source: Washington State Department of Natural Resources, Product Sales and Leasing.
Format: Vector digital data.
Date of Publication: Unknown. Updated weekly.
Source Scale: Unavailable.
Web Link: Unavailable.

LandTrendr has developed a raster dataset of disturbance in the Pacific Northwest US from 1985 through 2012. LandTrendr's three-band layer depicts the year of disturbance detection, the severity of disturbance (modeled as the percent of canopy cover loss) and the duration of disturbance. Open water, barren, rocky, and ephemeral snow conditions are sometimes mistaken for disturbances in LandTrendr data. To "clean" the LandTrender data, I used the LEMMA land cover attribute data to identify and extract pixels potentially misclassified as disturbed in the LandTrendr data. As a result, 1% of the pixels classified as disturbed were removed.

C.3.1 Fire

The LandTrendr data does not distinguish between types of disturbance. To separate out disturbances caused by wildfires, I used three historical fire perimeter GIS layers. One layer was developed by the US Forest Service and depicts fires that burned on Forest Service land prior to 2009. To identify other land ownerships and fires on Forest Service land since 2009, I used a data layer created by the Geospatial Multi-Agency Coordination Group (GeoMAC), which covers large US fires from 2000 to the present. To include non-Forest

Service land fires before 2000 I used the Washington historical fires data created by the Washington Department of Natural Resources.

I merged all three fire data layers together, including only fires that burned after 1984. I then used the merged fire perimeter layer to extract disturbed areas from the "cleaned" LandTrendr raster layers depicting severity of disturbance and the year the disturbance was detected. While some disturbed pixel extracted by the fire perimeter layer may actually have been disturbed by other factors such as wind, or beetle kill, I made the assumption that most areas within the fire perimeters and depicted by LandTrendr as disturbed were burned. As a result, I had one raster layer depicting the year of the fire and one depicting the severity of the fire.

I categorized the fire year layer into old fires (1985-1997) or new fires (1998-2012). The fire severity layer was categorized into low severity (canopy cover loss of 0-50%), or high severity (canopy cover loss of 51-100%). I also designated any unburned pixels as fire skips if they were surrounded by an area that had burned. Many of these fire skips are areas of forest that did not burn in the fire, often because they had been harvested or burned relatively recently. Other fire skips did not burn because they were not forested. These categorical fire year and fire severity layers were then merged into a single layer depicting each burned area as an old, low- severity burn, an old, high- severity burn, a new, low-severity burn, a new, high- severity burn, or a fire skip.

To convert the categorical fire harvest data into continuous data for the habitat analysis I extracted each disturbance category and made a binary layer for each one. A moving window was then applied to each binary layer to determine for every focal pixel the number of other like pixels within a 3x3 and 27x27 pixel window.

C.3.2 Timber Harvest

I used a process similar to the fire layers to create the timber harvest layers. I used several polygon layers of timber harvest history to extract timber harvest disturbances from the “cleaned” LandTrendr data. For Forest Service land, I used the FACTS data layer, which reliably identifies timber harvest units from 1996 forward, but less accurately identifies cuts made before 1996. For Department of Natural Resources land, I used the Forest Service Application and Sold and Completed Harvest layers. Through an examination in Google Earth I found that both the FACTS and Forest Service Application and Sold and Completed Harvest layers missed many harvest units or misrepresented their true shape. To improve the accuracy of the GIS layers, I used Google Earth to trace 1,278 missing or misshapen harvest units. Although clearcuts were easily observed in Google Earth, some thinned harvests may have been difficult to see and thus were not included in my hand-drawn harvest layer.

I merged the FACTS, Forest Service Application and Sold and Completed Harvest, and hand-drawn layers together into a single timber harvest polygon layer. The timber harvest polygon layer was then buffered by 50 m to allow for inaccuracies in the harvest boundaries. Next I used the merged harvest layer to extract the severity of disturbance data and the year of disturbance data from the LandTrendr dataset. Although some harvest units may have been missed by the timber harvest polygon layer and thus not included in the final raster layers, the LandTrendr data corrects for many inaccurate harvest unit shapes and for units included in the Forest Service and Department of Natural Resources harvest layers that were never actually cut.

I categorized the harvest year layer into old harvests (1985-1997) or new harvests (1998-2012). The harvest severity layer was categorized into thinned units (canopy cover loss of 0-50%), or clearcut units (canopy cover loss of 51-100%). These categorical harvest year and severity layers were then merged into a single layer depicting each harvested area as an old thin, an old clearcut, a new thin, or a new clearcut.

I erased any harvested pixels that the fire raster layer indicated as burned. Erasing harvested pixels ensured that harvested units that later burned were classified only as burned. Erasing harvest units that fell in a burned area also meant that any post-fire salvage-harvest units were classified only as burned.

To convert the categorical timber harvest data into continuous data for the habitat analysis I extracted each disturbance category and made a binary layer for each one. A moving window was then applied to each binary layer to determine for every focal pixel the number of other like pixels within a 3x3 and 27x27 pixel window.

C.4 Land Cover

Layer: GNN Species Size.
Source: Landscape Ecology, Modeling, Mapping and Analysis (LEMMA).
Format: Raster data.
Pixel Size: 30 meters.
Date of Publication: 2014.
Source Scale: Unavailable.
Web Link: http://lemma.forestry.oregonstate.edu/data/structure-maps

Layer: US Geological Survey, Gap Analysis Program (GAP). May 2011. National Land Cover, Version 2
Source: Northwest Gap Analysis Project.
Format: Raster data.
Pixel Size: 30 meters.
Date of Publication: June 2009.
Source Scale: Unavailable.
Web Link: http://gap.uidaho.edu/index.php/nw-gap/land-cover

The LEMMA layer is a raster dataset with a large attribute table so that each pixel represents many different habitat variables depicting forest tree species and structure. For non-forested areas, the layer creators assigned land cover types to each pixel using the Ecological Systems map developed for the US Geological Survey Gap Analysis Program. Satellite imagery from the year 2012 was used to create the LEMMA data layer.

The LEMMA data attribute FORTYPBA classifies forests into 40 types based on the dominant tree species. I reclassified the LEMMA data into six forest types and classified each side of the North Cascades crest slightly differently. West of the crest, forests were simply classified into either west-side sub-boreal forest or other forest. For forests east of the crest I classified forests to capture the general pattern of cool, moist sub-boreal forests (characterized by lodgepole pine [*Pinus contorta*], Engelmann spruce [*Picea engelmannii*], and subalpine fir [*Abies lasiocarpa*]), warmer, dry forests (characterized by Douglas fir [*Pseudotsuga menziesii*] and ponderosa pine [*Pinus ponderosa*]), and forests transitioning between the sub-boreal and dry forests (characterized by a mix of both sub-boreal tree species and dry forest tree species). Specifically, I reclassified forests east of the Cascade crest as west-side sub-boreal forests, lodgepole pine forest, Engelmann spruce-subalpine fir forest (referred to as spruce-fir), mixed sub-boreal forests and dry forests (referred to as mixed forest), dry forests, and forests dominated by deciduous trees.

Next, I used the ecological systems description attribute (ESLF_NAME) to reclassify non-forested areas as grassland, shrub land, rock or ice, open water, or agricultural areas. However, the LEMMA data incorrectly classified some non-forested areas as forested. I drew 621 missing forest openings and classified their cover type based on visually identifying their land cover in Google Earth as rock or ice, grassland, or shrub land. After converting my drawn forest openings to a raster dataset I incorporated the raster into the LEMMA land cover data.

The LEMMA data also misidentified some areas as grassland or shrub lands that were indicated by my timber harvest layer as harvested forest. Harvested forests misidentified as non-forest types (12% of the harvested forests) were reclassified as disturbed since I had no way to identify the species composition of the regenerating forest.

Areas with a canopy cover of less than 10% were not assigned a land cover value in the LEMMA data and were labeled REMNANT (6.5% of the North Cascades study area) For REMNANT pixels I used the GAP Analysis land cover data to assign these areas of low canopy cover a forest type or land cover type. I reclassified GAP Analysis land cover categories into the same land cover types used to reclassify the LEMMA data. Some of the REMNANT pixels were classified as disturbed by the GAP Analysis pixels. I reclassified the GAP Analysis disturbed categories as follows.

1. Harvested forest regenerating as trees, shrubs, or grass: I classified these areas as disturbed since there was no way of knowing the forest type.

2. Recently burned grassland or shrub land: I reclassified these areas as grassland or shrub land accordingly since the structure of a grassy or shrubby area is not significantly changed by fire and regeneration time is relatively short.

3. Recently burned forest: Most of these pixels were in high-elevation areas and interspersed with lodgepole pine forests. Lodgepole pine is an early succession species likely to be regenerating post-fire, and thus I reclassified recently-burned pixels as lodgepole pine. However, one small area of burn in the southern portion of the North Cascades study area was interspersed with areas of Douglas fir forest as well as lodgepole pine forest, making the reclassification of this area as lodgepole pine less certain.

I now had a categorical land cover layer in which each pixel was classified either by a forest type (six categories), or non-forested land cover type (five categories). All remaining pixels were those identified by the GAP Analysis data as either roads or developed areas (lumped into a single category called developed), or as an undefined disturbance. To convert this categorical land cover data into continuous data for the habitat analysis, I extracted each land cover type to be included in the analysis and made a binary layer for each. A moving window was then applied to each binary layer to determine for every focal pixel the number of other like pixels within a 3x3 and 27x27 pixel window. I did not make a continuous data layer for developed areas since these land covers are represented in the Roads layer and the Human Development layer.

C.5 Canopy Cover

Layer: GNN Species Size, Region 222, 221, and 1.
Source: Landscape Ecology, Modeling, Mapping and Analysis (LEMMA).
Format: Raster data.
Pixel Size: 30 meters.
Date of Publication: 2010. Updated as needed.
Source Scale: Unavailable.
Web Link: http://lemma.forestry.oregonstate.edu/data/structure-maps

I used the LEMMA GIS data to create the canopy cover layer. I used the attribute CANCOV to represent each forested pixel on the study area according to its percent canopy cover. I also used a moving window analysis to determine the average percent canopy cover within a 3x3 and 27x27 pixel window.

C.6 Topography and Climate

Layer: National Elevation Dataset.
Source: US Geological Survey.
Format: Raster data.
Pixel Size: 30 meters.
Date of Publication: 2011.
Source Scale: Unavailable.
Web Link: http://nationalmap.gov

Layer: Growing Season Precipitation, April to September.
Source: Moscow Forestry Sciences Laboratory, Nicholas Crookston and Gerald Rehfeldt.
Format: Raster data.
Pixel Size: 1,000 meters.
Date of Publication: Unpublished
Source Scale: Unavailable.
Web Link: http://forest.moscowfsl.wsu.edu/climate/current/

I used the US Geological Survey 30 m National Elevation Dataset to develop layers depicting slope. I also applied the ArcGIS Flow Accumulation tool to the US Geological Survey 30 m National Elevation Dataset to create a polyline layer depicting draws with a flow accumulation value greater than or equal to 500. I then converted the draw layer into raster formats and assigned each pixel a value indicating its distance to the nearest draw.

To create layers of Compound Topographic Index (Moore et al. 1993, Gessler et al. 1995) and Heat Load Index (McCune and Keon 2002), I used the Geomorphometry and Gradient Metrics tools developed by Evans (2011).

The climate data depicting total growing season precipitation were originally formatted with 1,000 meter pixels. Using program R (2.15.3), I reduced the pixel size to 30 meters using the elevation dataset to adjust the value of each new 30 meter pixel.

I used a moving window analysis to determine the average Compound Topographic Index and Heat Load Index values, and the average growing season precipitation within a 3x3 and 27x27 pixel window.

C.7 Patch Metrics

Three types of non-forested area were characterized by the patch metrics area and distance from edge. From my categorical land cover layer, I extracted all areas with a land cover of grassland, shrub land, agriculture, or developed. To prevent roads from dividing a forest opening into more than one patch, I reclassified developed pixels based on the values of the neighboring pixels. This reclassification eliminated most roads. I used FragStats 4.1 (McGarigal et al. 2012), to assign area values to each patch of forest opening and assigned each pixel within a forest opening the distance to the nearest edge of the opening, including forest edges created by forest patches within an opening (measured in meters). To examine patch metrics for harvested areas, I used FragStats 4.1 (McGarigal et al. 2012) to calculate the area of each harvest unit and the distance (meters) to edge was measured for each pixel within a harvest unit. Similarly, I calculated the distance from every pixel within a burn to the nearest edge of the burn. However, I did not calculate the area of each burn since the Tripod Burn, located partially in the Loomis study area, and the Whiteface Burn in the Black Pine Basin study area were the only significant burns included in the habitat model, making an analysis of burn area questionable.

APPENDIX D:Seasonal and Sex-Specific Core Habitat models

D.1 Results

The tests for multivariate redundancy identified and removed the variable depicting growing season precipitation within a small-scale area from the seasonal and sex-specific core habitat models. In addition, I removed several collinear variables from each of these model based on results of the Spearman-rank test (**Table D.1**).

The Summer, Winter, Male, and Female, Core Habitat models all demonstrated high model fit with out-of-bag error rates less than 30% and good model performance with accuracy values above 75%. Each of the models had somewhat higher sensitivity rates than specificity rates and each model was significant at $P<0.05$ (**Table D.2**).

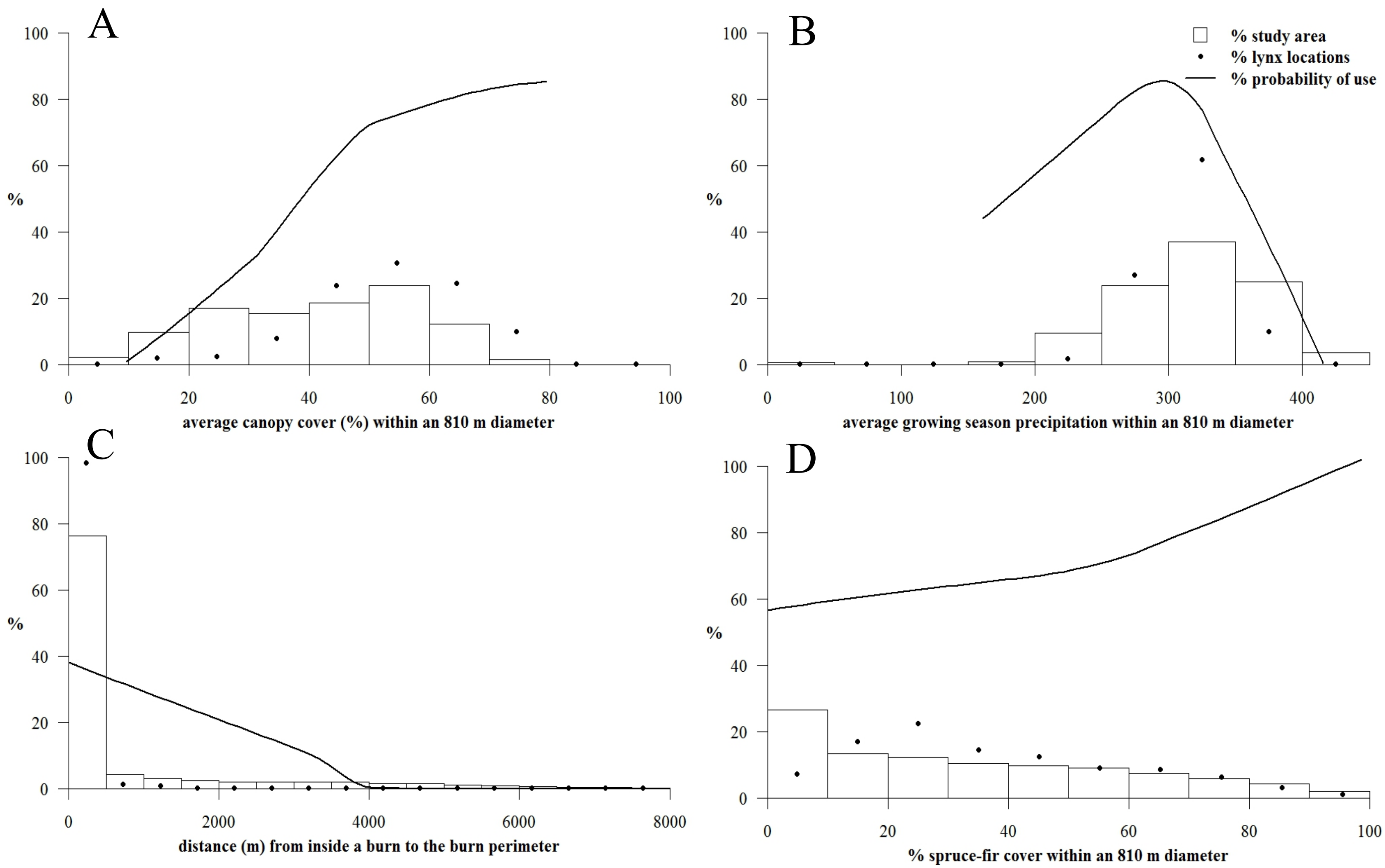
Table D.1. Collinear variable pairs as determined by Spearman rank tests (r>0.8). Variable descriptions are given in Table 2.2. The decision to retain one variable over another was based on the importance value of each variable as indicated by an initial Random Forest run using all variables; the more important variable was retained. In the case of collinear variables with very similar importance values, I retained the variable of higher ecological interest or one that added variety to the suite of variables tested in my models. Numbers after the variable name identify it as being portrayed at a large-scale (27x27 pixel area) or small-scale (3x3 pixel area).

Summer Core Habitat Model		**Winter Habitat Model**		**Females Habitat Model**		**Males Habitat Model**	
retained	eliminated	retained	eliminated	retained	eliminated	retained	eliminated
distedge_cut	area_cut	distedge_cut	area_cut	distedge_cut	area_cut	distedge_cut	area_cut
distedge_fo	area_fo	distedge_fo	area_fo	distedge_fo	area_fo	distedge_fo	area_fo
distedge_fire	fireskips27	distedge_fire	fireskip27	distedge_fire	fireskips27	distedge_fire	fireskips27
newhigh_f27	fireskips27					newhigh_f27	fireskips27
						newlow_f27	fireskips27
newhigh_f27	newlow_f27	newhigh_f27	newlow_f27	newhigh_f27	newlow_f27	newhigh_f27	newlow_f27
oldhigh_f27	oldlow_f27	oldhigh_f27	oldlow_f27				
						oldlow_f27	oldhigh_f27
new_cut27	new_thin27	new_cut27	new_thin27				
						new_thin27	new_cut27
old_cut27	old_thin27	old_cut27	old_thin27				
				old_thin27	old_cut27	old_thin27	old_cut27
				gsp27	dry27	gsp27	dry27
				gsp3	dry27	gsp3	dry27
hli27	hli3			hli27	hli3	hli27	hli3
				slope27	slope3		

Table D.2. Model validation and fit statistics for the Summer, Winter, Male, and Female Core Habitat models. Accuracy (%) indicates the overall performance of the model when predicting the withheld, validation dataset. Sensitivity and specificity show the proportion of used locations correctly predicted and the proportion of available locations correctly predicted. Area under the curve of a Receiver Operator Characteristic (AUC) scores are a measure of how evenly the model predicts sensitivity and specificity. The Kappa (k) statistic is a measure of how much better the model predicted used and available points than expected by random chance. P values indicate significance of each model and out-of-bag error rates (%) show the mean misclassification rate of trees when predicting the out-of-bag data.

Model Validation Statistics							Model Fit
Model	Accuracy (%)	Sensitivity	Specificity	*k*	AUC	*P* value	Out-of-bag error rate (%)
Summer	75.55	0.7955	0.725	0.5109	0.7555	$P < 0.001$	29.28
Winter	77.73	0.8355	0.7364	0.5546	0.7773	$P < 0.001$	26.52
Female	82.85	0.9192	0.7701	0.6571	0.8285	$P < 0.001$	22.12
Male	75.04	0.7931	0.7185	0.5008	0.7504	$P < 0.001$	28.64

The following figures are partial plots depicting the modeled probability of selection for habitat variables by lynx. I have included variables from each of the seasonal and sex specific models with importance values greater than ~ 0.20. For the Female and Male Core Habitat Models, I have reported partial plots for canopy cover, growing season precipitation, and spruce-fir forest at a large scale, and distance to the edge of a burn. Although slope at a large scale had an importance value > 0.20 in the Male Core Habitat Model, slope at a large scale had an importance value < 0.20 in the Female Core Habitat Model and was thus not included in the following group of figures.



A
B
C
D
% study area
% lynx locations
% probability of use
%
average canopy cover (%) within an 810 m diameter
average growing season precipitation within an 810 m diameter
distance (m) from inside a burn to the burn perimeter
% spruce-fir cover within an 810 m diameter

Figure D.1. Female lynx selection of habitat variables in the Loomis and Black Pine Basin study areas. Probability of use represents the effect of a focal habitat variable on female lynx habitat selection when the effect of all other habitat variables in the model are averaged. Histograms show the distribution of the focal habitat variable throughout the Loomis and Black Pine Basin study areas. The dots represent the percentage of female lynx points found within each histogram category of the focal habitat variable. Panels show female lynx selection for A) canopy cover at a large scale; B) growing season precipitation at a large scale; C) distance to the edge of a burn; and D) spruce-fir cover at a large scale.

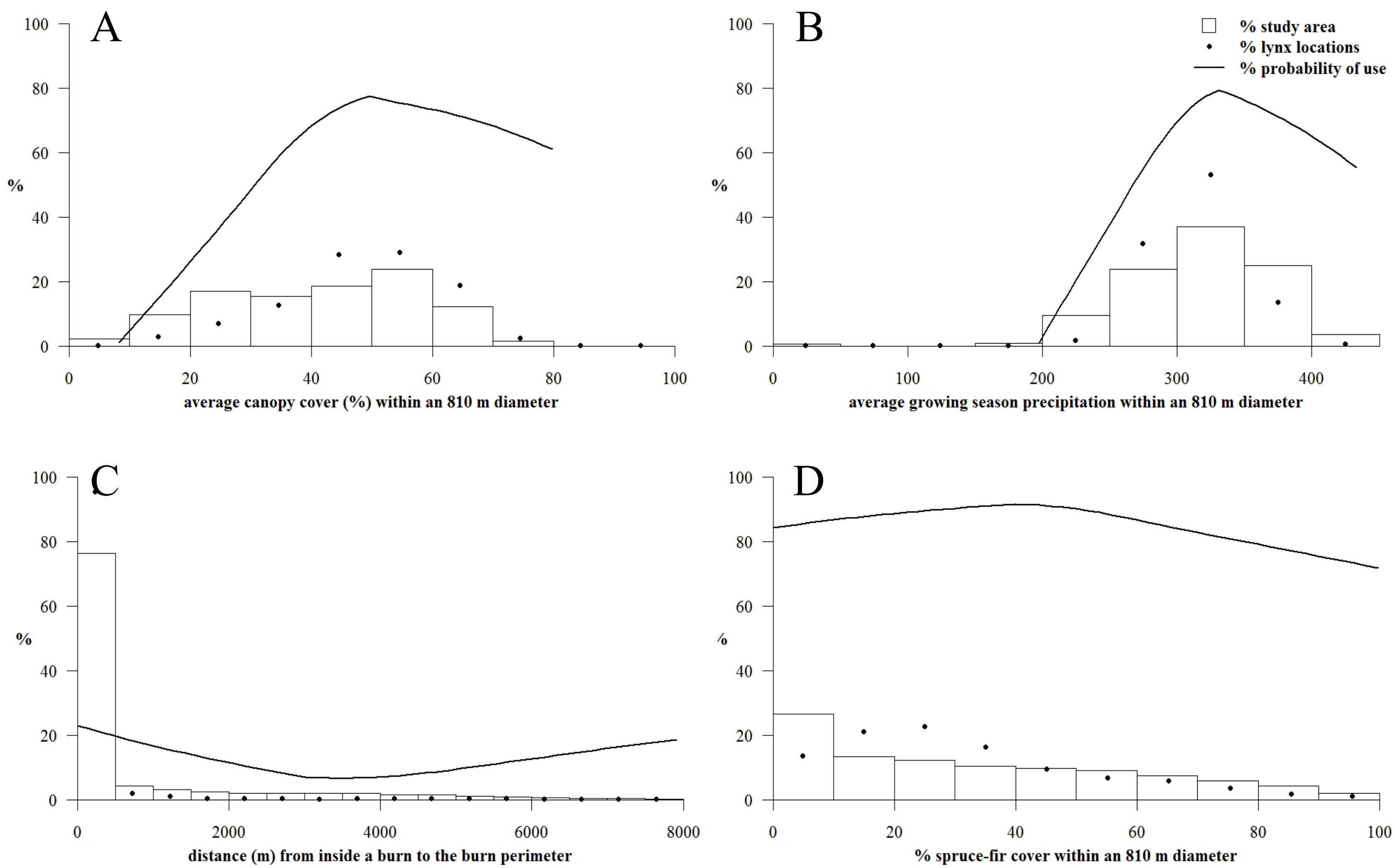
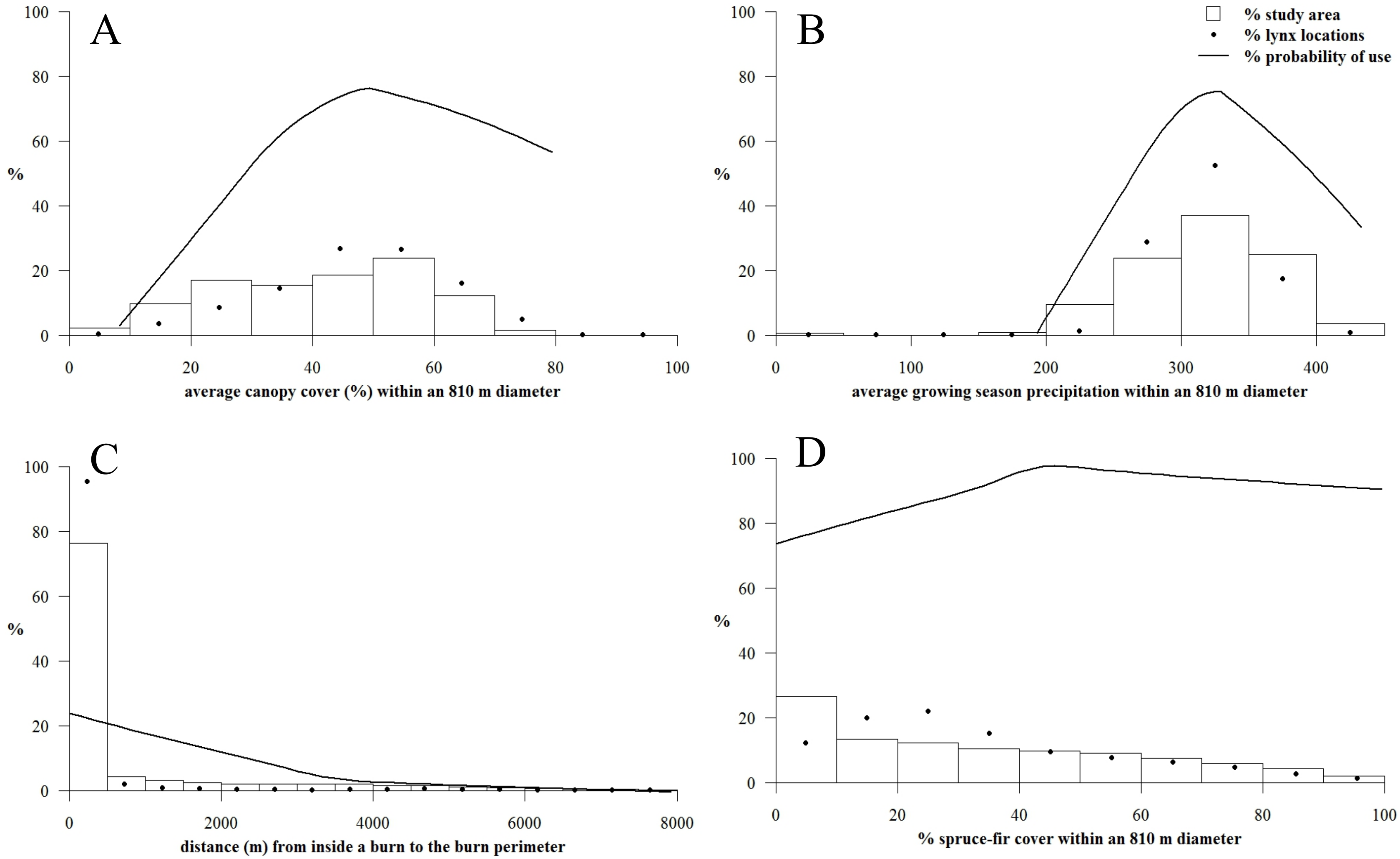

A
B
C
D
% study area
% lynx locations
% probability of use
%
100
80
60
40
20
0
average canopy cover (%) within an 810 m diameter
average growing season precipitation within an 810 m diameter
distance (m) from inside a burn to the burn perimeter
% spruce-fir cover within an 810 m diameter

Figure D.2. Male lynx selection of habitat variables in the Loomis and Black Pine Basin study areas. Probability of use represents the effect of a focal habitat variable on male lynx habitat selection when the effect of all other habitat variables in the model are averaged. Histograms show the distribution of the focal habitat variable throughout the Loomis and Black Pine Basin study areas. The dots represent the percentage of male lynx points found within each histogram category of the focal habitat variable. Panels show male lynx selection for A) canopy cover at a large scale; B) growing season precipitation at a large scale; C) distance to the edge of a burn; and D) spruce-fir cover at a large scale.



A
100
80
60
%
40
20
0
0
20
40
60
80
100
average canopy cover (%) within an 810 m diameter
B
% study area
% lynx locations
% probability of use
0
100
200
300
400
average growing season precipitation within an 810 m diameter
C
0
2000
4000
6000
8000
distance (m) from inside a burn to the burn perimeter
D
% spruce-fir cover within an 810 m diameter

Figure D.3. Lynx selection of habitat variables in the Loomis and Black Pine Basin study areas during the summer. Probability of use represents the effect of a focal habitat variable on lynx habitat selection during the summer when the effect of all other habitat variables in the model are averaged. Histograms show the distribution of the focal habitat variable throughout the Loomis and Black Pine Basin study areas. The dots represent the percentage of summer lynx points found within each histogram category of the focal habitat variable. Panels show lynx selection for A) canopy cover at a large scale; B) growing season precipitation at a large scale; C) distance to the edge of a burn; and D) spruce-fir cover at a large scale.

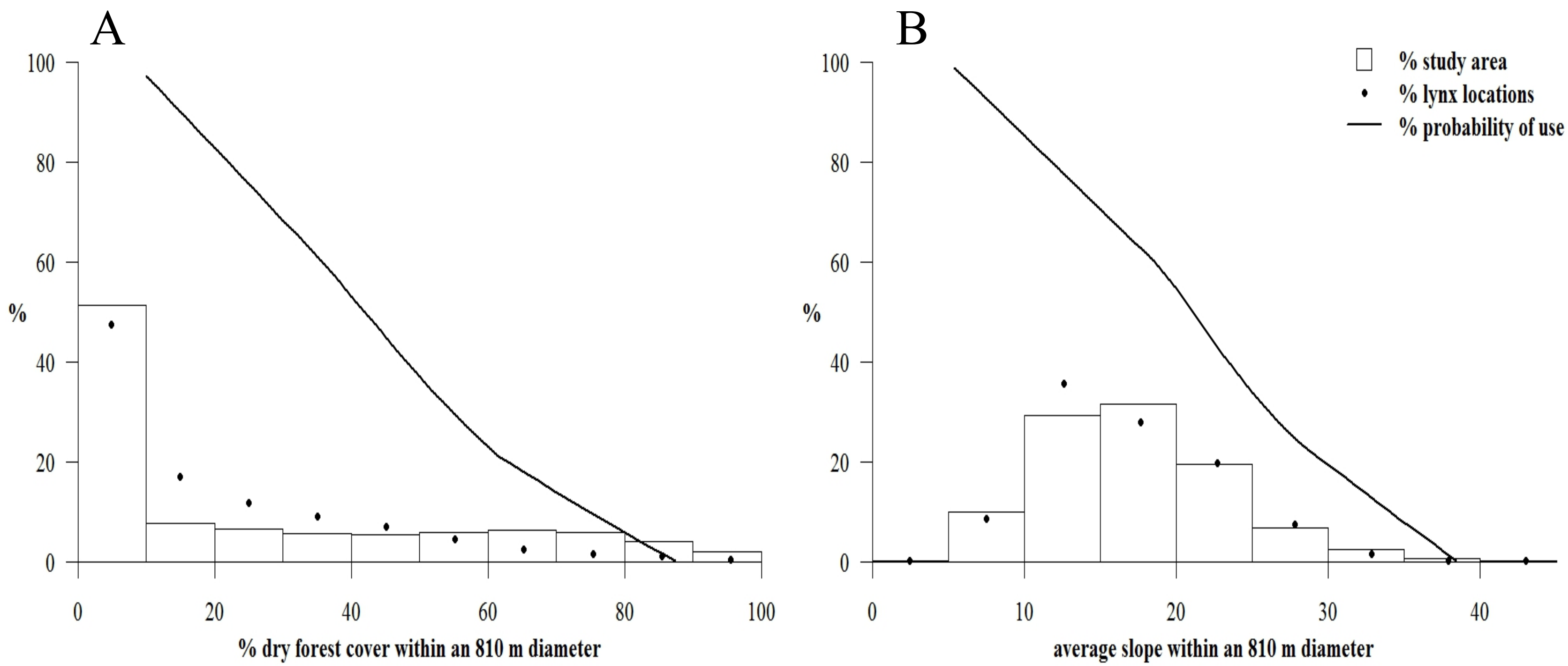


Figure D.4. Lynx selection of habitat variables in the Loomis and Black Pine Basin study areas during the summer. Probability of use represents the effect of a focal habitat variable on lynx habitat selection during the summer when the effect of all other habitat variables in the model are averaged. Histograms show the distribution of the focal habitat variable throughout the Loomis and Black Pine Basin study areas. The dots represent the percentage of summer lynx points found within each histogram category of the focal habitat variable. Panels show lynx selection for A) dry forest at a large scale; and B) average slope at a large scale.

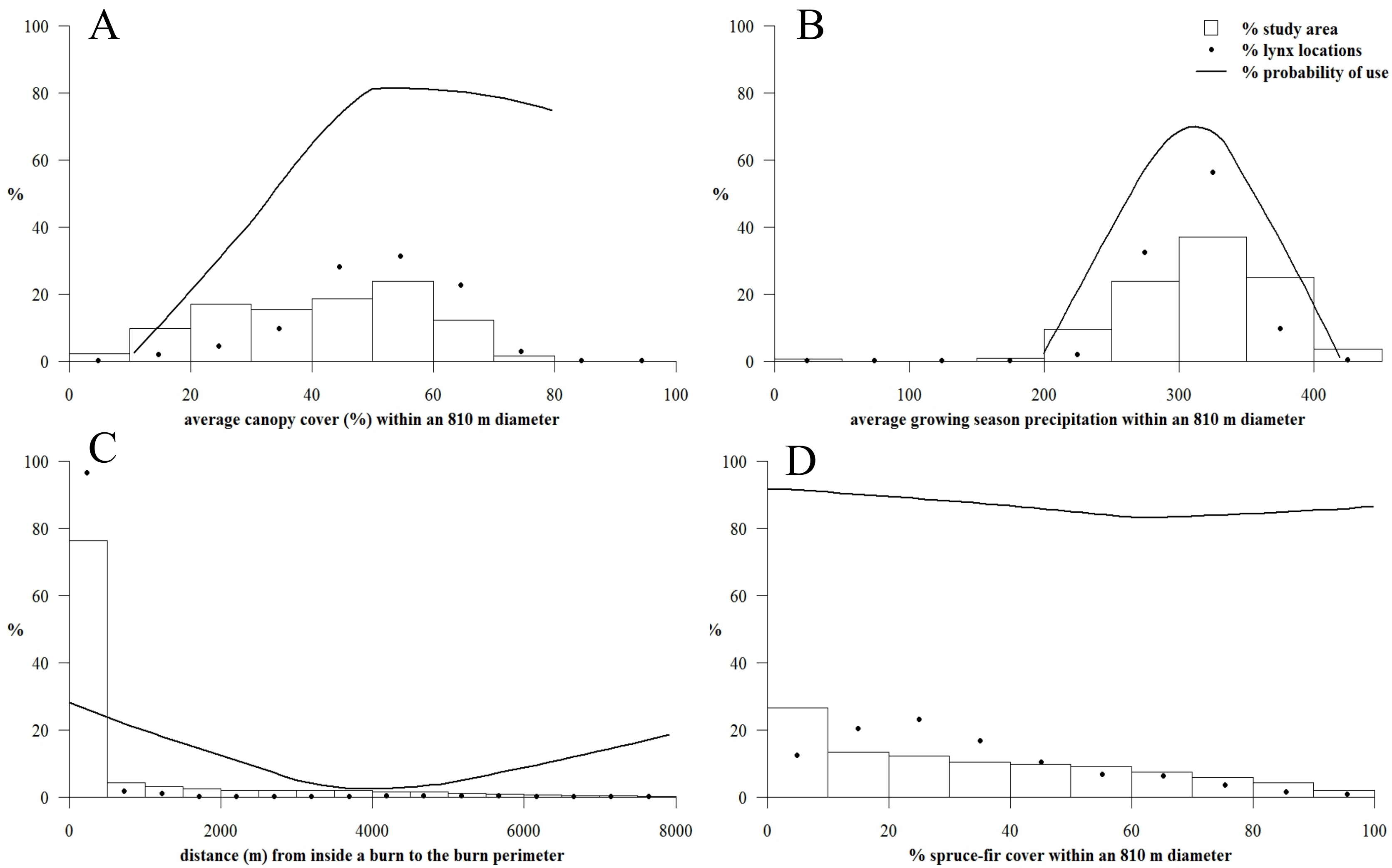

A
B
C
D
% study area
% lynx locations
% probability of use
%
average canopy cover (%) within an 810 m diameter
average growing season precipitation within an 810 m diameter
distance (m) from inside a burn to the burn perimeter
% spruce-fir cover within an 810 m diameter

Figure D.5. Lynx selection of habitat variables in the Loomis and Black Pine Basin study areas during the winter. Probability of use represents the effect of a focal habitat variable on lynx habitat selection during the winter when the effect of all other habitat variables in the model are averaged. Histograms show the distribution of the focal habitat variable throughout the Loomis and Black Pine Basin study areas. The dots represent the percentage of winter lynx points found within each histogram category of the focal habitat variable. Panels show lynx selection for A) canopy cover at a large scale; B) growing season precipitation at a large scale; C) distance to the edge of a burn; and D) spruce-fir cover at a large scale.

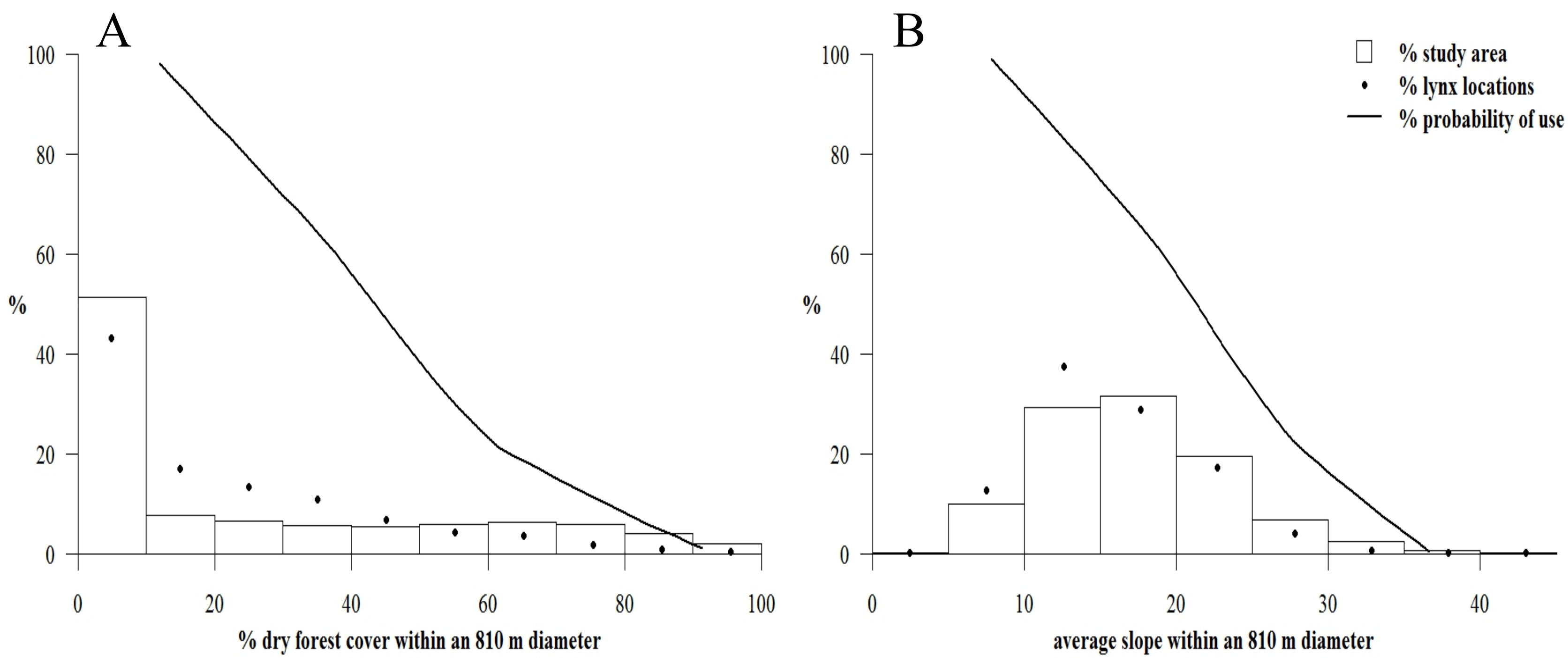


Figure D.6. Lynx selection of habitat variables in the Loomis and Black Pine Basin study areas during the winter. Probability of use represents the effect of a focal habitat variable on lynx habitat selection during the winter when the effect of all other habitat variables in the model are averaged. Histograms show the distribution of the focal habitat variable throughout the Loomis and Black Pine Basin study areas. The dots represent the percentage of winter lynx points found within each histogram category of the focal habitat variable. Panels show lynx selection for A) dry forest at a large scale; and B) average slope at a large scale.

D.2 Discussion

To reliably discover differences between two Random Forest models by comparing importance values and partial plots, one must consider that small differences between partial plots may be less an indication of actual habitat selection differences and more an artifact of the way Random Forest works. Model outputs will differ if the selected models use even a slightly different group of predictor variables since the interactions between included variables will differ. Thus I found that when comparing two models, drawing sound biological conclusions was only possible when regarding larger differences between models and required an in depth exploration of the landscape and ecological context of the selection patterns.

APPENDIX E: Data Obtained in the Whiteface and Tripod Burns

E.1 The Whiteface Burn

Much of the Whiteface Burn fell within male 329's home range and 478 of his 1,928 locations (24%) fell within the burn.

Male 311's home range was centered approximately 4 km east of the Whiteface Burn. 152 of 311's 2,251 locations fell within the Whiteface burn (7%).

Locations from female 330 indicate that while her home range bordered the burn and was within male 311's home range, she did not frequent the Whiteface Burn. Only nine of 330's 703 locations (1%) fell within the Whiteface Burn.

Although female 340 used a similar home range to female 330 and male 311, she made many trips outside of her home range, crossing though and spending time in the Whiteface Burn. Ninety-six of 340's 1,681 locations (6%) fell within the burn.

Male 312 did not have a well-established home range but spent approximately three months in the Black Pine Basin before leaving the area entirely, returning briefly, and then leaving again. Male 312 used the Whiteface Burn several times and 31 of his 1,311 locations (2%) fell within this burn.

E.2 The Tripod Burn

Male 312 also traveled out of the Black Pine Basin eastward through the Tripod Burn and into the Loomis area. Nine locations for male 312 were collected in the Tripod Burn (0.7%).

Locations from male 306 were only collected for 21 days. During this time he remained localized near the Tripod Burn, frequently using it but remaining within 900 m of the edge. Ninety locations for 306 were obtained, 33 of which were in the Tripod Burn (37%).

Locations for male 307 span one month and 129 locations were collected during this time. Although 307 remained in a localized area at the edge of the Tripod Burn only one location was collected within the burn, 250 m from the edge.

Male 308 lived in a home range adjacent to the Tripod Burn. 1,391 locations were collected from 308, only 15 of which fell within the Tripod Burn (1%). All 15 locations were within 200 m of the edge of the burn.

Male 309 had an established home range, the center of which was approximately 9 km from the edge of the Tripod Burn. Male 309 made many short forays out of his home range before dispersing to British Columbia, Canada. On several of these forays, 309 traveled near the edge of the Tripod Burn but only four of these foray locations were collected within the burn (0.2% of his 1,608 Washington locations). The location furthest inside the burn was 600 m from the edge.

Male 327 lived in a home range at the edge of the Tripod Burn and also included an island of forest that had previously burned in the 1970 Forks Fire but was not re-burned in the Tripod Fire. Locations from 327 were collected during his movements to and on the Forks fire skip, along the inside edge of the burn (within approximately 500 m of the edge), and on a few short forays into the Tripod Burn. Three hundred ninety of 327’s 824 locations fell within the Tripod Burn (47%).

Male 338’s home range bordered the Tripod Burn. Forty-seven of 338’s 1,263 locations (4%) fell within the burn, mostly within 500 m from the edge, although he ventured within approximately 1 km from the edge of the burn on 2 occasions.

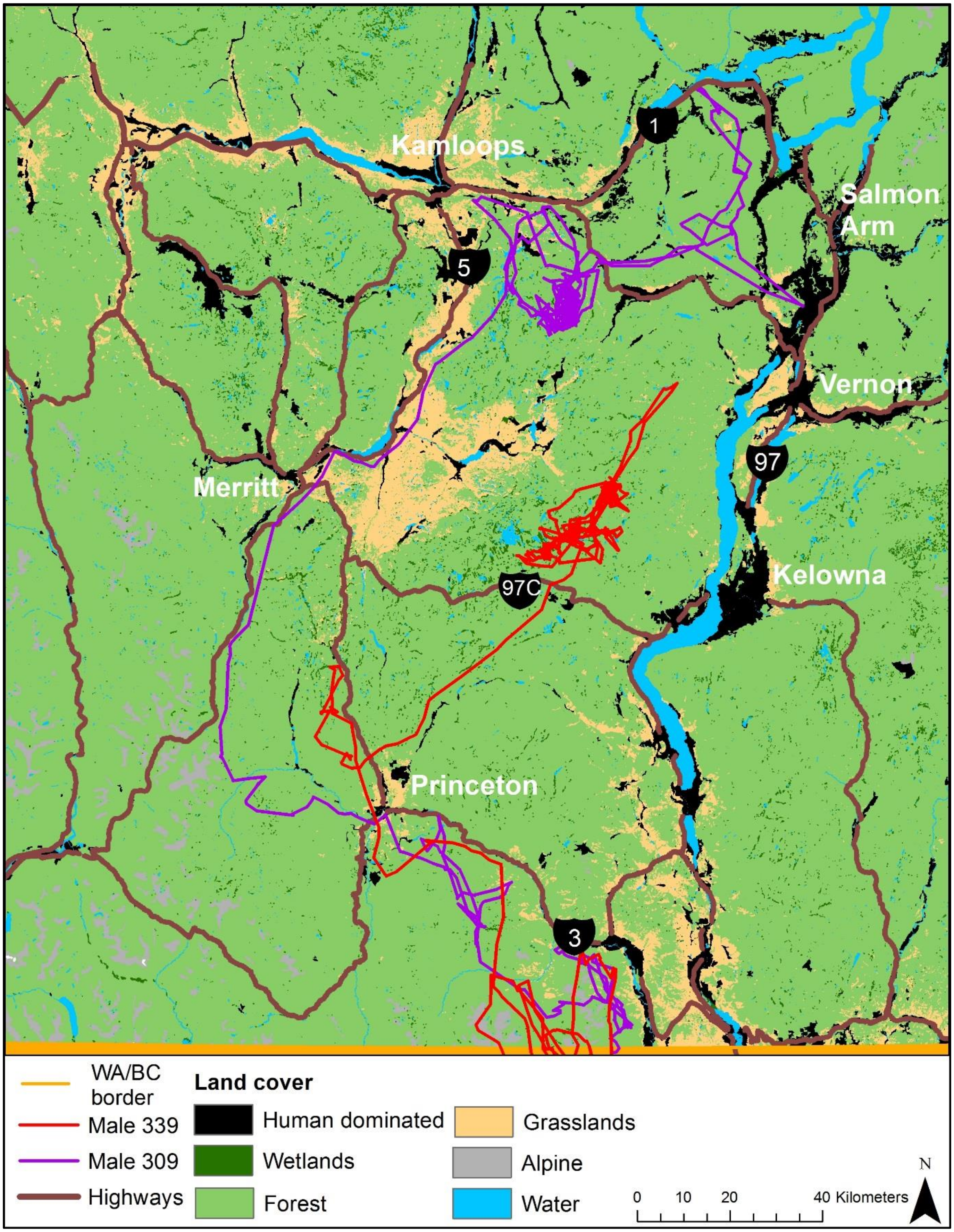
Male 339 lived in a home range mostly localized at the edge of the Tripod Burn and around a small isolated island of burn. Male 339 made many forays throughout the Loomis area before dispersing to British Columbia a year after he was collared. One hundred and seventy-one of 339's 1,694 Washington locations (10%) fell within the Tripod Burn. Locations in the burn were collected within 500 m of the burn edge, in an area of the Tripod Burn he frequently used as far as 2 km from the edge, and on several forays outside his home range. Male 339 also made five trips across the Tripod Burn to the Thunder Mountain Burn, staying there for three days on one occasion. Only 28 locations were collected in the Thunder Mountain Burn by 339 and he was the only lynx to record locations within the Thunder Mountain Burn.

Male 346's home range bordered the Tripod Burn and surrounded but avoided the same island of burn that male 339 avoided. Thirty-five of male 346's 2,990 locations fell within the burn (1%). Most of the locations within the burn were within 500 m of the edge though he sometimes ventured approximately 1 km into the burn. Male 346 also went on a foray nearly 7 km into the Tripod Burn and although he likely crossed through the Thunder Mountain Burn he did not linger there and no locations were recorded within the Thunder Mountain Burn. Male 346 also went on a longer exploratory movement to British Columbia, passing through the Tripod Burn on his way.

Male 347's home range bordered the Tripod Burn and 18 of his 1,381 locations (1%) fell within the burn. These locations were all within 500 m of the burn's inside edge.

Female 349's home range was adjacent to the Tripod Burn and 67 of her 1,345 locations were collected within the Tripod Burn (5%). All of her locations in the burn were within 800 m of the burn's inside edge.

APPENDIX F: Male 339 and 309's Dispersal Paths from Washington to British Columbia



Kamloops
Salmon Arm
Vernon
Merritt
Kelowna
Princeton
1
5
97
97C
3
WA/BC border
Male 339
Male 309
Highways
Land cover
Human dominated
Wetlands
Forest
Grasslands
Alpine
Water
0 10 20 40 Kilometers
N

Figure F.1. Male 339 and Male 309's dispersal pathways into British Columbia. Both of these males dispersed out of the Loomis study area and into British Columbia where they remained until they were legally harvested by trappers.