Co-Occurrence and Habitat Use Overlap of Snowshoe Hares (*Lepus americanus*) and American Martens (*Martes americana*) in the Boreal – Temperate Ecotone of the Northeastern U.S.

KATELYN A. COURTOT
B.S. Wildlife and Conservation Biology, University of Rhode Island, 2010

THESIS

Submitted to

PLYMOUTH STATE UNIVERSITY

In Partial Fulfillment of
the Requirements for the Degree of

Master of Science in Biology

Defended
March 18, 2022

Degree Conferred
May 2022

AN ABSTRACT OF THE THESIS OF

Katelyn A. Courtot for the degree of Master of Science in Biology
presented on

Title: Co-Occurrence and Habitat Use Overlap of Snowshoe Hares (*Lepus americanus*) and American Martens (*Martes americana*) in the Boreal – Temperate Ecotone of the Northeastern U.S.

Abstract approved:

Leonard R. Reitsma, Ph.D.

Managing forests for wildlife with different habitat preferences in addition to providing economic-based outcomes related to forest products poses a unique set of challenges for natural resource professionals. Snowshoe hares (*Lepus americanus*) are a keystone species influencing community dynamics, and American martens (*Martes americana*) are an umbrella species indicating ecosystem health. Hares prefer early-successional forest habitat in contrast to martens, which are typically associated with older forests. To evaluate the shared habitat preferences of both species, we collected forest structure data between May and November 2020 in 14 forested stands located in the Nulhegan Basin (NB), Vermont (n = 7) and the White Mountain National Forest (WMNF), New Hampshire (n = 7). My objective was to test the hypothesis that the co-occurrence of hares and martens is contingent on habitat availability at several scales. Specifically, I predicted that patches of early-successional forest within a matrix of mid- to late-successional forest allowed for habitat overlap of hares and martens. We measured basal area, canopy closure, diameter at breast height and counted stems at 45-50 plots within each of the 14 stands. We also measured coarse woody debris along three randomly selected transects in each stand. We compared these data with 2 years (2016 and 2017) of live-trapping data to determine what forest structure variables were associated with the habitat use overlap of hares and martens. The NB has a robust population of hares with few martens and the opposite pattern is observed in the WMNF, except that hares are relatively common, although at lower abundance in these forests. First, we fit a univariate, two-level categorical model (NB vs WMNF) to evaluate differences in second-order habitat selection. To evaluate fourth-order habitat selection, we fit 7 additive occupancy models for each species using forest structure variables and live-capture data. To further evaluate fourth-order habitat selection, we used three Principal Component Analysis (PCA) models to assess habitat use overlap. Results from the additive models suggest that hares selected areas with high stems counts and against areas with high basal area. Martens selected against areas with high stem counts, although basal area had only a weak effect. Visual-exploratory analysis using PCA suggested that deciduous stems accounted for

the habitat use overlap between hares and martens at a finer spatial scale. The WMNF experiences moderate amounts of disturbance that create small patches, typically resulting from windthrow events. This study suggests that these early-successional patches of forest within a later-successional landscape allow for the co-occurrence of both species, with deciduous stems driving the habitat use overlap. Deciduous stems have three phases that contribute to the habitat use overlap of hares and martens; seedlings/saplings, mature trees and coarse woody debris. The presence of keystone and umbrella species within the same community may increase biodiversity, and is consistent with the Intermediate Disturbance Hypothesis, however, more empirical support is needed to correctly guide and solidify future management.

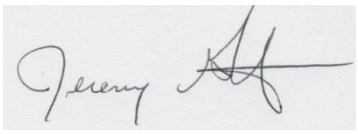
Master of Science thesis of Katelyn A. Courtot presented on 18 March 2022

APPROVED:

Thesis Co-advisor, Leonard Reitsma, Ph.D.
Professor of Biology, Plymouth State University
Department of Biology

Thesis Co-advisor, Alexej Sirén, Ph.D.
Postdoctoral Researcher, University of Vermont
Vermont Cooperative Fish and Wildlife Research Unit

Diana D. Jolles, Ph.D.
Associate Professor of Biology, Plymouth State University
Department of Biology



Jeremy Goetz, Forester

U.S. Fish and Wildlife Service

I understand that my thesis will become part of the permanent collection of Plymouth State University, Lamson Library. My signature below authorizes release of my thesis to any reader upon request.

Katelyn A. Courtot, Author

ACKNOWLEDGEMENTS

I would like to thank my field technicians, Sean Rabbitt and Jennifer Courtner, for their hard work in the rugged terrain and persevering through the swarms of blackflies during peak eruption! Field work was completed in a timely manner because of their dedicated effort.

Thank you to Jill Kilborn, for words of encouragement and advice along the way and to Rachel Cliché for sorting out the mountains of paperwork and making sure the process went smoothly.

I would like to acknowledge the Student Research and Creativity (SRAC) committee for the award that funded gear and equipment to conduct this study.

I would like to thank my committee members for their support and expertise. Thank you to my co-advisor Dr. Leonard Reitsma, for taking me under his wing as his last graduate student, for giving me a greater appreciation of ornithology and for guiding me through the intricate process of concise writing. Thank you to Jeremy Goetz for his expertise in forestry, and Dr. Diana Jolles for introducing me to the statistical program R. A special thank you to co-advisor Dr. Alexej Sirén, who has mentored me for many years and had faith in my potential when I doubted myself. His driven personality and work ethic is an incredible inspiration to push that little bit extra and to surpass all expectations, to be the best that one can be.

Thank you to my parents for always believing in me and my loving husband for listening to my countless adventures of chasing hares and martens through the forests and mountains! And thank you to all the snowshoe hares and martens; always a nice surprise to see one bounding through the brush or chattering in a tree, respectively...

CONTRIBUTION OF AUTHORS

Dr. Leonard Reitsma assisted with thesis revisions, and overall guidance.

Dr. Alexej Sirén assisted with project design, statistical analysis, thesis revisions and overall guidance.

Dr. Diana Jolles assisted with thesis revisions.

Jeremy Goetz assisted with training in forestry measurement techniques and thesis revisions.

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CHAPTER 1 – Ecological Importance and Habitat Use of Snowshoe Hares and American Martens in the Northeastern U.S.

The habitat requirements of two species with differing habitat preferences is often difficult to manage within the same forest matrix and poses a unique set of challenges for biologists, foresters, and natural resource managers. Biodiversity is thought to be regulated in part by disturbance, with the highest biodiversity occurring in areas that experience moderate amounts of disturbance in frequency and intensity (Connell 1978). This concept, referred to as the Intermediate Disturbance Hypothesis (*sensu* Connell 1978), potentially allows for the coexistence of species that typically have differing habitat preferences and competitive abilities. For example, snowshoe hares (*Lepus americanus*) and American martens (*Martes americana*) have disparate life histories and they do not typically coexist in comparable relative abundances within a landscape due to their different habitat preferences (i.e., early- to mid-successional vs mid- to late-successional forest habitat, respectively; Payer and Harrison 2003; Fuller and Harrison 2013). However, natural disturbances can create openings within a forest that generate various microhabitats with the potential for habitat use overlap (Kneeshaw and Bergeron 1998; Homyack et al. 2007; Reyes et al. 2010). In the northeastern U.S., the geographical overlap for hares and martens inhabiting their southern range limit is part of the deciduous forest-boreal forest ecotone (DBE) (Ferron and Ouellet 1992; Hodges 2000a; Goldblum and Rigg 2010; O'Brien et al. 2018). The unique forest conditions found in the DBE may allow these cold-adapted species to co-occur at finer spatial scales among landscapes. Identifying the habitat use overlap in forest structure preferred by keystone and umbrella species such as hares and martens, may provide valuable insight for managing multiple species within a common forest matrix; thus, areas with intermediate amounts of disturbance may increase overall biodiversity.

Community Level Dynamics

The impact of species on ecological communities is an important consideration when evaluating management approaches for promoting biodiversity. Hares and martens are ideal candidates given their ecological significance. For example, hares are primary prey for the Canada lynx (*Lynx canadensis*), a specialist predator that is federally threatened in the contiguous United States (USFWS 2000). Lynx were once valued for their fur before they became federally threatened in their southern range and biologists were intrigued by the distinct patterns and rhythms that were observed in the records from returns and sales during the fur trade with the Hudson's Bay Company (Elton and Nicholson 1942). Lynx populations in their southern range edge are limited due to biotic and abiotic factors and has caused interest among natural resource managers, as their density and distribution is not well understood (Ruggiero et al. 1999; Hornseth et al. 2014; King et al. 2020). Competition with other carnivores

(such as bobcats [*Lynx rufus*] and coyotes [*Canis latrans*]) combined with an insufficient hare population can have negative effects on this species (Ivan and Shenk 2016, Scully et al. 2018, Hostetter et al. 2020, Sirén et al. 2021, 2022). Understanding the factors that drive hare abundance in southern range limits may provide valuable insight to conserve populations of concern, such as the Canada lynx, which heavily rely upon hare density (>0.5 hares/ha; Simons-Legaard et al. 2013). Hares are also important prey for martens (whose conservation status varies by state) during the winter months when exposure to cold temperatures affects thermoregulation; larger prey provide greater caloric rewards for martens, which have high metabolic demands, however, hares may be available less frequently compared to smaller prey (Buskirk and McDonald 1989; Cumberland et al. 2001). Zielinski (1983) and Sirén et al. (2016) observed that martens were diurnal during spring and summer months, with increased nocturnal activity occurring in autumn and winter, potentially resulting in more frequent encounters with hares, which are also nocturnal during this time. However, not all studies support this idea of synchronized activity with prey, suggesting that encounters with hares in some regions of North America may be stochastic or more dependent on locating hare resting areas (Thompson and Colgan 1994).

The Snowshoe Hare

The snowshoe hare is a keystone herbivore and important prey for many predators such as Canada lynx, martens, bobcats, coyotes, red fox (*Vulpes vulpes*), fisher (*Pekania pennanti*), northern goshawks (*Accipiter gentilis*), barred owls (*Strix varia*) and great-horned owls (*Bubo virginianus*) (Spencer et al. 1983; Zielinski et al. 1983; Arthur et al. 1989; Dibello et al. 1990; Keith et al. 1993; Krebs et al. 2001; Berg et al. 2012; Sirén 2020). Their diet consists of both coniferous and deciduous browse and they consume a greater proportion of herbaceous vegetation during summer months, in contrast to the ligneous tissue of bark and twigs that are more readily available during winter (Wolff 1978; Hodges 2000b; Ewacha et al. 2014; Feierabend and Kielland 2014). In the northeastern U.S., preferred and abundant browse for hares is associated with early-successional forests and these habitats lack dense protective overhead canopy closure compared to more mature conifer forests (Litvaitis et al. 1985; Fuller and Harrison 2005; Homyack et al. 2007). Managing forests for these conditions that provide food and cover are imperative to sustain hares at moderate abundances within the northeastern U.S.

Snowshoe Hare Habitat Associations

Forest structure greatly influences hare abundance throughout the contiguous United States. Midwestern and northeastern states have high densities of hares in regenerating forests (Bittner and Rongstad 1982; Fuller et al. 2007) and western states appear to have higher densities in mature, multistoried forests (Koehler et al. 2008; Hodges et al. 2009). Studies show that hare density is highest in large contiguous

habitat with extensive lateral cover, however, they will utilize small patches if the habitat is sufficient (Hodges 2000a; Lewis et al. 2011; Berg et al. 2012; Sirén et al. 2021). The dense forest structure in southern areas that constitute the preferred habitat structure for hares is often fragmented due to anthropogenic activities such as logging and urban development, resulting in a variety of forest matrices of poor to high quality habitats (Sirén et al. 2021). Hares living in the northern boreal forest display pronounced peaks and lows in abundance and distribution in contrast to populations found in their southern range limit (Wolff 1980; Keith et al. 1993; Wirsing et al. 2002). For example, in the northeastern U.S., hare populations in the White Mountain National Forest of New Hampshire are relatively stable and they inhabit small yet adequate patches (< 1 ha) within a forest matrix of less suitable habitat (Sirén et al. 2021).

Although hares prefer early-successional stages of forest, residual mature forest patches with dense understory may be imperative to sustain hare populations immediately after logging (St-Laurent et al. 2008). For instance, studies show that it often takes 8-10 or more years before hares will fully utilize a regenerating boreal forest stand after clear-cut logging (Thompson 1988; De Bellefeuille et al. 2001; Potvin et al. 2005). Once regrowth becomes sufficiently dense, the understory that regenerates after timber harvesting provides cover that is an important habitat component and may facilitate dispersal into logged areas from viable source populations that took refuge in mature, undisturbed, residual patches (Potvin et al. 2005; St-Laurent et al. 2008). St. Laurent et al. (2008) found that hare activity was concentrated in uncut forest > 20 m from the edge of clear-cuts and observed greater daily movements in cut habitat (> 300m). Species such as spruce (*Picea* spp.) and balsam fir (*Abies balsamea*) provide effective cover from predators during this dispersal process (St-Laurent et al. 2008; Ewacha et al. 2014).

The American Marten

Martens are small mustelids with morphological features adapted to deep snow due to their ratio of body mass to foot size (Krohn et al. 1995; Carroll 2007). These adaptations give them an advantage over sympatric competitors and potential predators, such as the fisher (Daniel 1960; Krohn et al. 1995). Primary prey for martens includes mice (*Peromyscus* spp. and *Zappus* spp.), voles (*Microtus* spp. and *Myodes*), shrews (*Sorex* spp.) and red squirrels (*Tamiasciurus hudsonicus*), with larger prey (e.g., hares) consumed during the colder months (Zielinski et al. 1983). Their euryphagous diet will also opportunistically include human refuse, amphibians, birds, insects, beechnuts, raspberries (*Rubus* spp.), and American mountain ash (*Sorbus americana*) berries (Steventon and Major 1982; Cumberland et al. 2001; Jensen et al. 2012). Marten mortality is often a result of trapping, raptor predation or predation from mammals such as fisher, canids or other martens (Hodgman et al. 1997; Sirén 2013). Marten conservation status varies considerably in the northeastern U.S. For

example, martens are a furbearer species in Maine, endangered in Vermont, and recently removed from the list of threatened species in New Hampshire (Ritter 1986; DiStefano et al. 1990; WAP 2015a; NHFG 2017).

American Marten Habitat Associations

Martens show a positive association with older forests, which are correlated with high canopy closure and abundant coarse woody debris (Sherburne and Bissonette 1994). The structural characteristics of coarse woody debris offer subnivean openings that may be exploited for hunting (Sherburne and Bissonette 1994), used as refuge for resting and denning (Buskirk et al. 1989; Ruggiero et al. 1998), and provide protection from predators (Hargis and McCullough 1984; Carroll 2007). The presence of coarse woody debris may also provide martens with sensory cues regarding the location of hidden prey (Sherburne and Bissonette 1994; Andruskiw et al. 2008). Deep snow and contiguous mixedwood or boreal habitat of montane forests typically have rugged terrain and may provide martens with a climatic refugia (Carroll 2007; Sirén et al. 2017). They generally avoid open areas, and although they were previously believed to be a specialist of old coniferous forests (Ruggiero et al. 1994), recent studies in eastern North America show that martens utilize a variety of forest habitats based on predator avoidance, special habitat features and prey availability (Chapin et al. 1997; Fuller and Harrison 2005; Cheveau et al. 2013). For example, open areas such as clear cuts often have an abundance of small mammals and seasonally available foods such as raspberries, which could provide reliable hunting and foraging opportunities that martens occasionally exploit (Steventon and Major 1982; Hargis et al. 1999). However, uncut habitat is essential for winter survival and forests comprised of a high proportion of unsuitable habitat (e.g., large clear cuts) may negatively affect landscape connectivity for martens, with populations declining rapidly after > 35% forest loss (Steventon and Major 1982; Chapin et al. 1998; Hargis et al. 1999; Moriarty et al. 2016).

Research Objectives

Hares are keystone herbivores found in boreal and northern temperate forests (Hodges et al. 1999; Krebs et al. 2001). Identifying factors that influence hare populations at several spatial scales is critical because this species influences community-level dynamics of predation, competition, and herbivory due to direct and indirect interactions among a variety of wildlife across its range (Homyack et al. 2006). Many studies have consistently reported a correlation between key habitat features, such as understory density, and hare abundance (Litvaitis et al. 1985; Berg et al. 2012; Fuller and Harrison 2013), thus, managing and sustaining hares while considering the needs of late-successional species is critical to maintaining a balanced ecosystem.

Martens are both a predator and prey species, linked to the productivity of boreal forest ecosystems and are often considered an umbrella species of the northern Appalachians (Lambeck 1997; Carroll 2007; Buskirk 1992; Hodgman et al. 1997). If

an umbrella species is protected, all other biotic components within that particular ecological community may also be protected, thus the presence of martens may indicate the overall health of forest communities (Lambeck 1997; Carroll 2007; Aylward et al. 2018).

Few studies have measured forest structure with the intent to identify suitable habitat for species with differing habitat requirements within a landscape on the same spatial and temporal scale (Estevo et al. 2017; Jedlikowski and Brambilla 2017). The objective of this thesis is to identify forest structure variables that affect the co-occurrence and habitat use overlap of hares and martens at several spatial scales while considering their habitat preferences. Typically, studies have focused on one species of interest or the habitat in which it occupies. The importance of keystone and umbrella species is crucial and the identification of key forest structure characteristics that influence their coexistence will greatly affect the success of future management strategies that aim to increase biodiversity with consistent and desired results.

Study Area

The two study areas were located in the northeastern U.S., in northern Vermont (Nulhegan Basin (N 44.83576, W 71.73641); hereafter NB) and northcentral New Hampshire (White Mountain National Forest (N 44.31608, W 71.34871); hereafter WMNF) (Figure 1.1). This region is characterized by long winters with deep snowpack (244 – 406 cm of annual snowfall) and average -11°C (-15 to -2°C) in the coldest month of January (USDA 2007; Davis et al. 2013). Summers are warm and rainy (100 – 160 cm annual precipitation) and average 18°C (11 - 27°C) in the warmest month of July (USDA 2007; Davis et al. 2013). The NB is a low elevation area, ranging from 300 - 850 m (USFWS 2018). The WMNF is a high elevation area, ranging from 450 – 1,917 m and contains the highest peaks with some of the oldest boreal forests in the northeastern U.S. (Seidel et al. 2009; Foster and D'Amato 2015).

Forest communities vary greatly by elevation in the region with montane (≥ 823 m) and lowland (< 823 m) classifications based on the New Hampshire Wildlife Action Plan Classification System (WAP 2015b). Species in montane habitats above 823 m included American mountain ash, balsam fir, red spruce (*P. rubens*), and birches (*Betula* spp.). Tree species that dominated lowland habitats below 823 m included aspen (*Populus* spp.), American beech (*Fagus grandifolia*), red maple (*Acer rubrum*), sugar maple (*A. sacharrum*), white birch (*B. papyrifera*), yellow birch (*B. alleghaniensis*), tamarack (*Larix laricina*), black spruce (*P. mariana*), red spruce, white spruce (*P. glauca*) and balsam fir. Shrub species included hobblebush (*Viburnum lantanoides*), northern wild raisin (*V. nudum*), lowbush blueberry (*Vaccinium angustifolium*), S*piraea sp.*, northern bush honeysuckle (*Diervilla lonicera*) and speckled alder (*Alnus incana*).

We sampled these areas because the NB has a robust population of hares, with few martens and the opposite pattern persists in the WMNF, except that hares are relatively common with low abundance (Sirén 2020). Both study areas clearly display the contrast between landscapes with their differing forest structure. The NB is comprised of early- to mid-successional forest stands and the WMNF is comprised of mid-to late-successional forest. We consider the NB to be resource rich for hares and the WMNF to be resource poor, based on hare habitat preferences in northeastern North America (Homyack et al. 2007; Hodson et al. 2011).

FIGURES

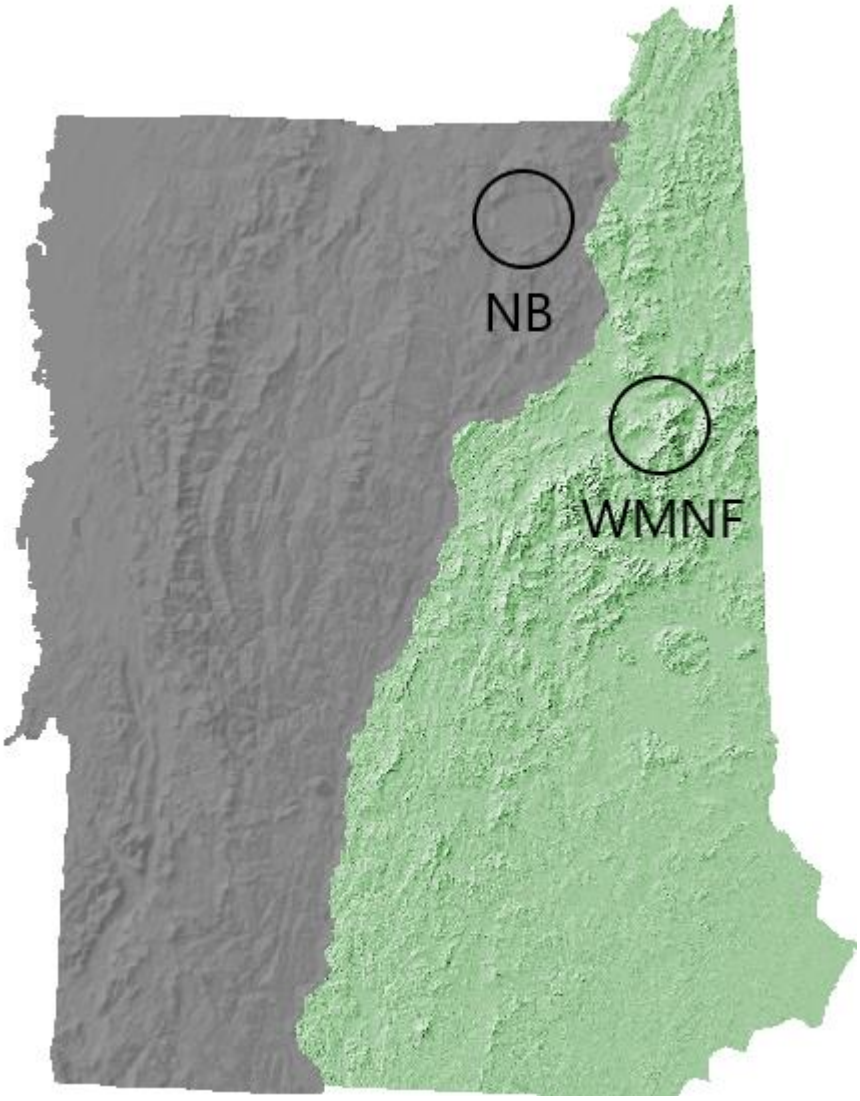

Figure 1.1: Location of the two study areas; the Nulhegan Basin, Vermont and the White Mountain National Forest, New Hampshire.

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CHAPTER 2 –Forest Stands and Landscapes in the Northeastern U.S. Affecting Ecologically Significant Species

INTRODUCTION

The landscapes of northern New England have been shaped by humans for several centuries and do not reflect the pre-settlement era when old-growth forests dominated the region, with major changes in forest structure influenced mostly by natural disturbances (Cronon and Demos 1983; Cogbill 2000; Cogbill et al. 2002). Landscapes that were once dominated by boreal forests have been converted to mixedwood and hardwood stands in various successional stages as a result of differing parcel size and management decisions made by a large number and diversity of landowners (Boucher et al. 2006; Boucher and Grondin 2012; Sass et al. 2021). Forest fragmentation has also occurred due to the individual management approaches and decisions accompanied with changing landownership over the last few decades (Litvaitis 2003; Lorimer and White 2003; Sass et al. 2021). However, recent advances in ecological restoration and forest management provide the opportunity to restore landscapes and wildlife communities and repair the long history of anthropogenic disturbances (Carey and Johnson 1995; Homyack et al. 2004). Ecological forestry is an approach that prioritizes timber harvesting according to natural processes and patterns, despite economic difficulties (Seymour and Hunter 1999). Specifically, ecological forestry suggests that native species diversity is linked to the natural disturbances within an area and forests should be managed within the limits of these natural phenomena to maintain biodiversity and long-term productivity (Bergeron and Harvey 1997; Seymour and Hunter 1999). For example, many regions in the northeastern U.S. are characterized by patches of forest in various successional growth stages and the unique conditions that support the co-occurrence of early- and late-successional wildlife species is not well understood (Gerhardt and Foster 2002; Hunter and Schmiegelow 2011). Nonetheless, managing for increased wildlife diversity and optimum forest health is an integral part of natural resource management.

Forests and Disturbances

Climate is a strong determinant of vegetation and has influenced the distribution and abundance of numerous plant species over time (Iverson and Prasad 2001). Abundance and distribution of tree species is regulated by many factors including soil composition, temperature and precipitation, all of which vary by elevation (Reiners et al. 1984; Lee et al. 2005). This is evident when observing mountain vegetation, as regeneration patterns differ with changes in elevation (Varga and Klinka 2001). In general, there is a decline in soil fertility with increased elevation in mountain environments in the northeastern U.S. and cold environments are found at high elevations and northern latitudes (Bond 1989; Lee et al. 2005). Average seasonal temperatures and length of growing season also decline with increased elevation and

at northern latitudes (Reiners et al. 1984). Further, precipitation increases with elevation for many of the mountains in the northeastern U.S., resulting in more snow and longer snow seasons, which directly affects the presence of wildlife communities (Dingman 1981; Krohn et al. 2004; Seidel et al. 2009).

Boreal, mixedwood and northern hardwood forests comprise the main cover types in northeastern North America. Boreal forests form a continuous belt east to west and north to south between 45 and 65 degrees latitude, dominated by various coniferous species and is the only forest biome to encompass the Earth (Rowe 1972; Woodward 2003). Young boreal stands include intolerant species such as aspen (*Populus* spp.), that are later replaced by more shade-tolerant conifers (Kneeshaw and Bergeron 1998). Northern hardwood forests are found in areas that have 120 - 150 frost free days and include American beech (*Fagus grandifolia*), maple (*Acer* spp.), and birches (*Betula* spp.) (Lull 1968; USDA 2007). Shade-tolerant conifers such as eastern hemlock (*Tsuga canadensis*) are commonly interspersed throughout northern hardwood stands (Lorimer and White 2003). Forest cover types can intermix; for example, according to MacDonald (1995), a boreal mixedwood forest is defined as an area in which no single species comprises more than 80 % of the basal area within a stand (MacDonald 1995). The edaphic, topographic and climatic conditions associated with boreal mixedwood forests often include the following five tree species that dominate in various successional stages, creating closed canopies (Chen and Popadiouk 2002). Trembling aspen (*Populus tremuloides*) and white birch (*B. papyrifera*) are found in early-successional stages, American beech, red maple (*A. rubrum*), sugar maple (*A. saccharum*), yellow birch (*B. alleghaniensis*), black spruce (*Picea mariana*) and white spruce (*P. glauca*) in mid-successional stages, and balsam fir (*Abies balsamea*) and red spruce (*P. rubens*) in late-successional stages (Leak 1991; Chen and Popadiouk 2002). These forests are important for biodiversity, and the northeastern U.S. is part of the deciduous forest-boreal forest ecotone (DBE) (Goldblum and Rigg 2010). The DBE sustains wildlife such as snowshoe hares (*Lepus americanus*) and American martens (*Martes americana*) in their southernmost range, and the unique forest structure characteristics associated with the DBE may allow these cold-adapted species to co-occur at finer spatial scales among landscapes, despite limiting factors such as interspecific competition (Ferron and Ouellet 1992; Hodges 2000; O'Brien et al. 2018).

Defoliating insects are among the natural disturbances with the potential to impact large landscapes during cyclic outbreaks, in contrast to more stochastic and localized events, such as wildfire or windthrow, that often catalyze stand level changes (Blais 1983; Reyes et al. 2010). The spruce budworm (*Choristoneura fumiferana*) is a well-known defoliating insect that has profound effects on the productivity of boreal and mixedwood forests in eastern North America, with outbreaks occurring every few decades, at minimum (Blais 1983; Royama et al. 2005; Morin et al. 2007). They are

the most destructive of any insect found in this region and they cause high, rapid mortality of mature balsam fir trees (MacLean 1984; Morin 1994; Parent et al. 2003). The seedlings that survive an outbreak experience a growth release and fill the opening caused by the dead trees and they continue to mature until future outbreaks or other disturbances (Johnson et al. 2003).

Other disturbances include windthrow and fire. Windthrow is the most common disturbance in the northeastern U.S. and is characterized by damaging winds that vary in frequency and intensity (Rich et al. 2007). Spruce and fir are often found in areas with thin soils, and their shallow root system makes them susceptible to windthrow (Lorimer and White 2003). Severe wind storms can create large openings in coniferous forests and stimulate abundant regeneration if the gap is large enough to allow adequate sunlight (Qinghong and Hytteborn 1991). Fire can start several ways and can profoundly alter the landscape by changing soil composition and by removing existing vegetation, thus stimulating successional processes (Fox 1978; Parshall and Foster 2002). Historically, Native Americans utilized fire in northern New England, however, it is unclear if they had a significant impact on fire frequency or vegetation composition compared to the increase in fires observed after the arrival of European settlers (Kozlowski and Ahlgren 1974; Parshall and Foster 2002). The development and increased use of fire suppression practices has limited the amount of areas burned and overall occurrence; thus, windthrow and insect outbreaks likely have a greater influence on southern boreal forest ecosystems (Cumming 2005; Couillard et al. 2013). Worrall and Harrington (1988) examined the causes of canopy gaps in high elevation old-growth spruce-fir forest in northern New Hampshire and found that wind stress was responsible for up to 72% of the gap area created.

Despite the source of disturbance, forest openings may provide adequate resources for wildlife species that prefer early-successional forest conditions, and these gaps may be temporarily utilized until forest succession progresses to a later stage (Lorimer and White 2003). Hares are a keystone species that prefer early- to mid-successional forests and their presence influences community dynamics (Krebs et al. 2001). Large gaps created by spruce budworm outbreaks may provide optimal habitat for hares by providing dense understory cover and abundant browse with the regenerating spruce-fir, thus increasing their population (Fuller et al. 2007; Ewacha et al. 2014). Smaller openings (e.g., <1 ha) created by more localized windthrow may still benefit hares, but also sustain martens by providing a stable prey base if the disturbance occurs in more mature forests (Fuller and Harrison 2013).

Research Objectives

My objective was to document forest structure in 14 stands located in the Nulhegan Basin, Vermont (NB) and the White Mountain National Forest (WMNF), New Hampshire. I collected data to explore the differences in forest structure between stands and landscapes in the two study areas. NB is dominated by early-successional

forest due to an intensive logging history and the WMNF is characterized by late-successional forest with greater structural complexity due to its rugged terrain in the higher elevations that restrict intensive timber harvesting. Specifically, I predicted that the WMNF would have higher basal area and more coarse woody debris (CWD) than the NB, with variation in structural diversity among individual stands due to natural or anthropogenic disturbances, which may also potentially affect wildlife diversity that depend upon unique structural features.

METHODS

Data Collection

We collected forest structure data within 14 forested stands established for snowshoe hare fecal pellet monitoring in the NB and the WMNF between May and November of 2020 (Figure 2.1 - 2.2). We sampled 7 stands in the NB within the towns of Brunswick, Ferdinand, Bloomfield, and Lewis and 7 stands in the WMNF, located in Jefferson, Randolph, Low and Burbanks Grant, Thompson and Meserve's Purchase, and Chandlers Purchase. Stand size was either 18 ha (540 m x 340 m) or 20 ha (590 m x 340 m). This included a 70 m buffer to reduce edge effects (Newbury and Simon 2005), which provided distance between the most outer sampling points within the stand from the stand perimeter. There were 9–10 points, each represented by a wooden stake painted blue, along each of 5 parallel transects, spaced 50 m apart, resulting in 45–50 points per stand, hereafter, referred to as plots (Figure 2.3). These plots were also used to count hare fecal pellets within 1 m^2 of plot center between 2015 and 2019 (Sirén 2020). Stands were spaced > 500 m apart to satisfy assumptions of independence, taking into consideration the upper threshold of average hare home range diameter and mean dispersal distances (Mills et al. 2005; Homyack et al. 2006; Feierabend and Kielland 2014). Stand types consisted of hardwood, mixedwood, lowland spruce-fir (softwood) and high elevation spruce-fir (montane softwood) (Table 2.1). High elevation montane habitats were ≥ 823 m and lowland habitats < 823 m, based on the New Hampshire Wildlife Action Plan classification system (WAP 2015a). Basal area, diameter at breast height (DBH), overhead canopy closure and stem density were sampled at every plot (45–50) within each of the 14 stands and CWD was sampled along 3 randomly selected 200 m transects within each stand (Table 2.2). We measured canopy closure during the leaf-off season using spherical densiometers and recorded four measurements in each cardinal direction with the densiometer centered 1 m above the ground and centered over each plot. We used 10 factor English prisms centered above each plot to calculate basal area of coniferous and deciduous trees, and a metric diameter tape to measure the DBH of trees ≥ 7.6 cm that were counted using the prism. We counted all woody stems ≤ 7.6 cm DBH within a 2 m radius at each plot and differentiated between coniferous, deciduous and shrub stems. We measured CWD on 3 randomly selected 200 m transects in each stand, using calipers to record the diameter of fallen logs at the point of intersection as we walked the transect.

Statistical Analysis

Prior to analyzing vegetation variables, we used histograms for exploratory analysis to determine how the data were distributed and what models would be appropriate based on the type of data. We used Poisson Generalized Linear Models (GLMs) for stem counts, beta-binomial GLMs for canopy closure and linear models for basal area to evaluate the differences in forest structure between the two study areas (NB and WMNF). We conducted a correlation analysis on stem counts, canopy closure and basal area to determine the strength of relationships between these variables. Finally, we used Principal Component Analysis (PCA) to investigate multivariate structural patterns among forest variables (Zimmerman 1999). Principal components with eigenvalues >1 were retained according to the Kaiser Criterion (Kaiser 1960; Braeken and Van Assen 2017) and all statistical analyses were conducted using the statistical program R (R Core Team 2020).

RESULTS

We counted a total of 60,420 stems in the NB and the WMNF. In the NB, we counted 18,188 coniferous stems, 1,828 deciduous stems and 20,724 shrub stems, totaling 40,740 stems (mean = 127,313 stems/ha). We counted less than half the number of total stems in the WMNF (19,640 stems; mean = 62,476 stems/ha), with 12,921 coniferous stems, 5,511 deciduous stems and 1,248 shrub stems. The average DBH for coniferous trees was 17.8 cm in the NB and 21.2 cm in the WMNF; deciduous trees were 22.5 cm and 24.5 cm, respectively. Canopy closure averaged 70% in the NB and 75% in the WMNF during the leaf-off season. Coniferous basal area averaged 18 m^2/ha in the NB, however, it was much higher (25.2 m^2/ha) in the WMNF. Deciduous basal area was comparable in both study areas, averaging 11 m^2/ha in the NB and 11.2 m^2/ha in the WMNF. CWD was twice as high in the WMNF (n = 791 intersections) than in the NB (n = 383 intersects), yet the diameters were nearly identical (14.6 cm, and 14.5 cm, respectively) (Table 2.3).

Poisson Generalized Linear Models (GLMs) for stem counts indicate that the NB had a significantly greater number of stems than the WMNF ($p < 0.0001$), with an estimated mean of 127.3 stems in the NB and 62.5 stems in the WMNF. Stems were categorized into coniferous, deciduous and shrub to differentiate between any observable patterns. Coniferous stems were abundant in both study areas, but greater in the NB than in the WMNF with an estimated mean of 56.8 stems in the NB and 41.0 stems in the WMNF ($\beta = 4.04$, SE = 0.08, $P < 0.0001$ and df = 634, $\beta = -0.33$, SE = 0.12, $P = 0.005$, respectively). Deciduous stem counts were uncommon and significantly less in the NB than in the WMNF ($p < 0.0001$), with an estimated mean of 5.7 stems in the NB and 17.5 stems in the WMNF ($\beta = 1.74$, SE = 0.09, $P < 0.0001$ and $\beta = 1.12$, SE = 0.12, $P < 0.0001$, respectively). Deciduous stems were the second most abundant stems in the WMNF following coniferous stems. Shrub stems surpassed all other stem counts and were significantly greater in the NB than in the

WMNF ($p < 0.0001$), with an estimated mean of 64.8 stems in the NB and 4.0 stems in the WMNF ($\beta = 4.17$, SE = 0.12, $P < 0.0001$ and $\beta = -2.79$, SE = 0.17, $P < 0.0001$, respectively). The NB is therefore characterized by high shrub stem densities and the WMNF is characterized by high deciduous stem densities (Figure 2.4).

The results from the beta-binomial GLM indicate that canopy closure was significantly less in the NB than in the WMNF ($\beta = 0.79$, SE = 0.05, $P < 0.0001$ and $\beta = 0.18$, SE = 0.07, $P = 0.02$, respectively). Both study areas were dominated by conifers, however, the estimated mean canopy closure was 68.6% in the NB and 72.1% in the WMNF (Figure 2.5). Measurements were recorded on a scale of 0 – 100%.

Basal area was significantly less in the NB than in the WMNF (df = 633, $R^2 = 0.22$, $P < 0.0001$); specifically, the estimated mean basal area was 20.1 m^2/ha in the NB and 32.4 m^2/ha in the WMNF. To further investigate the differences between study areas, basal area was evaluated separately for coniferous trees and deciduous trees. Coniferous basal area was significantly less in the NB than in the WMNF (df = 633, $R^2 = 0.08$, $P < 0.0001$). The estimated mean coniferous basal area was 16.3 m^2/ha in the NB and 23.7 m^2/ha in the WMNF. Deciduous basal area was also significantly less in the NB than in the WMNF (df = 633, $R^2 = 0.08$, $P < 0.0001$). The estimated mean deciduous basal area was 3.9 m^2/ha in the NB and 8.8 m^2/ha in the WMNF (Figure 2.6).

Correlation analysis suggests that canopy closure and coniferous basal area had the highest positive correlation of all forest structure variables ($r = 0.61$). Canopy closure was positively correlated with total basal area ($r = 0.43$) and negatively correlated with deciduous basal area ($r = -0.23$). Coniferous trees were abundant in both study areas, thus coniferous basal area was highly and positively correlated with total basal area ($r = 0.77$). Shrub stems were negatively correlated with coniferous basal area ($r = -0.24$), deciduous basal area ($r = -0.28$) and basal area ($r = -0.42$). All other forest structure variables had a correlation coefficient ≤ 0.40 (Figure 2.7).

PCA resulted in retaining PC1, PC2 and PC3, and accounted for 71.6 % of the cumulative variation. PC4–6 had eigenvalues < 1 and were discarded (Table 2.4). PC1 displays the contrast between deciduous stems and shrub stems among landscapes and indicates that the NB is characterized by high shrub stem counts and the WMNF is characterized by deciduous stems, higher canopy closure and higher coniferous basal area (Figure 2.8). PC1 explains 35% of the variation. PC2 indicates that both the NB and the WMNF are characterized by coniferous stems, with less in the WMNF. PC2 explains 21.7% of the variation (Figure 2.9). PC3 indicates that the WMNF is characterized by deciduous stems, however, it explains only 14.9% of the variation (Figure 2.10).

Stand types included hardwood, lowland softwood, mixedwood, and montane softwood (Table 2.1). Stand types were categorized by the forest structure variable that was most dominant. Stands identified as SFF had the most shrub stems, stands identified as LSF, HSF and MW had the most deciduous stems and stands identified as SFU had the most coniferous stems. Stands identified as SFW and KM had the highest coniferous basal area and NHF and HD had the highest deciduous basal area. Stands identified as SFW and SFU had the highest canopy closure. Stands with counts of CWD >100 intersections along all transects included HSF, SFW, KM and MW. Stands with counts of CWD < 100 intersections along all transects included LSF, SFF, HD, NH, SFU. Overall, the stand identified as HSF3 had the most CWD (172) and SFU1 had the least (2). It is important to note, however, that there were not enough replicates to conclude any definitive patterns (Figure 2.11).

DISCUSSION

Forest succession is generalized as a process of sequential colonization and dominance with younger trees having smaller diameters and structural diversity increasing as succession continues (Hibbs 1983). The data collected supports my assumption that the NB is dominated by early-successional forest habitat due to a more recent and intensive logging history and the WMNF is characterized by late-successional forests with greater structural complexity. Overall, results from the PCA suggest that the NB is characterized by higher shrub and coniferous stem counts and lower canopy closure compared to the WMNF, which is characterized by higher basal area, deciduous stems and abundant CWD. In summation, the forest structure data collected from my research captured the structural differences between two landscapes that are at different stages of forest succession in the deciduous forest-boreal forest ecotone of northern New England.

Coniferous and Deciduous Trees

Conifers are dominant in cold environments with nutrient-poor soils (Bond 1989) and coniferous trees were more abundant than deciduous trees in both study areas (NB and WMNF). Conifers have lower water uptake and transport which limit their growth rate; however, they have a longer leaf lifespan compared to deciduous trees, which may result in more efficient nutrient absorption (Bond 1989; Piper et al. 2018). The DBH of deciduous trees in the NB was larger than coniferous trees, except for the softwood stand identified as SFF3, which had marginally larger coniferous trees (21.2 cm and 21.4 cm, respectively) (Figure 2.12). In the WMNF, coniferous trees had a larger DBH than deciduous trees in 4 out of 7 stands (Figure 2.13). The WMNF is approximately 80 km southeast of the NB, however, most stands sampled in the WMNF were located at higher elevation, which results in lower seasonal temperatures and shorter growing seasons compared to the surrounding landscape (Reiners et al. 1984).

Angiosperms, such as deciduous trees, are thought to have been restricted to historically warm environments and evolved traits that allowed their distribution to spread into areas that have an extended period of freezing (Wing and Boucher 1998). Woody tissue in some species such as beech, birch and sugar maple, may restrict hardwood distribution due to a low tolerance of minimum temperature, although such low temperatures are likely well below the threshold of temperatures that occur in New England (George et al. 1974). In the WMNF, the only stand dominated by deciduous trees was HD2 and the only northern hardwood stand sampled in that study area. It was located at the lowest elevation compared to the other 6 stands. The deciduous species that were present in the highest elevation stands in the WMNF were limited to American mountain ash and birch. American mountain ash provides mast crops for a variety of wildlife species including martens, which are known to persist in the WMNF and fluctuations in mast crop productivity are often synchronous with predator prey abundance (Jensen et al. 2012).

Two cold-adaptations of deciduous species include dormancy and leaf abscission to increase survival during unsuitable seasons (Zanne et al. 2014). Although there was only one northern hardwood stand sampled in the NB, tamarack (*Larix laricina*) was very common in the NB and has characteristics of both coniferous and deciduous trees. It is often found in wet, boggy areas and is considered a deciduous conifer, which may be an adaptive advantage in more extreme or disturbed environments. However, it is not an important dietary component for many wildlife species; nonetheless, hares will occasionally browse on the bark and twigs (Fowells 1965; Damman and French 1987).

Stem Counts

The relative growth rate or slow seedling hypothesis states that angiosperms grow more rapidly than gymnosperms in the juvenile stages of development, thus giving them a competitive advantage over gymnosperms when coexisting in the same environment (Bond 1989). Nonetheless, there are some hypotheses stating that gymnosperms, such as coniferous species, are successful in more stressful environments due to their adaptive biological features, such as smaller diameter tracheids relative to vessels and high leaf longevity (Brodribb et al. 2012). This is likely a resource conservation trait due to the greater efficiency of processing nutrients (Piper et al. 2018); energy conservation occurs when conditions are not ideal, during times of freezing or when there is limited photosynthesis (Brodribb et al. 2012). Coniferous stems were more abundant than deciduous stems in the NB and the WMNF, and both areas have nutrient poor soils that may not be ideal for many angiosperm species to thrive (Leak 1976; USFWS 2018). Regardless, all stem types provide some degree of lateral cover and are an important food source for many mammals (Potvin et al. 2005). For example, the NB had numerous lowbush blueberry shrubs (*Vaccinium angustifolium*), a highly preferred browse species for hares and

both deciduous and shrub stems provide greater lateral cover during the leaf-on season, which may have seasonal effects on habitat use for a variety of wildlife (Wolff 1978; Litvaitis et al. 1985; Olson 2015). Overall, coniferous stems offer consistent protection regardless of season, with greater thermal protection from climatic extremes and superior cover from predators (Litvaitis et al. 1985).

Higher growth rates of angiosperms over gymnosperms appear to be restricted to early-successional species in the northern hemisphere (Becker 2000). Shrub stems greatly surpassed all other stem counts in the NB, which is the early-successional study area (Figure 2.14). Shade and competition are also mechanisms that reduce survival and the growth of saplings and high accumulations of CWD may prevent germination of various species due to the layers of downed organic material that prevent adequate sunlight from reaching the ground (Pagès et al. 2003; Reyes et al. 2010). On the other hand, CWD provides an important substrate for the establishment of various plant species by providing additional moisture compared to the surrounding landscape, reduced competition, and longer snow-free periods (Feller 2003; Harmon et al. 1986). Further, soil composition and disturbance history can influence germination and the abundance of seedlings (McRae et al. 2001). Regardless, these factors may explain why species such as wild blueberry (*Vaccinium* spp.) and spiraea (*Spiraea* spp.) were abundant in the moisture rich environment of the NB and comparatively uncommon in the stands sampled in the WMNF, which had more CWD associated with coniferous stems and lower shrub stem counts associated with ample sunlight or disturbance (Figure 2.15).

Canopy Closure

Canopy closure was measured during the leaf-off season. Although the NB and the WMNF were both dominated by coniferous trees, many of those conifers were tamaracks and canopy closure was significantly less in the NB. Large openings or gaps were abundant in the NB, due to the interspersed patches of peatlands, bogs and swamps (USFWS 2018). The WMNF had only occasional forest openings, likely created by sporadic storm events and blowdowns. Martens have a strong presence in the WMNF and have often been considered a specialist of old forests with closed canopies (Ruggiero et al. 1994). There is a positive association between martens with these forest types, which most often have high canopy closure (Sherburne and Bissonette 1994). Northern hardwood stands have the greatest variation in overhead canopy closure dependent upon season, and seasonal shifts of wildlife species such as hares and martens have been observed (Chapin et al. 1997; Katnik 1992; Olson 2015; Sirén et al. 2016). For example, Olson (2015) found that deciduous trees had negative effects on leaf-off pellet densities and positive effects on leaf-on densities, which may also seasonally influence the presence of martens that rely on hares as important prey. Northern hardwood stands are usually associated with more mature forests and the mean DBH of NHF2 and HD2 were the highest out of all stands sampled.

Basal Area

Agricultural expansion over the last several centuries has eliminated most old-growth forests in New England, which are characterized as having dominant trees >100 years old (Mosseler et al. 2003; Harrison et al. 2010). Areas where older forests persist are typically small isolated patches that are inaccessible due to rugged terrain, or protected and regulated (Mosseler et al. 2003), such as the WMNF. The higher elevations associated with steep terrain in the WMNF are not ideal for timber harvesting, and these forests have continued to progress through their natural successional processes.

The southeastern portion of the boreal forest is dominated by balsam fir, which is less susceptible to atmospheric deposition compared to species such as red spruce, and has increased in abundance due to fire suppression and changing forest management practices; however, it is highly susceptible to spruce budworm outbreaks (Kneeshaw and Bergeron 1998; Foster and D'Amato 2015). Basal area was significantly less in the NB than in the WMNF and the NB was extensively harvested in the 1970s and 1980s following the most recent spruce budworm epidemic, which created early-successional forest conditions (Chen et al. 2017). Although there have been extensive studies on spruce budworm outbreaks due to their ability to create large scale disturbances, the dynamics of periodicity, synchronicity and amplitude are not well understood, which makes proactive wildlife management planning difficult (Morin et al. 2007). However, it is well-established that balsam fir is the preferred host species of spruce budworms and mature balsam fir stands are most susceptible to mortality compared to other conifers such as spruce (Mott 1963; MacLean 1980; MacLean and Ostaff 1989). This may potentially impact wildlife such as martens in areas with high basal area, (e.g., the WMNF) if a spruce budworm outbreak occurred in southern fringes of the boreal forest. Martens are an umbrella species typically found in more mature forests, and the impacts of a spruce budworm outbreak may negatively affect their abundance and distribution (Lambeck 1997; Carroll 2007; WAP 2015b). However, Chapin (1997) found that martens selected for areas impacted by spruce budworm where no salvage cutting occurred, despite decreased canopy closure. The abundance of CWD, snags, root masses, stumps and regeneration may increase structural diversity, and thus provide greater opportunities for resting, denning, and hunting. Regardless, the landscape in the NB is transitioning into a late-successional stage that may alter wildlife diversity. For example, the NB currently has a robust population of hares and rare occurrences of martens. Payer and Harrison (2003) suggested that ≥ 18 m^2/ha is the minimum basal area threshold for martens to occur in Maine, and the mean coniferous basal area in the NB is currently 18 m^2/ha. This may lead to a changing wildlife community over the next few years, depending upon future forestry management practices and natural disturbances, with the surrounding high elevation areas increasing the likelihood of marten occurrences within the NB.

It is also important to note that DBH is not a reliable predictor of basal area (Elledge and Barlow 2010). For example, coniferous trees with a mean DBH of 10 cm were measured at a total of two plots (plot 30 in SFF6 of the NB and plot 15 in KM1 of the WMNF), however, basal area measured 32.1 m^2/ha and 16.1 m^2/ha, respectively. Further, Potvin et al. (2005) found that clear-cut logging may temporarily negatively affect the density of wildlife such as moose and hares, in response to the lack of canopy closure and reduced basal area.

Coarse Woody Debris

CWD was more abundant in the WMNF than in the NB. High accumulations of CWD suggest forest stands may have gone through a thinning process as part of their successional stage (Sturtevant et al. 1997). Overall, the NB is a younger forest than the WMNF and has yet to reach maturity, hence the low accumulations of CWD. The comparable mean diameter of CWD also suggests that tree species reach senescence in a similar time interval in both study areas, with more forest thinning already occurring in the WMNF. For example, Bouchard (2005) suggested that certain species may be more prone to environmental stresses in varying regions (e.g., windthrow in high elevations) when they are close to reaching maturity or senescence. However, older stands typically have multiple cohorts of varying age, thus challenging our assumptions of forest stand senescence (Bergeron et al. 1999; Kuttner et al. 2013). Regardless, the presence of CWD provides resting, nesting and foraging or hunting opportunities for a variety of wildlife including their prey, and allows for a network of subnivean refugia in areas with long winters and deep snowpack (Sherburne and Bissonette 1994).

GENERAL CONCLUSIONS

Each study area can be characterized by their most prominent forest structure features. The NB has a large proportion of shrub stems and the WMNF is characterized by high canopy closure, high coniferous basal area and abundant CWD. Both study areas have a robust number of coniferous stems intermixed with deciduous and shrub stems, which reflects the region's location as part of the deciduous forest - boreal forest ecotone (Goldblum and Rigg 2010).

Windthrow will likely continue to be the primary source of disturbance in the WMNF, creating a mosaic of early-successional forest gaps dispersed among older growth. The NB may continue to mature if timber harvesting is attenuated, and basal area should increase until senescence, however, there is a high amount of uncertainty in this outcome. The last spruce budworm epidemic occurred over 40 years ago in the northeastern U.S. and studies suggest their expected return interval is approximately 34-60 years, with longer intervals dependent upon the abundance of their preferred host species, balsam fir (Baskerville 1975; Royama 1984; Royama et al. 2005; Fraver et al. 2007; Boulanger and Arseneault 2012). Currently, eastern Quebec is experiencing the most recent outbreak in eastern Canada and moth counts are steadily

increasing and moving southward (Wagner et al. 2016). Blais (1983) documented the history of spruce budworm outbreaks in eastern Canada and concluded that the severity and average land area affected has increased throughout the 1900s compared to the previous 100 years (1800s), potentially due to forest management practices, which resulted in greater densities of balsam fir, their preferred host species (Blais 1983). Regardless, another outbreak can drastically reshape the region's forest structure and affect resource economics. Forestry practices in the northeastern U.S. may adapt by utilizing logging techniques involving selection. These methods can create small patches of regenerating spruce-fir and reduce balsam fir to mitigate such threats, resulting in a more complex landscape. Partial cuts may also be implemented to maintain the core forest structure (Boucher and Grondin 2012). This may potentially increase wildlife diversity or allow for the co-occurrence of early- and late-successional wildlife species within a heterogeneous forest matrix.

Despite the threat of defoliating insects, balsam fir is regulated in-part by temperature and spruce-fir forests may be at risk of extirpation in the northeastern U.S. if temperatures continue to increase (Iverson and Prasad 2001). These tree species only recently expanded southwards over the last few centuries and colonized New England during the Little Ice Age (DeHayes et al. 2000). Many wildlife species rely on spruce-fir forests, which could result in even greater ecological losses if these forests decline (Iverson and Prasad 2001). On the contrary, Foster and D'Amato (2015) found that montane spruce and fir are expanding downslope, indicating a strong recovery from historically intensive timber harvesting. Duveneck (2017) also found similar results, suggesting that many species may benefit from an increased and warmer growing season despite lower optimal temperatures. Regardless, there are several land-use factors not attributed to climate change that are projected to have a large influence on carbon dynamics and forest composition in the northeastern U.S. (Duveneck and Thompson 2019). These include development and timber harvesting, with the latter projected to have the greatest effect on carbon stores, forest biomass and species composition due to corporate-owned forests accounting for over one-quarter of New England (Duveneck and Thompson 2019). However, compounding factors and model discrepancy make the future unclear, thus indicating high uncertainty and the need to collect more data (Bormann and Likens 1979; Tyrrell and Crow 1994; Keeton et al. 2011; Wang et al. 2017).

Forest management in the northeastern U.S. commonly includes even-aged and uneven-aged harvesting techniques (Solomon and Gove 1999). Silvicultural practices that manage for uneven-aged forests include stands with at least three age classes of regrowth, and ideally include several treatments of partial cuts allowing for continuous regeneration (Nolet et al. 2017). Therefore, older forested stands typically have an age structure that allows for the coexistence of younger, middle-aged and older-aged cohorts and may increase biodiversity (Gauthier et al. 2009). Succession is a perpetual

process, and forests will continually evolve through natural influences and human disturbances. Structural complexity is believed to have a greater influence on wildlife than plant species composition (Litvaitis et al. 1985; Ferron and Ouellet 1992) and both study areas have distinct forest structures that currently benefit a variety of flora and fauna. Thus, future management has the potential to maximize desired wildlife communities, increase biodiversity and achieve optimum forest health.

TABLES

Table 2.1: Stand identification associated with stand types in the two study areas located in the Nulhegan Basin (NB) and the White Mountain National Forest (WMNF).

Study Area	Grid	Stand ID	Stand Type
NB	179	NHF2	Hardwood
NB	179	SFF3	Lowland Softwood
NB	179	SFF4	Lowland Softwood
NB	179	SFF6	Lowland Softwood
NB	179	SFU1	Lowland Softwood
NB	179	SFU2	Lowland Softwood
NB	180	SFU1	Lowland Softwood
WMNF	106	HD2	Hardwood
WMNF	106	HSF3	Montane Softwood
WMNF	106	KM1	Montane Softwood
WMNF	106	LSF1	Lowland Softwood
WMNF	106	LSF3	Lowland Softwood
WMNF	106	MW4	Mixedwood
WMNF	106	SFW1	Montane Softwood

Table 2.2: Forest structure variables measured in all stands sampled in the Nulhegan Basin (NB; n = 7) and White Mountain National Forest (WMNF; n = 7) with description and methods.

Variable	Description	Method
Canopy Cover (%)	4 cardinal directions, plot center	Spherical Densiometer
Basal Area (m^2/ha)	Plot center	10 Factor English Prism
DBH (cm)	Fixed area plot, trees ≥ 7.6 cm	Diameter Tape
Stem Density (stems/ha)	Fixed area plot, ≤ 7.6 cm, 2 m radius	Count
Coarse Woody Debris (cm)	Line intersect, ≥ 7.6 cm, ≥ 1 m long	Calipers

Table 2.3: Mean (S.E.) values of forest structure variables measured in the two study areas Nulhegan Basin (NB) and the White Mountain National Forest (WMNF).

Variable	NB	WMNF
Stem Density (stems/ha)	127313 (9268)	62476 (3931)
coniferous	56838 (8032)	41019 (3495)
deciduous	5713 (710)	17495 (1623)
shrub	64763 (4558)	3962 (755)
DBH (cm)	18.7 (0.2)	22.3 (0.2)
coniferous	17.8 (0.2)	21.2 (0.2)
deciduous	22.5 (0.4)	24.5 (0.3)
Basal Area (m^2/ha)	29.0 (0.5)	36.4 (0.5)
coniferous	18.0 (0.6)	25.2 (0.7)
deciduous	11.0 (0.8)	11.2 (0.6)
Canopy Cover (%)	70.0 (1.4)	75.0 (1.1)
Coarse Woody Debris		
number of intersects	383	791
diameter (cm)	14.6 (0.3)	14.5 (0.2)

Table 2.4: Results of Principal Component Analysis on forest structure data comparing vegetation variables. The highest loadings are given in bold type.

Forest Structure Variable	Factor Loadings		
	F1	F2	F3
Coniferous Stems	-0.120	0.310	0.370
Deciduous Stems	-0.040	-0.099	**0.902**
Shrub Stems	0.352	0.390	-0.085
Basal Area	**-0.556**	-0.262	-0.038
Coniferous Basal Area	**-0.566**	0.237	0.004
Deciduous Basal Area	-0.012	**-0.741**	-0.063
Canopy Closure	**-0.479**	0.260	-0.190
Eigenvalue	2.45	1.52	1.04
Variability %	35.0	21.7	14.9

FIGURES

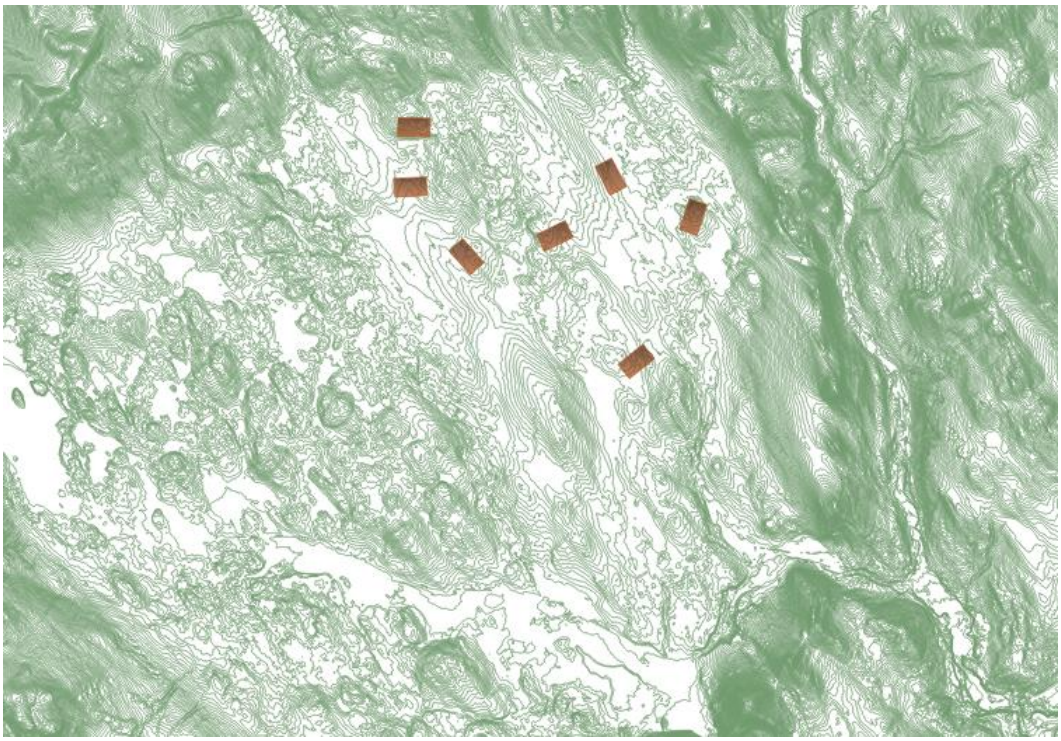

Figure 2.1: Contour map depicting the spatial arrangement and surrounding topography of stands sampled (n = 7) in the Nulhegan Basin, Vermont.

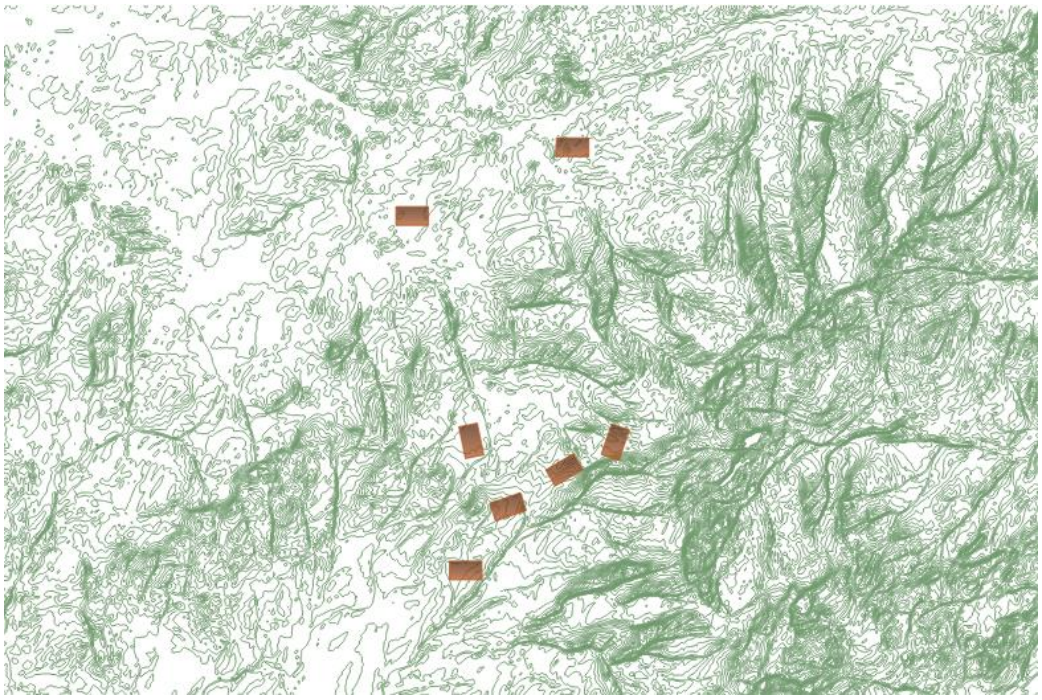

Figure 2.2: Contour map depicting the spatial arrangement and surrounding topography of stands sampled (n = 7) in the White Mountain National Forest, New Hampshire.

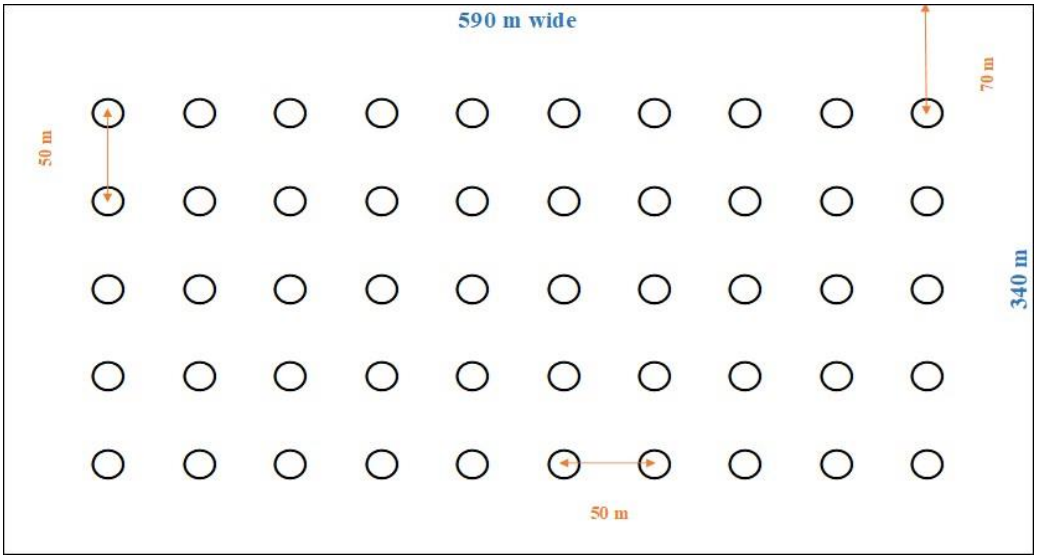

Figure 2.3: Individual plots (45 – 50) within a single forested stand (n = 14) in the Nulhegan Basin, Vermont and the White Mountain National Forest, New Hampshire. Stem counts, diameter at breast height, basal area and canopy closure were measured at each plot (Sirén 2020). Coarse woody debris was measured along three randomly selected transects out of ten.

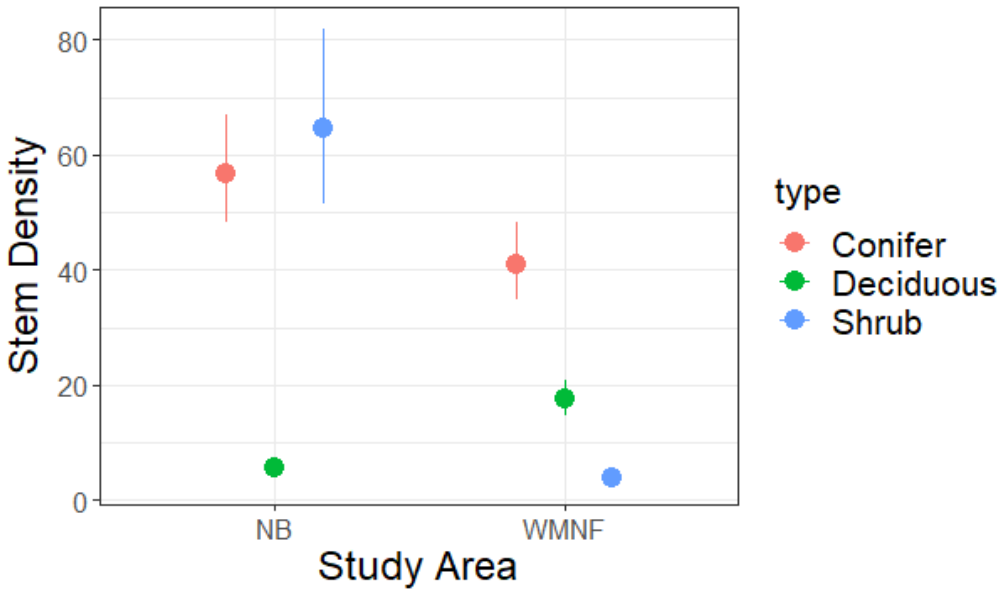

Figure 2.4: Poisson Generalized Linear Model (GLM) for stem counts in Nulhegan Basin (NB) and the White Mountain National Forest (WMNF). Coniferous stems estimated mean of 56.8 stems in NB and 41.0 stems in the WMNF; deciduous stems estimated mean of 5.7 stems in NB and 17.5 stems in the WMNF; shrub stems estimated mean of 64.8 stems in NB and 4.0 stems in the WMNF.

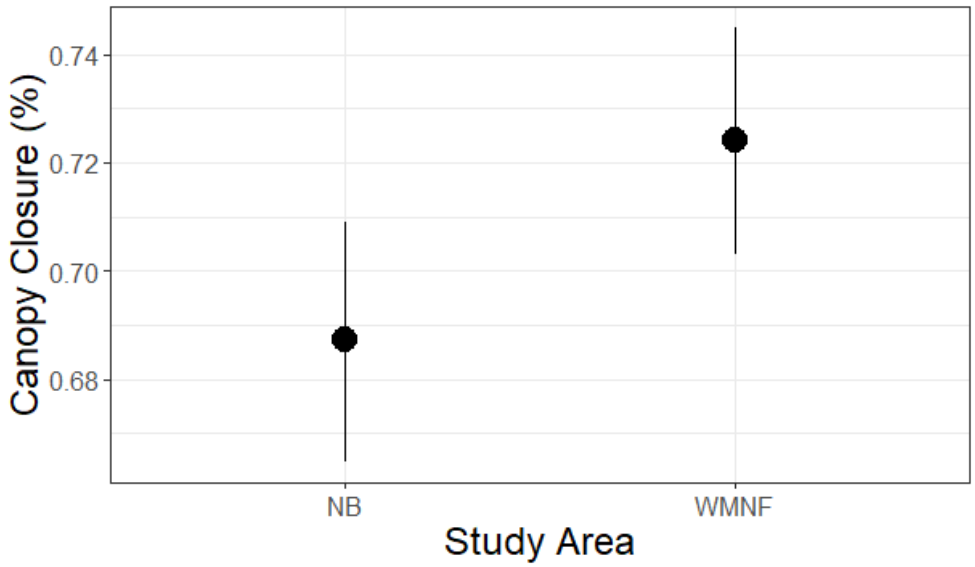

Figure 2.5: Beta-binomial GLM suggests that canopy closure was significantly less ($p < 0.02$) in Nulhegan Basin (NB) than in the White Mountain National Forest (WMNF). Both study areas were dominated by conifers, however, the estimated mean canopy closure was 68.6% in NB and 72.1% in the WMNF.

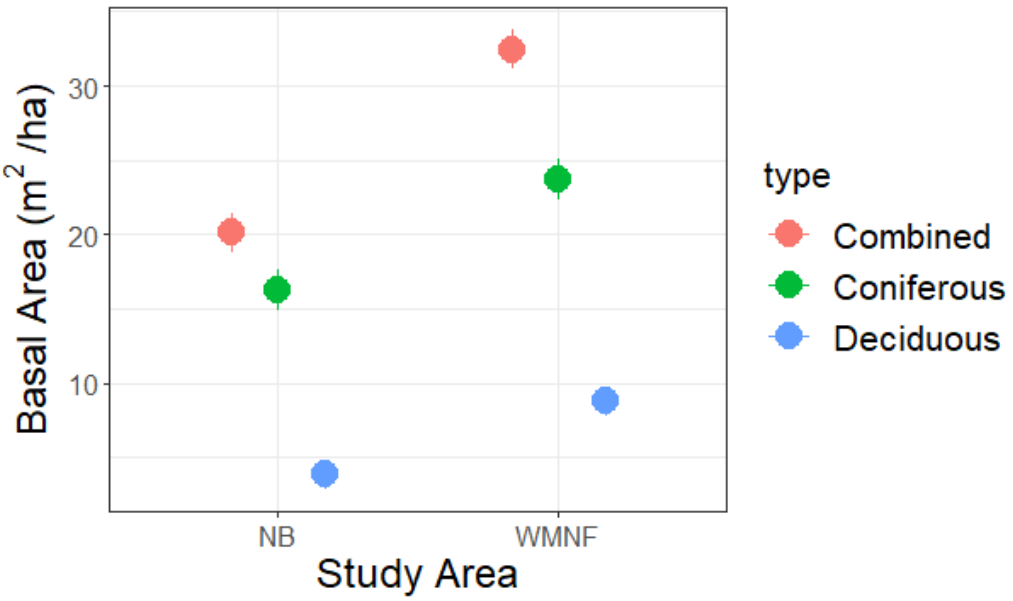

Figure 2.6: Linear model for basal area in the Nulhegan Basin (NB) and the White Mountain National Forest (WMNF). The estimated mean basal area was 20.1 m^2/ha in NB and 32.4 m^2/ha in the WMNF. The estimated mean coniferous basal area was 16.3 m^2/ha in NB and 23.7 m^2/ha in the WMNF. The estimated mean deciduous basal area was 3.9 m^2/ha in NB and 8.8 m^2/ha in the WMNF.

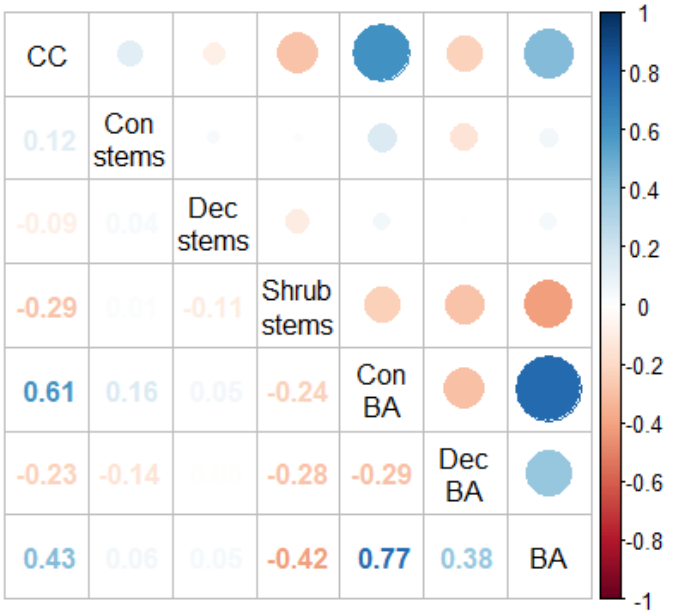

Figure 2.7: Correlation analysis of forest structure variables measured in the Nulhegan Basin and the White Mountain National Forest indicate that canopy closure (CC) and coniferous (Con) basal area (BA) had the highest positive correlation of all forest structure variables (r = 0.61). CC was positively correlated with total BA (r = 0.43) and negatively correlated with deciduous (Dec) BA (r = -0.23). Shrub stems were negatively correlated with coniferous BA (r = -0.24), deciduous BA (r = -0.28) and BA (r = -0.42).

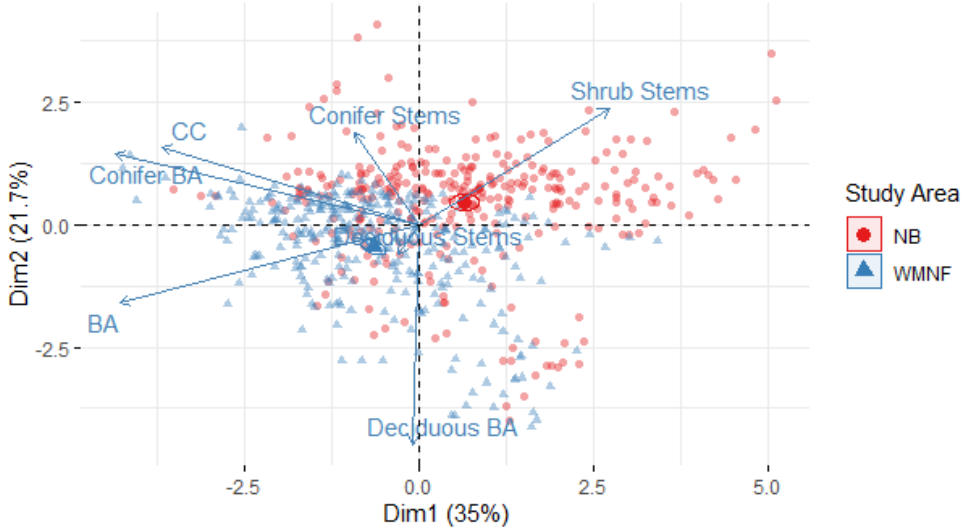

Figure 2.8: PCA biplot comparing PC1 (Dim1) and PC2 (Dim2), including stem counts, basal area (BA) and canopy closure (CC) in the Nulhegan Basin (NB) and the White Mountain National Forest (WMNF). PC1 indicates that the NB is characterized by high shrub stem counts and the WMNF is characterized by higher canopy closure and coniferous BA. PC1explains 35% of the variation.

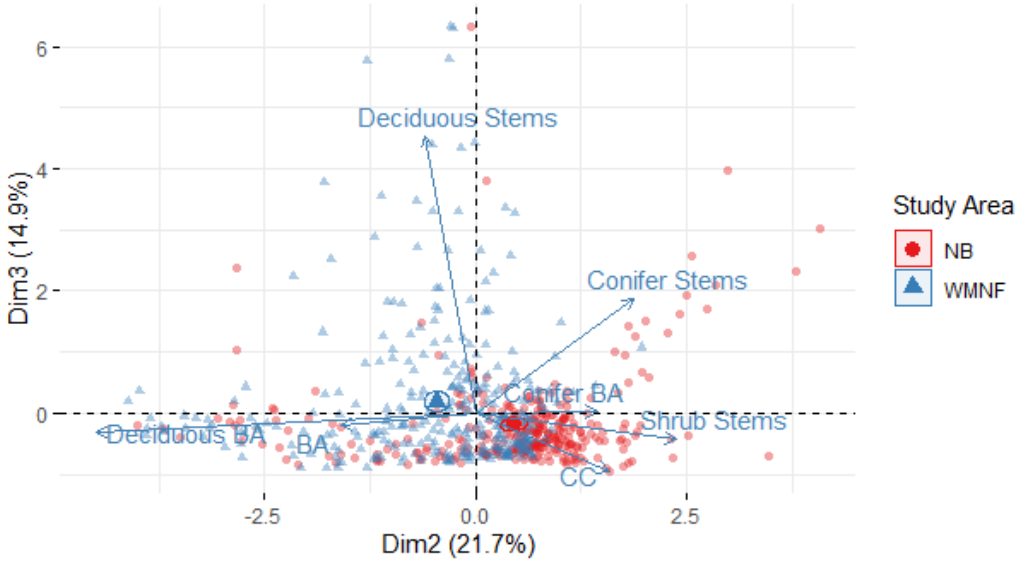

Figure 2.9: PCA biplot comparing PC2 (Dim2) and PC3 (Dim3) including stem counts, basal area (BA) and canopy closure (CC) in the Nulhegan Basin (NB) and the White Mountain National Forest (WMNF). PC2 indicates that both the NB and the WMNF are characterized by coniferous stems, with less in the WMNF. PC2 explains 21.7% of the variation.

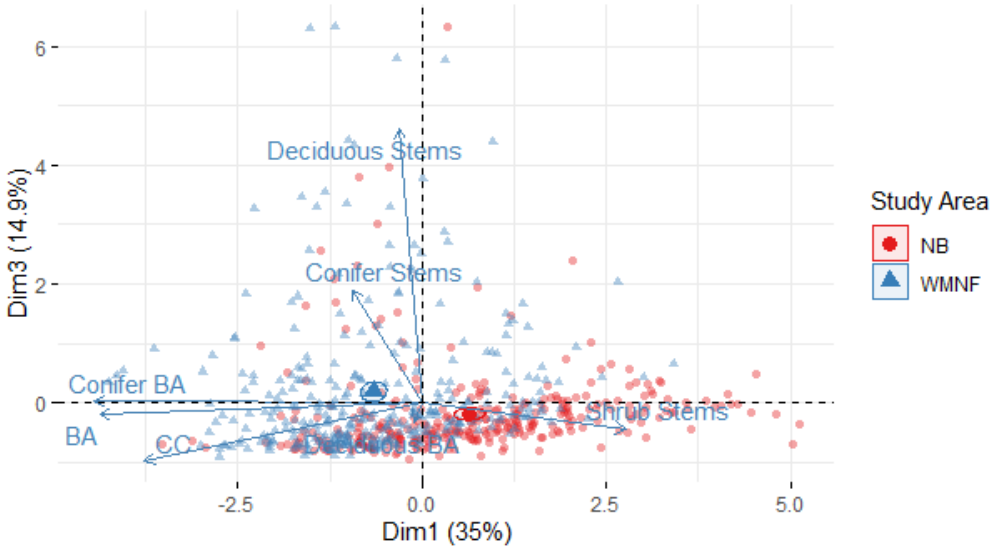

Figure 2.10: PCA biplot comparing PC1 (Dim1) and PC3 (Dim3) including stem counts, basal area (BA) and canopy closure (CC) in Nulhegan Basin (NB) and the White Mountain National Forest (WMNF). PC3 indicates that the WMNF is characterized by deciduous stems in comparison to PC1, which indicates shrub stems in the NB, however, PC3 explains only 14.9% of the variation.

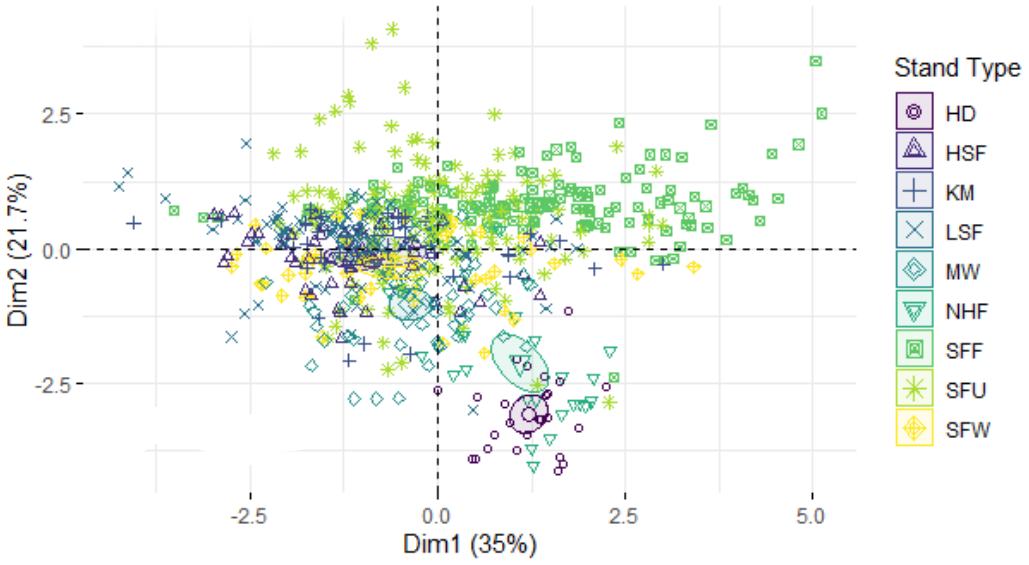

Figure 2.11: PCA analysis of forest structure according to stand types in Nulhegan Basin (NB) and the White Mountain National Forest (WMNF). Stands identified as SFF had the most shrub stems, stands identified as LSF, HSF and MW had the most deciduous stems and stands identified as SFU had the most coniferous stems. Stands identified as SFW and KM had the highest coniferous basal area and NHF and HD had the highest deciduous basal area. Stands identified as SFW and SFU had the highest canopy closure.

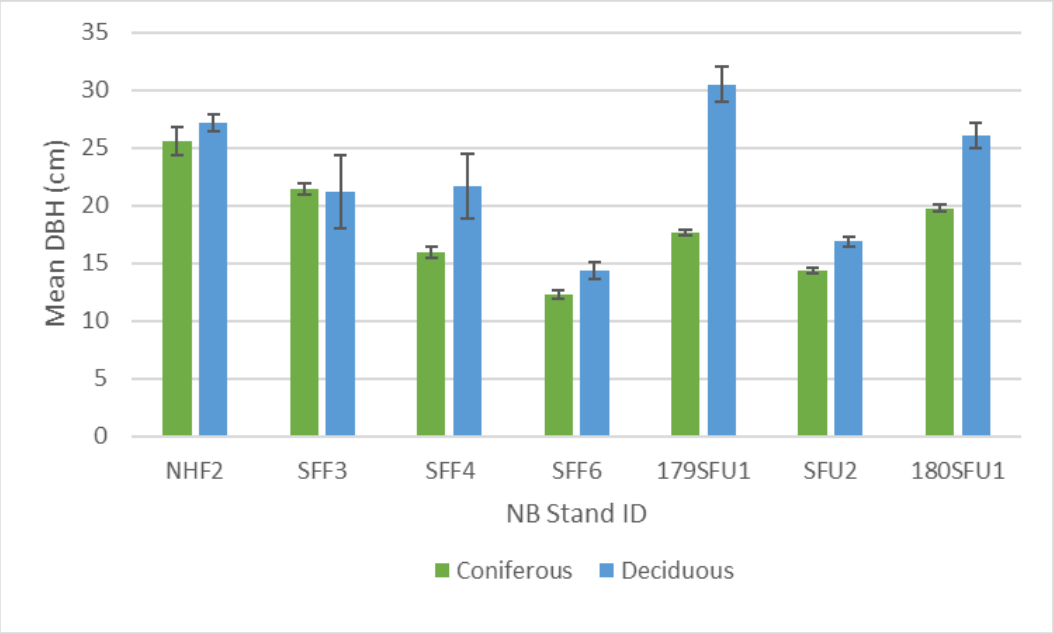

Figure 2.12: Mean diameter at breast height (DBH) of coniferous and deciduous trees in the Nulhegan Basin (NB).

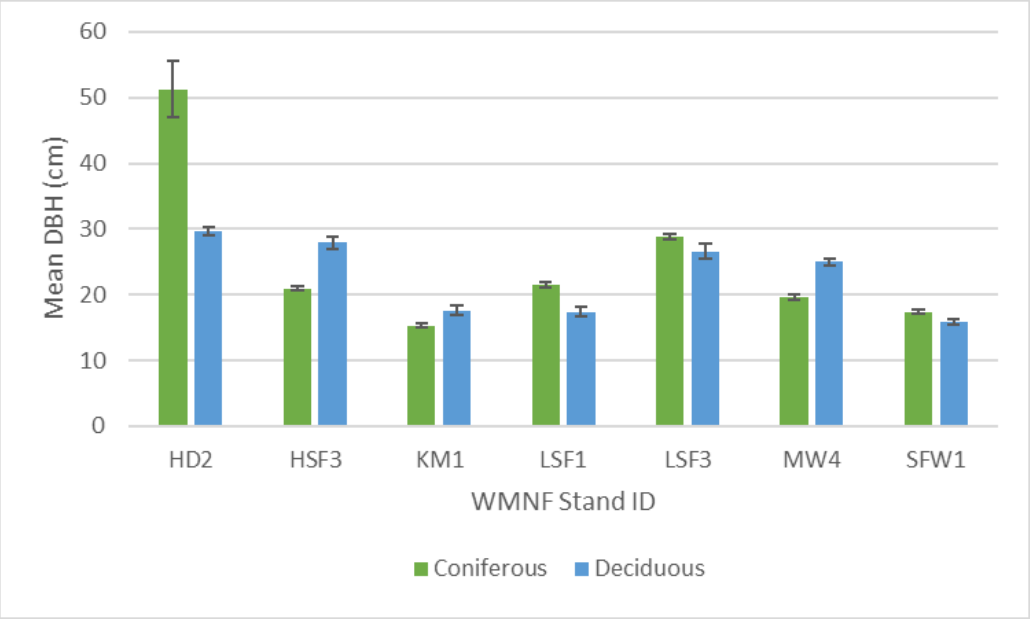

Figure 2.13: Mean diameter at breast height (DBH) of coniferous and deciduous trees in the White Mountain National Forest (WMNF).

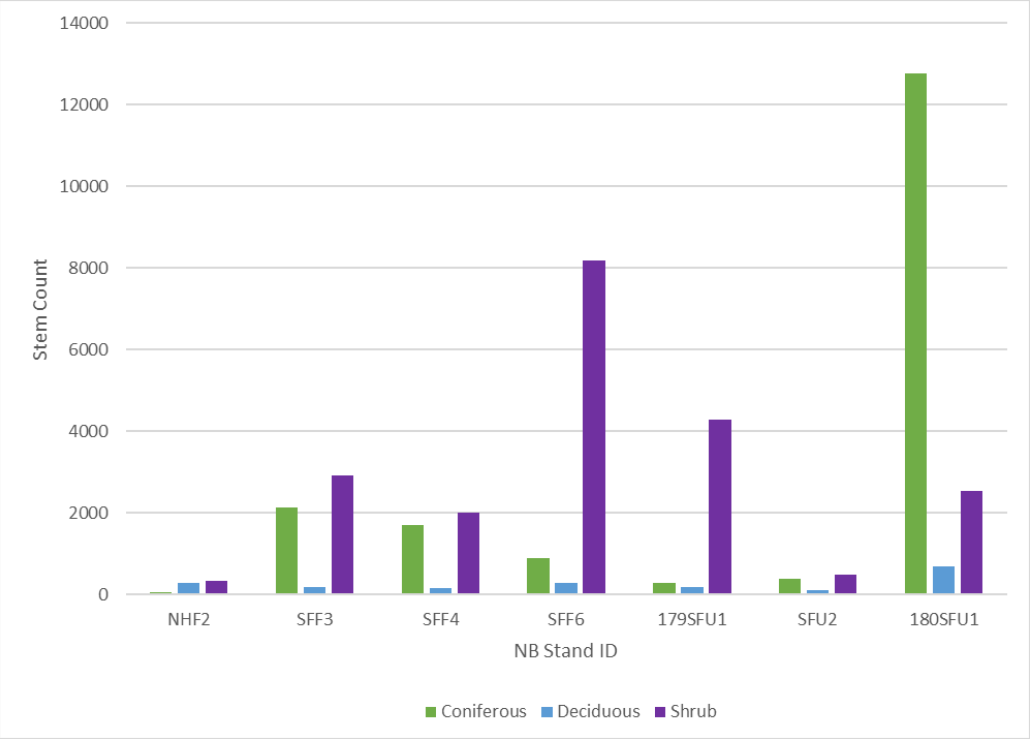

Figure 2.14: Stem counts (coniferous, deciduous and shrub) in the Nulhegan Basin (NB). Shrub stems were most abundant with deciduous stems the least abundant, except for one stand that had a disproportionately large number of coniferous seedlings (180SFU1). The single northern hardwood stand (NHF2) had the least number of all stem types.

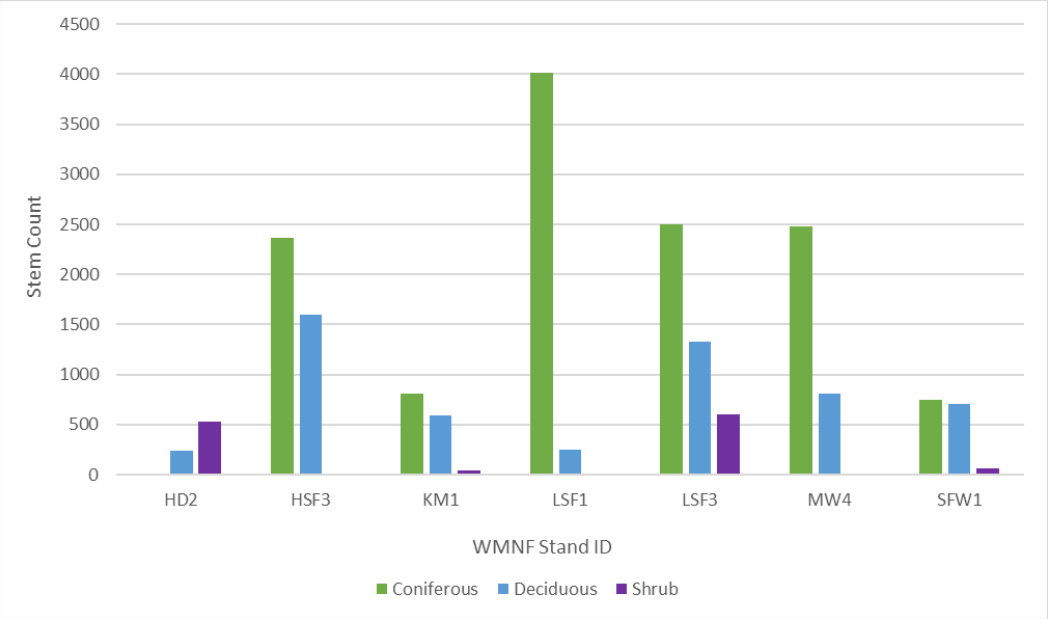

Figure 2.15: Stem counts (coniferous, deciduous and shrub) in the White Mountain National Forest (WMNF). Coniferous stems were most abundant with shrub stems the least abundant.

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CHAPTER 3: Co-Occurrence and Habitat Use Overlap of Snowshoe Hares and American Martens in Boreal, Mixedwood and Northern Hardwood Forests of the Northeastern U.S.

INTRODUCTION

Increasing biodiversity is a common goal shared among conservation groups, natural resource managers and numerous landowners (Harrison et al. 2010; Butler et al. 2021; Sass et al. 2021). The presence of keystone and umbrella species within the same community may increase biodiversity, however, empirical support is needed to guide management decisions (Johnson et al. 2017). It is important to understand how forest structure influences the co-occurrence of keystone and umbrella species, such as snowshoe hares (*Lepus americanus*) and American martens (*Martes americana*) at several spatial scales. Hares and martens are associated with a broad spectrum of forest characteristics, due to their different habitat preferences (Payer and Harrison 2003; Fuller and Harrison 2013). Identifying key forest structure characteristics may allow for their co-occurrence at several spatial scales and increase biodiversity. An understanding of these relationships is critical for informing management to promote and maintain biodiversity along the deciduous-boreal ecotone of the northeastern U.S. (Goldblum and Rigg 2010).

Hierarchical selection of preferred habitat and food resources is dependent upon availability; however, an abundant resource does not guarantee high usage (Johnson 1980). Johnson (1980) ordered usage through spatial scales and defined habitat selection as the use of a habitat component disproportionate to its availability. First-order selection is the geographical range of a species. Second-order selection is the distribution of home ranges or social groups within that geographical range. Third-order selection is the use of habitat components within individual home ranges. Habitat components are the areas where a species is active, including microhabitats within patches or stands. Fourth-order selection is the procurement of resources such as food items and microhabitat features (e.g., shelter for resting and denning) within that particular habitat component (Johnson 1980; Morin et al. 2005). For example, selection of a habitat type is of higher order than selection of home range because the habitat type and availability is determined by the selected home range (Johnson 1980). Selection of available food resources is of higher order than selection of feeding locations because a particular feeding location is limited in the abundance and availability of its food resources (Johnson 1980). Martens may be present on the landscape (second-order selection), but they may not be present on the smaller stand scale where hares are abundant, due to certain characteristics of habitat components (third- and fourth-order selection). However, observable patterns on one scale do not necessarily predict patterns on other scales (Morin et al. 2005).

Prey abundance is typically used to predict predator habitat suitability, home range size, diet and fitness, however, the presence of prey does not guarantee successful prey acquisition, just as an abundant resource does not guarantee high usage (Johnson 1980; Andruskiw et al. 2008). Predator success among a variety of wildlife is largely dependent upon the structural complexity of the habitat (the horizontal and vertical distribution of woody vegetation including ground cover), and forest structure has a stronger influence on wildlife responses than stand age (Carey and Johnson 1995; Homyack et al. 2004; Andruskiw et al. 2008). Hares and predators such as martens are a good example of this. For instance, even if there is a purported high density of hares in early-successional patches, there may be no martens to prey on those hares if the habitat is lacking key forest structure characteristics (Fuller et al. 2007). Fuller (2007) found that stands with a high density of hares were not always associated with the presence of Canada lynx (*Lynx canadensis*), and this was attributed to limited access to prey in stands with very dense vegetative structure.

The objective of this chapter is to identify forest structure characteristics that affect the co-occurrence of hares and martens at several spatial scales. Specifically, we were interested in evaluating forest structure variables that were associated with habitat use overlap based on their preferred habitats. We collected forest structure data in two study areas that are characterized by early-to-mid-successional growth (Nulhegan Basin [NB]) and mid- to late-successional growth (White Mountain National Forest [WMNF]). I hypothesized that the habitat use overlap of hares and martens is contingent on habitat availability at several scales. Accordingly, I predicted that early-successional forest patches within a matrix of forest in the mid- to late-successional growth stage allows for co-occurrence of hares and martens. However, even if mid- to late-successional forests contain patches of early-successional habitat for hares, and the surrounding habitat is hypothetically suitable for martens, future studies may reveal that the lack of contiguous forests on the landscape may prevent martens from establishing home ranges despite the potential for suitable forest structure among smaller patches (i.e., second order habitat seleciton; Johnson 1980). Thus, scale is an important consideration in managing mosaics of older and younger forests.

METHODS

Data Collection

We used two years (2016 and 2017) of hare and marten live-trapping data to create occupancy models based on forest structure data collected between May and November of 2020 from pellet plot stands in northern Vermont (n = 7) and New Hampshire (n = 7) (see Chapter 2 for methods on collecting forest structure data). Stands of similar age classes were selected since hare density is variable and dependent upon age class (Hodson et al. 2011; Sullivan et al. 2012), and stands ranged in age from 25–60 yrs (early- to mid-regenerating) in the NB and 89–295 yrs (mid- to late-regenerating/mature) in the WMNF. Traps (n = 25–50 per stand) were placed at

or within 5 m of pellet plots for two summers (20 June–13 August 2016 and 6 June–28 July 2017) and baited with alfalfa cubes, pellets, and apple slices, including vanilla extract used as an olfactory attractant to lure animals inside. For more information on trapping and handling, see Sirén (2020). All activities associated with trapping, handling, and radio-collaring were done in accordance with an animal care and use protocol (University of Massachusetts, Amherst, IACUC Protocol # 2016-0024) (Sirén 2020).

Statistical Analysis

We used site occupancy models that account for imperfect detection using live-trap data to evaluate several hypotheses on habitat use. Due to the close spacing of live traps that resulted in >1 traps per average hare and marten home ranges, we interpreted "occupancy" as probability of use rather than probability of occurrence (Mackenzie et al. 2017). First, we fit a univariate, two-level categorical model (NB vs WMNF) to evaluate differences in second-order habitat selection. We fit a single variable (Julian day) in the detection submodel to account for seasonal changes in activity associated with breeding, forage availability, and behavioral responses to capture. To evaluate fourth-order habitat selection, we fit occupancy models for each species by assessing their presence or absence from live-trapping data based on forest structure variables. Specifically, we fit seven additive models using plot level forest structure measurements from Chapter 2 as predictors of occupancy, accounting for potential multicollinearity among variables. We evaluated three models separately using principal components (PC1, PC2 and PC3; see Chapter 2) as predictors for overlap in habitat use between species. Models were ranked using Akaike's Information Criterion (AIC), choosing the most parsimonious model with the lowest AIC score as the top model. Our primary interest was to evaluate habitat use overlap between hares and martens. To evaluate potential areas in fine-scale habitat use overlap, we examined the intersection of predicted habitat use based on the primary principal components (PC1 and PC2) that had the most unbiased estimates of occurrence and an influential effect on hares and martens. Specifically, we calculated the intersection of the fitted lines where PC1 and PC2 intersected. We then created a biplot for visual-exploratory analyses to interpret landscape and microhabitat forest characteristics that were associated with use by both species. To this end, we fit a multivariate co-occurrence model that allows us to identify areas of use between species. Forest succession between 2016 and 2020 was assumed negligible. We did not have enough stand replicates to evaluate third-order habitat selection, so we provided summaries of each stand to evaluate stand-level trends. All occupancy analyses were conducted using the "unmarked" package in the statistical program R (R Core Team 2020).

RESULTS

In the NB, we tallied 191 and 0 captures of hares and martens, respectively (Table 3.1). However, in the WMNF, captures were more evenly distributed (hares = 45,

martens = 46; Table 3.1). Hares often had one or more instances of recapture in most stands in the NB, however, this trend was not consistent with capture in the WMNF (Table 3.2). In the NB, hares were captured the most (79) in the softwood stand identified as SFF6 and the least (5) in the northern hardwood stand identified as NHF2. In the WMNF, hares were captured the most (23) in the high elevation spruce-fir stand identified as HSF3 and the least (0) in the northern hardwood stand HD2. In the WMNF, martens were captured the most (12) in the softwood stand identified as SFW1 and captured the least (1) in the northern hardwood stand HD2.

Landscape scale: second-order habitat selection

We found landscape-scale differences between martens and hares. Specifically, hares were more likely to be captured in traps in the NB than the WMNF, whereas the opposite pattern occurred for martens (Figure 3.1). Julian day had no apparent effect on hare occurrence; they were just as likely to be captured year-round. Martens, however, were more likely to be detected later during the trapping period, which may be attributed to the time of year when trapping occurred in the WMNF (Figure 3.2).

Stand scale: fourth-order habitat selection

Snowshoe hares

The top two additive models (hare3 and hare4) were within 2 AIC units of each other (Table 3.3). Hare3 indicated that occupancy was positively associated with shrub stem counts and negatively associated with high basal area ($\beta = 1.5$, SE = 0.69, $P = 0.03$ and $\beta = -0.28$, SE = 0.16, $P = 0.08$ respectively; $\psi = 0.52$, $p = 0.82$) (Table 3.4; Figure 3.3). Hare4 indicated that occupancy was also positively associated with shrub stem counts, however, canopy closure was not significant ($\beta = 2.22$, SE = 0.79, $P = 0.005$ and $\beta = 0.11$, SE = 0.16, $P = 0.5$ respectively; $\psi = 0.59$, $p = 0.90$).

American martens

The top two additive models (marten3 and marten4) were within 2 AIC units, mirroring the top two models for hares (Table 3.5). Marten3 indicated that martens had a higher probability of selecting areas with low shrub stem counts, however, basal area had a relatively weak positive effect on marten occupancy in this study ($\beta = -4.70$, SE = 2.36, $P = 0.05$ and $\beta = 0.09$, SE = 0.27, $P = 0.73$ respectively; $\psi = 0.06$, $p = 0.01$) (Table 3.6; Figure 3.5). Marten4 also indicated that occupancy was negatively associated with shrub stem counts, however, canopy closure was not significant ($\beta = -4.83$, SE = 2.39, $P = 0.04$ and $\beta = 0.03$, SE = 0.35, $P = 0.94$ respectively; $\psi = 0.06$, $p = 0.01$).

Hares and Martens

The top model for hares (hare9) with principal components as predictors indicated a positive relationship with PC2, suggesting that hare occupancy was positively associated with shrub and conifer stems and negatively associated with high deciduous basal area ($\beta = 0.72$, SE = 0.14, $P < 0.001$; $\psi = 0.43$, $p = 0.67$) (Figure 3.4). The top

model for martens (marten8) with principal components as predictors indicated a strong negative relationship with PC1, suggesting that martens selected against areas with high shrub stem counts, and were more likely to occupy areas with higher coniferous basal area and canopy closure, although that relationship was not as strong (β = -0.33, SE = 0.16, P = 0.04; ψ = 0.29, p = 0.42) (Figure 3.6). However, no martens were captured in the NB, thus zero probability and complete uncertainty of them occurring there despite the same trapping effort as the WMNF (the parameters are unidentifiable because they are estimated at 0, which means complete uncertainty in the estimate due to no captures since these models account for imperfect detection).

Visual-exploratory analysis indicated that the greatest habitat use overlap for hares and martens was where PC1 was approximately 0 and where PC2 was slightly negative, however, there was high uncertainty in these estimates (Figure 3.7). Visual examination of the biplot with PC1 and PC2 (from Chapter 2) at the multivariate intersection of the fitted occupancy lines where PC1 and PC2 crossed suggested that areas with higher deciduous stem counts were the forest structure variable associated with the highest overlap in habitat use at finer spatial scales for hares and martens (Figure 3.8). This was the multidimensional space associated with deciduous stem counts.

DISCUSSION

I hypothesized that the habitat use overlap of hares and martens is contingent on habitat availability at several scales. Accordingly, I predicted that early-successional patches of forest regeneration within a matrix of forest in the mid- to late-successional growth stage may allow the co-occurrence of both species. My hypotheses were supported by data from the WMNF, where there are early-successional patches of regeneration within a matrix of mid- to late-successional forest. Here, there are low hare populations with a presence of martens dispersed within the landscape. Other studies have shown that medium-sized trees with a diameter at breast height (DBH) of 10.3 – 27.9 cm provide protection from predators for hares and also have sufficient understory growth to provide reliable browse (Lewis et al. 2011; Thornton et al. 2012).

The early-successional forest patches observed in the WMNF are regulated by stochastic windthrow events and these moderate amounts of disturbance may promote the habitat use overlap of hares and martens on finer spatial scales and increase biodiversity; thus, these results are consistent with the Intermediate Disturbance Hypothesis (Connell 1978; Worrall and Harrington 1988; Lorimer and White 2003; Rich et al. 2007). Areas that experience a disturbance typically result in prominent forest structure characteristics. For example, low basal area and low canopy closure in certain stands may indicate a gap created by windthrow (WMNF) or an area impacted by logging (NB). Trees with larger DBH may suggest that stands have not experienced a significant disturbance and smaller DBH may indicate a more recent

event. However, tree diameter is not a reliable indicator of tree age, as exposure to harsh environments may limit growth (Sprugel 1984). Hares and martens are positively associated with a broad spectrum of forest characteristics and are impacted by varying amounts of disturbance.

Consistent with my predictions, habitat use of both species was scale-dependent. Martens were not detected in the NB, indicating a divergence in occurrence at larger spatial scales, likely explained by differing forest structure between study areas and lack of contiguous habitat. Indeed, as discussed earlier in Chapter 2, mean basal area in the NB was 18 m^2/ha which is the minimum threshold that Payer and Harrison (2003) suggested for martens to occur in Maine. Hares, however, are found in a variety of forest types and age classes in eastern North America (Hodson et al. 2011).

What structural features are associated with hare occupancy?

Forest structure within a habitat has a greater influence on hares than species composition (Litvaitis et al. 1985; Ferron and Ouellet 1992). For example, stem counts were positively associated with hare occupancy and stems provide dense understory lateral foliage for cover from predators, thermal protection from exposure to climatic events and available browse (Litvaitis et al. 1985; Fuller and Harrison 2013). Specifically, shrub stem counts had the greatest influence on hares in the NB compared to coniferous and deciduous stems in the WMNF. All stems under 7.6 cm DBH were counted in this study, including seedlings. There is often a minimum stem diameter that studies utilize when counting stems that disregard the presence of seedlings (Lee et al. 2005; Fuller et al. 2007; Berg et al. 2012). The diameter at point of browsing for hares is normally ≤ 3 mm (Pease et al. 1979). Pease (1979) found a direct correlation between undernutrition and larger diameter twigs; thus, the importance of seedlings may be overlooked as a source of browse. To better understand trends, future studies may consider including a seedling category and a sapling category. Saplings may provide lateral cover, while seedlings may provide more nutritious browse. The NB had a large proportion of lowbush blueberry (*Vaccinium angustifolium*), a highly preferred browse species for hares with many branches < 3 mm (Wolff 1978), and these stems may have been disregarded had there been a minimum DBH for counting stems within the protocol.

The diverse processes that reduce basal area and create patches of early, regenerating boreal and mixedwood forests among older stands in the northeastern U.S. are contingent upon weather events, insects, disease, forest fires, senescence and logging (Kneeshaw and Bergeron 1998; Chen and Popadiouk 2002). Windthrow is the most common of these natural disturbances and destructive weather events with high wind include microbursts, ice storms and occasional tornadoes (Rich et al. 2007). Hare occupancy was negatively associated with basal area, which can be significantly reduced in forest stands that experience a windthrow event or other disturbance. However, these stochastic events may be too intermittent or mild to significantly reduce basal area in places like the WMNF; thus, the limited number and size of regenerating forest patches may restrict an increase in hare populations.

Wave-regeneration is a phenomenon observed in high elevation montane environments, resulting in an ascending pattern of succession (Sprugel 1976). Standing dead trees occupy the space above a growth release of regenerating seedlings and saplings, and steadily increase to mature forest (Sprugel 1976). These areas are typically dominated by balsam fir (*Abies balsamea*) and are attributed to disturbances and extreme exposure fueled by the prevailing winds (Sprugel 1976; WAP 2015). For instance, rime ice or winter desiccation can cause wave-edge mortality, which continuously causes trees to die off on the leading edge of a wave (Sprugel 1976; Foster 1988). Although these fir waves are dynamic, they take years to move through the forest and may provide hares with reliable patches of early-successional conditions, with reduced basal area and high stem counts (Sprugel 1984).

Similar to basal area, patch size may affect survival, extirpation, and extinction of hare populations. Keith et al. (1993) observed extirpation in 3 out of 5 patches that were ≤ 7 ha of prime habitat, but none on 2 larger patches ≥ 23 ha. It is important to note, however, that Keith et al. (1993) conducted his study in matrix habitat dominated by upland hardwoods and wetlands. Regardless, patches of optimal hare habitat (i.e. higher stem counts and lower basal area) in the WMNF that have reduced basal area may not be large enough to sustain more than a few hares with adequate resources. Logging has been the primary major disturbance in the NB, especially with extensive harvesting after the spruce-budworm infestation of the 1970s and 1980s, resulting in a resource rich environment with low overstory basal area and abundant spruce-fir regeneration, where hares typically thrive and are most abundant (Litvaitis et al. 1985; Chen et al. 2017).

What structural features are associated with American marten occupancy?

The WMNF contains some of the oldest forests, deepest snowpack and highest elevations in the northeastern U.S. (Seidel et al. 2009; Foster and D'Amato 2015), which provide martens with a refugium less susceptible to climate change and human alterations (Carroll 2007; Sirén et al. 2017). In areas similar to the NB, forestry has both direct and indirect impacts on landscape and species responses; the complexity of forest structure is reduced in certain applications and species fecundity may be affected due to increased access by predators and humans to previously remote areas (Chapin et al. 1998; Carroll 2007). However, uneven-aged silviculture can promote greater structural complexity through SCE (structural complexity enhancement) and this method may accelerate the development of late-successional characteristics within a stand (Keeton 2006). The early-successional forest conditions and high stem density in the NB are considered less complex than the older forests found in the WMNF (Clark et al. 1998; Andruskiw et al. 2008). Martens selected against areas with high shrub stems and although martens are present in the higher elevations surrounding the NB, zero were captured within the basin itself, despite available prey. Stem counts were negatively correlated with canopy closure and basal area, both of which were significantly greater in the WMNF (see Chapter 2). We found only a weak relationship between basal area and marten occupancy, suggesting that the size-class

of trees may have a greater influence on occupancy than basal area, although this was not evaluated in this study. For example, plot level comparisons show that two plots had a mean DBH of 10 cm for coniferous trees (one plot in the NB (stand ID: SFF6 plot 30) and one plot in the WMNF (stand ID: KM1 plot 15), however, coniferous basal area measured 32.1 m^2/ha and 16.1 m^2/ha in those plots, respectively. Similarly, multiple plots had a coniferous basal area of exactly 18.4 m^2/ha, and each of those plots had a mean coniferous DBH that ranged from 9.4 cm to 39 cm DBH per plot. Thus, forested stands can have the same basal area and look completely different; therefore, high basal area may not always be associated with marten occupancy. Future studies may wish to investigate the size-class of trees within these forested stands to better understand and evaluate species responses.

The structural complexity of a given habitat may regulate the probability of predator success in prey acquisition, regardless of a high prey abundance (Andruskiw et al. 2008). Movement patterns are a result of foraging strategies to obtain maximum efficiency in resource acquisition with minimal risk (Barton and Hovestadt 2012). Predators are predicted to move sinuously through localized areas with anticipated and abundant prey, compared to the direct, fast and less sinuous movements through large areas with low prey density (Barton and Hovestadt 2012; Moriarty et al. 2016). Martens travel sinuously through complex forests, compared to linear movements through less complex habitats, with the potential to cover significant distances per day (Moriarty et al. 2016). The WMNF had nearly twice the amount of coarse woody debris compared to the NB (see Chapter 2) and may aid martens in the visual deception of predators and potential prey by allowing them to appear and disappear while traveling sinuously in areas with high abundance of coarse woody debris. Coarse woody debris is ecologically important within forested stands due to the benefits it provides for wildlife such as habitat, winter insulation, protection from predators, refugia and subnivean corridors for numerous species (Harmon et al. 1986). Martens may select for rugged terrain combined with high amounts of coarse woody debris, which could provide superior structural complexity that amplify these benefits (Sirén et al. 2016). Thompson and Colgan (1994) found that their data did not support the hypothesis that logged boreal forests with minimal subnivean openings are a limiting factor for martens, thus restricting population growth. However, these findings oppose the views of other researchers (Koehler and Hornocker 1977; Steventon and Major 1982; Lofroth and Steventon 1990). This may be due to the compounding effects of logging as observed in the NB; even if there are minimal subnivean openings associated with coarse woody debris, there is typically less canopy closure to protect martens from predation during their daily movements. Thus, the availability of denning habitat provided by coarse woody debris is critical for the recruitment and success of marten populations (Ruggiero et al. 1998) and disturbances caused by timber harvesting can have profound effects on martens, whose sensitivity to logging varies regionally (Hargis et al. 1999; Cheveau et al. 2013; Sirén et al. 2016).

What structural features are associated with the co-occurrence of hares and martens?

Deciduous stems were associated with the habitat use overlap supporting the co-occurrence of hares and martens and unrelated to other forest structure variables (see Chapter 2). Deciduous stems are a viable food source for hares in early successional stages, however, they can grow significantly larger than shrub stems, and may contribute to complex forest structure and coarse woody debris in later successional stages. Further, hares are restricted to ground level, which makes the low lateral cover that all stem types provide, imperative for their survival. However, when deciduous stems mature into larger trees, they provide canopy closure that may benefit martens, whose arboreal habits do not restrict them to ground level. Thus, deciduous stems may have three phases that contribute to the habitat use overlap of hares and martens: seedlings/saplings, mature trees, and coarse woody debris. Mixedwood stands often include deciduous species such as maple (*Acer* spp.) and birch (*Betula* spp.), and have been suggested as key habitats within a boreal landscape for martens because they provide dense cover, denning sites, and increased prey availability, while reducing the risk of avian predation (Cheveau et al. 2013). Red maples (*A. rubrum*) were the most common deciduous stems in both study areas and the seedlings and saplings often had evidence of herbivory from hares (personal observation). Red maple is considered a minor climax species with intermediate tolerance, and often persists in older softwood stands (Leak 1991).

Hares and martens in the WMNF

Hare populations inhabiting the southern edges of their range are typically less dense and acyclic, and do not display the pronounced cyclic population fluctuations that are observed throughout the northern boreal forests of Alaska and Canada; the peaks and lows of these cycles are greatly attenuated farther south (Keith et al. 1993; Wirsing et al. 2002; Newey et al. 2007). Low-density hare populations may have higher survival rates and may remain in areas of their preferred browse due to less competition for food and minimal predation (Wolff 1980; Sirén 2020). The low stem counts in the WMNF may be adequate for hares to persist; however, if martens are present within the same forest matrix, the habitat use overlap may allow martens to prey on hares more frequently and limit their population growth (Sirén 2020). Sirén (2020) found that martens were the most common predator of hares in the WMNF, and yet survival was significantly less for hares in the NB compared to the WMNF; thus, dynamic hare populations may directly affect marten occupancy and fourth-order habitat selection (Sirén et al. 2021).

An abundance of preferred browse or increased food availability has been shown to decrease home range size, and hares have been observed to shift their ranges into safer areas that provide greater cover in response to increased pressure due to predation, despite potential decreases in optimum browse availability (Wolff 1980; Boutin 1984;

Feierabend and Kielland 2014). Although hare abundance is significantly lower in the WMNF than in the NB (Sirén 2020), hares in the WMNF may have been restricted to the few areas that provide cover in early-successional patches with a reliable food source, resulting in lower captures. The development of early, regenerating forest patches with high stem counts as a result of windthrow in older forested stands may provide hares with reliable browse and cover from predators by reducing visibility (Fuller et al. 2007). This may limit daily and seasonal movements. On the other hand, when resources are depleted, this may trigger greater shifts in search for other resource rich patches. Sirén (2020) observed significantly greater movements of hares in the WMNF compared to the NB, which may be related to resource acquisition. Further, seasonal shifts may result in occupying areas that have reduced basal area and canopy closure in summer when sunlight exposure stimulates abundant herbaceous and deciduous browse at ground level (lateral cover) and selecting areas with greater coniferous cover in winter after deciduous abscission (Adams 1959; Feierabend and Kielland 2014). Additionally, direct light only reaches the ground level of the largest gaps created from disturbances due to the low sun angle in northern latitudes and this may also stimulate a seasonal surplus of herbaceous vegetation in these open patches (Kneeshaw and Bergeron 1998). Martens may avoid these exposed areas, allowing hares to persist and coexist in small patches within a common forest matrix.

Marten occurrence patterns in the NB and the WMNF

A lack of contiguous area due to fragmentation from roads and unsuitable forest conditions may prevent martens from establishing home ranges, despite ideal forest structure. Home range size for martens is highly variable and they do not adhere to any specific geographic patterns (Buskirk and McDonald 1989). However, the home range of martens is disproportionately large compared to their body mass relative to other carnivores (Lindstedt et al. 1986; Chapin et al. 1998). The NB consists of a network of roads accessible year-round and a large-proportion of early-successional forest.

The WMNF is a large contiguous area, dominated by spruce and fir mixedwood forests, with moderately low stem counts and minimal shrubs. There is a considerable distance between the WMNF and other large, contiguous areas of similar habitat, e.g., the Connecticut Lakes Region. Although studies suggest that martens will utilize small patches, large contiguous residual areas of uncut habitat (> 15 ha) have the greatest potential to be inhabited by martens, with the ability to sustain home ranges, especially in areas that experience intensive logging (Snyder and Bissonette 1987; Chapin et al. 1998; Sirén et al. 2016). Proximity of small patches to large contiguous forest and forest connectivity is critical to maintain marten populations, whose demographics naturally fluctuate due to resource availability (Chapin et al. 1998; Jensen et al. 2012). For example, the natural fluctuation of mast crops influences the abundance of small mammals that serve as a prey source for martens and thus affects demographic responses (Jensen et al. 2012). Further, traveling between patches or beyond their natural home range in search of resources may expose martens to the risk

of predation (Chapin et al. 1998). If the resources within an isolated area are unknown, the energy expenditure and caloric reward may not be worth the associated risks of traveling through less ideal habitat to reach a particular area.

Snyder and Bissonette (1987) captured only 5 of 51 martens in residual patches of undisturbed forest habitat < 15 ha within a heavily clear-cut area in Newfoundland, suggesting the importance of patch size when surrounded by less ideal habitat. The opposite is observed in the NB; the high elevation areas surrounding the basin have martens (Sirén et al. 2022), indicating more ideal forest structure surrounding less ideal habitat. Although hares are abundant in the NB, the less ideal habitat may deter martens from pursuing this available resource. Patches of uncut forest > 15 ha in the NB where martens could take refuge may not exist. Additionally, tamarack (*Larix laricina*) is a deciduous conifer in the NB, and there is a significant loss of canopy closure in winter when this species sheds its needles. This may also contribute to habitat avoidance compounded with high shrub stem counts that were negatively correlated with canopy closure and basal area (see Chapter 2; Figure 2.7). Other studies indicate that martens will avoid areas with < 30 - 40% canopy closure in winter within their home range (Koehler and Hornocker 1977; Spencer et al. 1983; Chapin et al. 1998; Potvin et al. 2000).

Additional factors that may limit martens in the NB may depend on predator-prey interactions along range limits. Sirén et al. (2021) found that coyotes had a negative effect on martens and the vast network of established logging roads and skid trails throughout the NB may provide coyotes greater accessibility to prey, and thus minimize the negative effect of snow depth on cold-limited populations along range edges. Regardless, if 18 m^2/ha is indeed the minimum threshold for marten occupancy in the northeastern U.S. (Payer and Harrison 2003), the martens in the higher elevations surrounding the NB may expand into the lower elevations in the coming years if management practices allow basal area to increase.

Trapping implications

Live-trapping can be an invasive method of obtaining data with the potential to create unnatural behavioral responses and biased population estimates (Green et al. 1981). Trap shyness can result in trap avoidance or species may become trap happy and visit traps more frequently in search of available bait (Pollock et al. 1990). Further, certain individuals or other species may be more vulnerable to capture or procure bait without capture (Strickland and Douglas 1987; Noyce et al. 2001). Sirén (2020) observed hares were more likely to be trapped repeatedly after their first capture, suggesting a trap-happy response in certain individuals (Pollock et al. 1990). Humans may also have indirect effects on captures. For example, the stand identified as SFW1 in the WMNF had a hiking path towards the southern end, and hikers (including domestic dogs) routinely traveled through the area, leaving food scraps and human scent. Live trapping occurred in this stand throughout the summer months, during peak hiking

season. Snow tracks and scent marking reveal avid use of the trail by hares and martens in winter and may be seasonally dependent. SFW1 had the most marten captures, however, there was only one hare captured in the trap located farthest away from the hiking trail in this stand. This response may also reflect the behavioral nature of each species; hares are an herbivorous prey animal that instinctually shy away from danger, and martens are a more aggressive and carnivorous predator at a higher trophic level (Havens 1993; Tirok et al. 2011; Jensen et al. 2012). Both species may have their own bias towards capture, regardless of their response to direct or indirect human interaction.

Future Management

It is important to evaluate entire ecosystems rather than focusing on single biotic or abiotic factors for effective management. Hares are a keystone species and martens are an umbrella species. Their different habitat preferences provide unique management challenges to sustain populations of both species within a common forest matrix. Accurately identifying suitable habitat for hares and martens could lead to future and successful reintroduction programs, habitat restoration, increased biodiversity, and prey availability for species of concern (e.g., Canada lynx).

Timber harvesting can result in a matrix of forest in various successional stages and the method in which forests are harvested is contingent upon the mechanics of the logging operation, the potential impacts of major disturbances (storm events, wildfire and pests), the amount of biodiversity desired and is largely driven by landowner goals (Franklin and Forman 1987). Studies have consistently shown that timber harvesting affects the distribution and demographic rates of martens (Chapin et al. 1998; Payer and Harrison 2003; Carroll 2007) and influences hare abundance (Homyack et al. 2007; St-Laurent et al. 2008; Lewis et al. 2011). Future studies utilizing LiDAR (Light Detection and Ranging) may guide foresters in their decisions regarding patch size and scale. LiDAR may indicate what portion of a stand to harvest and what size openings are appropriate for maximizing targeted wildlife populations. LiDAR may also quantify the concept of moderate in terms of optimal disturbance size. State, federal and private agencies may consider giving landowners incentives to meet desired biological results while evaluating any significant economic gains or losses. Landowners who own large parcels of mid to late-successional forests that connect to core areas like the WMNF, could collaborate with natural resource managers to create early-successional patches of habitat for hares while maintaining the forest structure for martens. Connectivity between core habitats may potentially result in increased hare and marten populations and thus increase overall biodiversity. Landowners with large stands of early successional forest could allow areas of older growth to develop if they have no interest in timber harvesting.

PCA was an effective method to analyze the large data set associated with extensive field measurements, and to evaluate large-scale trends. Additional statistical analyses combined with more specific field measurements focused on hotspots may clarify the connection between disturbance patterns and biodiversity. Future studies may wish to examine small patches within the WMNF where small-scale disturbances are evident to determine how these hotspots influence biodiversity and if the Intermediate Disturbance Hypothesis is scale dependent (*sensu* Connell 1978). Places like the NB reflect a large-scale disturbance and have a robust population of hares but are lacking the complex forest structure and habitat connectivity required to sustain martens. However, mean basal area for coniferous trees in sampled stands within the NB is 18 m^2/ha and Payer and Harrison (2003) suggested that martens may select stands in Maine with basal area > 18 m^2/ha. Therefore, new forest management strategies and the development of habitat connectivity with adapted logging practices could give places like the NB the potential to increase biodiversity and support both hares and martens in the years to come.

TABLES

Table 3.1: Number of hares and martens captured in the Nulhegan Basin (NB) and the White Mountain National Forest (WMNF) between 20 June–13 August 2016 and 6 June–28 July 2017. The number of captures indicates how many times a hare or marten was captured (e.g., 99 hares were captured once, 26 hares were captured twice, 12 hares were captures three times).

Study Area	Species	Number of captures					Total
		0	1	2	3	4	
NB	hare	230	99	26	12	1	191
WMNF		373	39	3	0	0	45
NB	marten	368	0	0	0	0	0
WMNF		374	36	5	0	0	46

Table 3.2: Number of hares and martens captured in each stand in the Nulhegan Basin (NB; n = 7) and the White Mountain National Forest (WMNF; n = 7) between 20 June–13 August 2016 and 6 June–28 July 2017.

Study Area	Stand ID	Species	Number of captures					Total
			0	1	2	3	4	
NB	G179_NHF2	hare	21	3	1	0	0	5
NB	G179_SFF3	hare	29	16	3	2	0	28
NB	G179_SFF4	hare	33	12	3	2	0	24
NB	G179_SFF6	hare	49	30	14	7	0	79
NB	G179_SFU1	hare	41	6	1	0	0	8
NB	G179_SFU2	hare	37	11	1	1	0	16
NB	G180_SFU1	hare	25	21	3	0	1	31
NB	G179_NHF2	marten	25	0	0	0	0	0
NB	G179_SFF3	marten	50	0	0	0	0	0
NB	G179_SFF4	marten	50	0	0	0	0	0
NB	G179_SFF6	marten	100	0	0	0	0	0
NB	G179_SFU1	marten	48	0	0	0	0	0
NB	G179_SFU2	marten	50	0	0	0	0	0
NB	G180_SFU1	marten	50	0	0	0	0	0
WMNF	G106_HD2	hare	25	0	0	0	0	0
WMNF	G106_HSF3	hare	79	19	2	0	0	23
WMNF	G106_KM1	hare	37	3	0	0	0	3
WMNF	G106_LSF1	hare	38	11	1	0	0	13
WMNF	G106_LSF3	hare	48	2	0	0	0	2
WMNF	G106_MW4	hare	47	3	0	0	0	3
WMNF	G106_SFW1	hare	99	1	0	0	0	1
WMNF	G106_HD2	marten	24	1	0	0	0	1
WMNF	G106_HSF3	marten	94	6	0	0	0	6
WMNF	G106_KM1	marten	36	3	1	0	0	5
WMNF	G106_LSF1	marten	45	5	0	0	0	5
WMNF	G106_LSF3	marten	45	4	1	0	0	6
WMNF	G106_MW4	marten	41	7	2	0	0	11
WMNF	G106_SFW1	marten	89	10	1	0	0	12

Table 3.3: Results of occupancy (Ψ) models with all possible covariates, including the number of model parameters (K), Akaike Information Criterion Score (AICc), delta AIC (ΔAICc) and model weights (w_i) for fourth-order habitat selection. Seven additive models (hare1- hare7) used plot level forest structure measurements as predictors of occupancy and accounted for potential multicollinearity among variables. Hare8 – hare10 used principal components from PCA (PC1, PC2 and PC3) as predictors. Occupancy models for hares used live-trapping data based on forest structure variables. Hare3 was the top model with the lowest AIC score.

Model	Occupancy covariates	K	AIC_c	ΔAIC_c	w_i
hare3	ψ (~ Julian day ~ SC shr[a] + BA[b])	5	1689.66	0.00	0.79
hare4	ψ (~ Julian day ~ SC shr[a] + CC[c])	5	1692.32	2.66	0.21
hare9	ψ (~ Julian day ~ PC2[d])	4	1700.24	10.58	0.00
hare1	ψ (~ Julian day ~ SC con[e] + BA[b])	5	1702.82	13.16	0.00
hare5	ψ (~ Julian day ~ SC dec[f] + BA[b])	5	1709.42	19.75	0.00
hare8	ψ (~ Julian day ~ PC1[g])	4	1713.02	23.36	0.00
hare7	ψ (~ Julian day ~ SC con[e] + BA con[h])	5	1723.03	33.37	0.00
hare2	ψ (~ Julian day ~ SC con[e] + CC[c])	5	1724.13	34.47	0.00
hare6	ψ (~ Julian day ~ SC dec[f] + CC[c])	5	1729.29	39.63	0.00
hare10	ψ (~ Julian day ~ PC3[i])	4	1734.78	45.11	0.00

[a] SC shr = number of shrub stems counted
[b] BA = basal area
[c] CC = overhead canopy closure
[d] PC2 = second principal component
[e] SC con = number of coniferous stems counted
[f] SC dec = number of deciduous stems counted
[g] PC1 = first principal component
[h] BA con = coniferous basal area
[i] PC3 = third principal component

Table 3.4: Hare model estimates, standard errors (SE), z-values, and probability statistics (*P*) for fourth-order habitat variables.

Model	Variable	Estimate	SE	z-value	*P*	
hare1	intercept	-0.213	0.207	-1.030	0.302	
	SC con	0.560	0.293	1.910	0.056	·
	basal area	-0.700	0.138	-5.060	0.000	**
hare2	intercept	0.042	0.269	0.157	0.875	
	SC con	0.603	0.469	1.286	0.198	
	canopy closure	-0.408	0.154	-2.652	0.008	**
hare3	intercept	0.096	0.358	0.267	0.790	
	SC shr	1.497	0.687	2.179	0.029	*
	basal area	-0.281	0.158	-1.778	0.076	·
hare4	intercept	0.371	0.405	0.916	0.360	
	SC shr	2.222	0.789	2.815	0.005	**
	canopy closure	0.114	0.162	0.699	0.484	
hare5	intercept	-0.243	0.199	-1.222	0.222	
	SC dec	-0.007	0.124	-0.061	0.952	
	basal area	-0.649	0.134	-4.861	0.001	**
hare6	intercept	-0.035	0.227	-0.155	0.877	
	SC dec	-0.078	0.128	-0.613	0.540	
	canopy closure	-0.376	0.155	-2.423	0.015	*
hare7	intercept	-0.040	0.232	-0.173	0.862	
	SC con	0.609	0.363	1.677	0.093	
	conifer basal area	-0.418	0.134	-3.129	0.002	**
hare8	intercept	-0.190	0.202	-0.940	0.347	
	PC1	0.348	0.081	4.290	0.001	**
hare9	intercept	-0.287	0.201	-1.430	0.153	
	PC2	0.729	0.143	5.090	0.001	**
hare10	intercept	-0.021	0.223	-0.094	0.925	
	PC3	0.092	0.147	0.626	0.531	

Significance is indicated by an (*) and marginally significant values are indicated by (·).

Table 3.5: Results of occupancy (ψ) models with all possible covariates, including the number of model parameters (K), Akaike Information Criterion Score (AICc), delta AIC (ΔAICc) and model weights (w_i) for fourth-order habitat selection. Seven additive models marten1- marten7) used plot level forest structure measurements as predictors on occupancy and accounted for potential multicollinearity among variables. Marten8 – marten10 used principal components from PCA (PC1, PC2 and PC3) as predictors. Occupancy models for hares used live-trapping data based on forest structure variables. Marten3 was the top model with the lowest AIC score.

Model	Occupancy covariates	K	AIC_c	ΔAIC_c	w_i
marten3	ψ (~ Julian day ~ SC shr[a] + BA[b])	5	452.32	0.00	0.51
marten4	ψ (~ Julian day ~ SC shr[a] + CC[c])	5	452.43	0.11	0.48
marten8	ψ (~ Julian day ~ PC1[d])	4	463.67	11.35	0.00
marten9	ψ (~ Julian day ~ PC2[e])	4	464.46	12.14	0.00
marten1	ψ (~ Julian day ~ SC con[f] + BA[b])	5	465.09	12.77	0.00
marten5	ψ (~ Julian day ~ SC dec[g] + BA[b])	5	465.69	13.37	0.00
marten6	ψ (~ Julian day ~ SC dec[g] + CC[c])	5	467.44	15.12	0.00
marten2	ψ (~ Julian day ~ SC con[f] + CC[c])	5	467.86	15.54	0.00
marten7	ψ (~ Julian day ~ SC con[f] + BA con[h])	5	468.15	15.83	0.00
marten10	ψ (~ Julian day ~ PC3[i])	4	468.55	16.23	0.00

[a] SC shr = number of shrub stems counted
[b] BA = basal area
[c] CC = overhead canopy closure
[d] PC1 = first principal component
[e] PC2 = second principal component
[f] SC con = number of coniferous stems counted
[g] SC dec = number of deciduous stems counted
[h] BA con = coniferous basal area
[i] PC3 = third principal component

Table 3.6: Marten model estimates, standard errors (SE), z-values, and probability statistics (*P*) for fourth-order habitat variables.

Model	Variable	Estimate	SE	z-value	*P*	
marten1	intercept	-0.872	0.600	-1.450	0.146	
	SC con	-0.398	0.379	-1.050	0.294	
	basal area	0.582	0.288	2.020	0.044	*
marten2	intercept	-0.733	0.628	-1.168	0.243	
	SC con	-0.207	0.311	-0.666	0.505	
	canopy closure	0.447	0.302	1.480	0.139	
marten3	intercept	-2.801	1.140	-2.458	0.014	*
	SC shr	-4.700	2.358	-1.993	0.046	*
	basal area	0.091	0.267	0.341	0.733	
marten4	intercept	-2.825	1.150	-2.458	0.014	*
	SC shr	-4.839	2.388	-2.027	0.043	*
	canopy closure	0.027	0.345	0.077	0.939	
marten5	intercept	-0.814	0.967	-0.842	0.400	
	SC dec	0.262	0.646	0.406	0.685	
	basal area	0.514	0.315	1.633	0.103	
marten6	intercept	-0.628	1.336	-0.470	0.638	
	SC dec	0.303	0.914	0.331	0.740	
	canopy closure	0.502	0.471	1.065	0.287	
marten7	intercept	-0.755	0.605	-1.250	0.212	
	SC con	-0.349	0.372	-0.940	0.347	
	conifer basal area	0.368	0.263	1.400	0.163	
marten8	intercept	-0.898	0.579	-1.550	0.121	
	PC1	-0.329	0.160	-2.050	0.040	*
marten9	intercept	-0.661	0.779	-0.849	0.396	
	PC2	-0.529	0.404	-1.307	0.191	
marten10	intercept	-0.699	0.590	-1.184	0.236	
	PC3	0.071	0.217	0.326	0.744	

Significance is indicated by an (*).

FIGURES

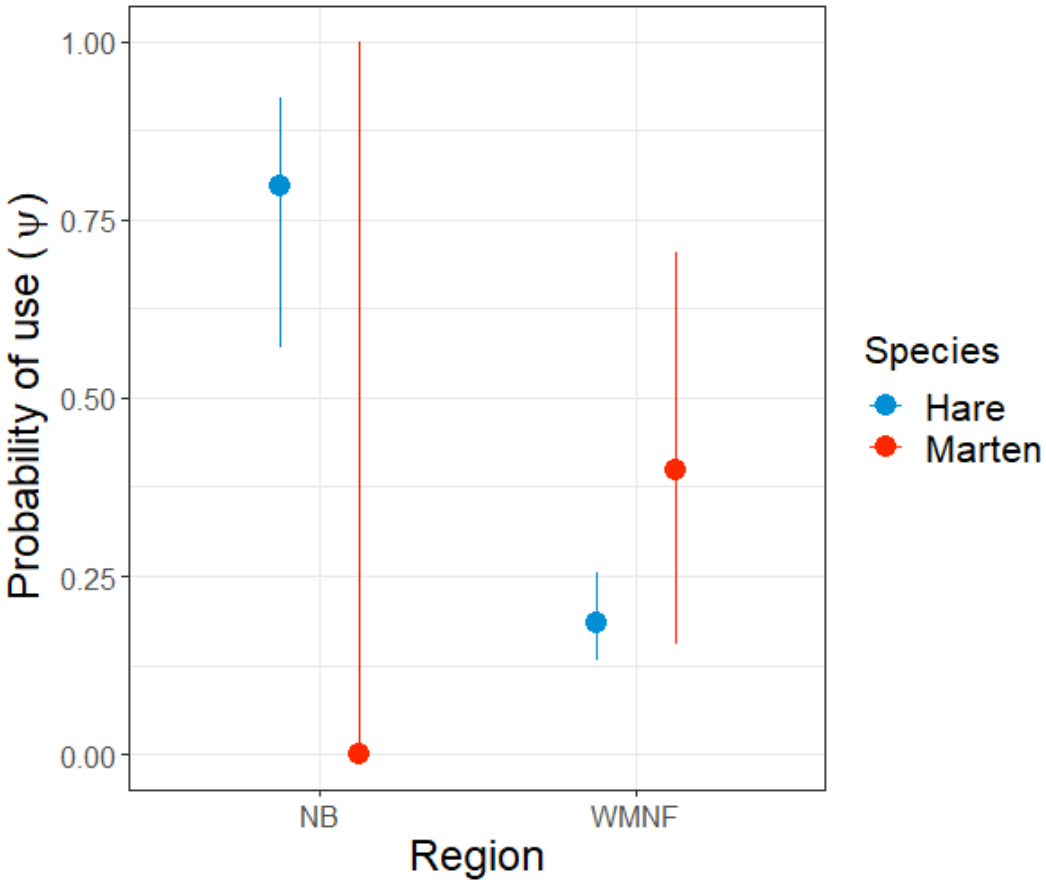

Figure 3.1: Hares selected for areas with forests characterized by structure found in the Nulhegan Basin (NB) and martens had a higher probability of selecting areas with forests characterized by structure found in the White Mountain National Forest (WMNF). Zero martens were captured in the NB, indicating complete uncertainty.

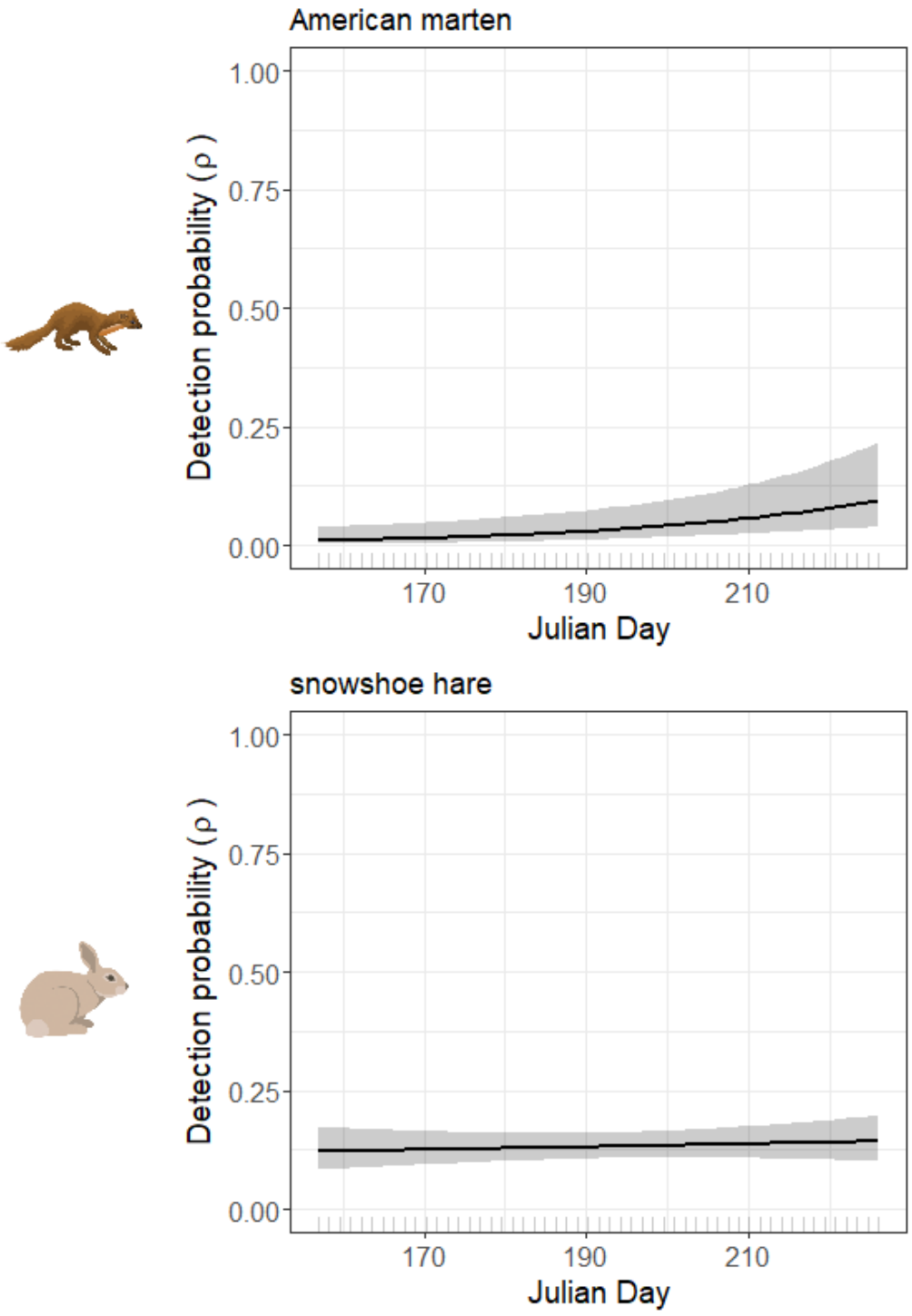

Figure 3.2: Julian day had no apparent effect on hare occurrence; they were just as likely to be captured year-round. Martens, however, were more likely to be detected later during the trapping period, which may be attributed to when trapping occurred in the WMNF.

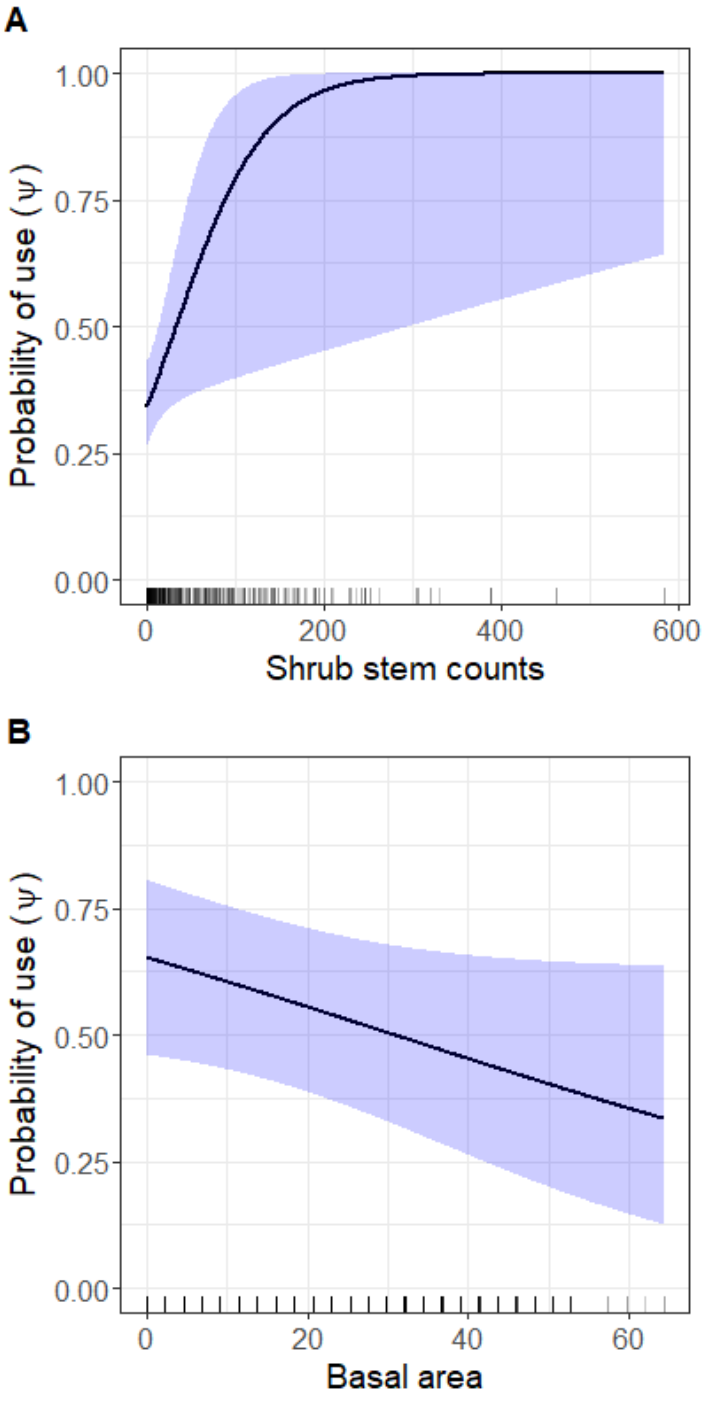

Figure 3.3: The two top models for hares (hare3 and hare4) within 2 AIC units of each other indicated that occupancy was positively associated with shrub stem counts and negatively associated with high basal area.

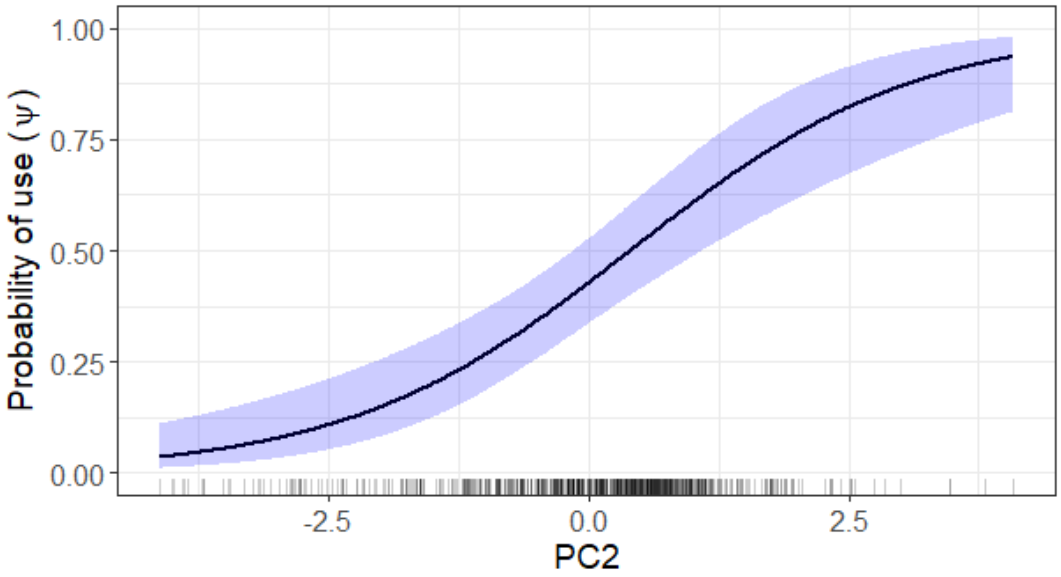

Figure 3.4: The top model for hares with principal components as predictors (hare9) indicated a positive relationship with PC2, suggesting that hare occupancy is positively associated with shrub and conifer stems and negatively associated with high deciduous basal area.

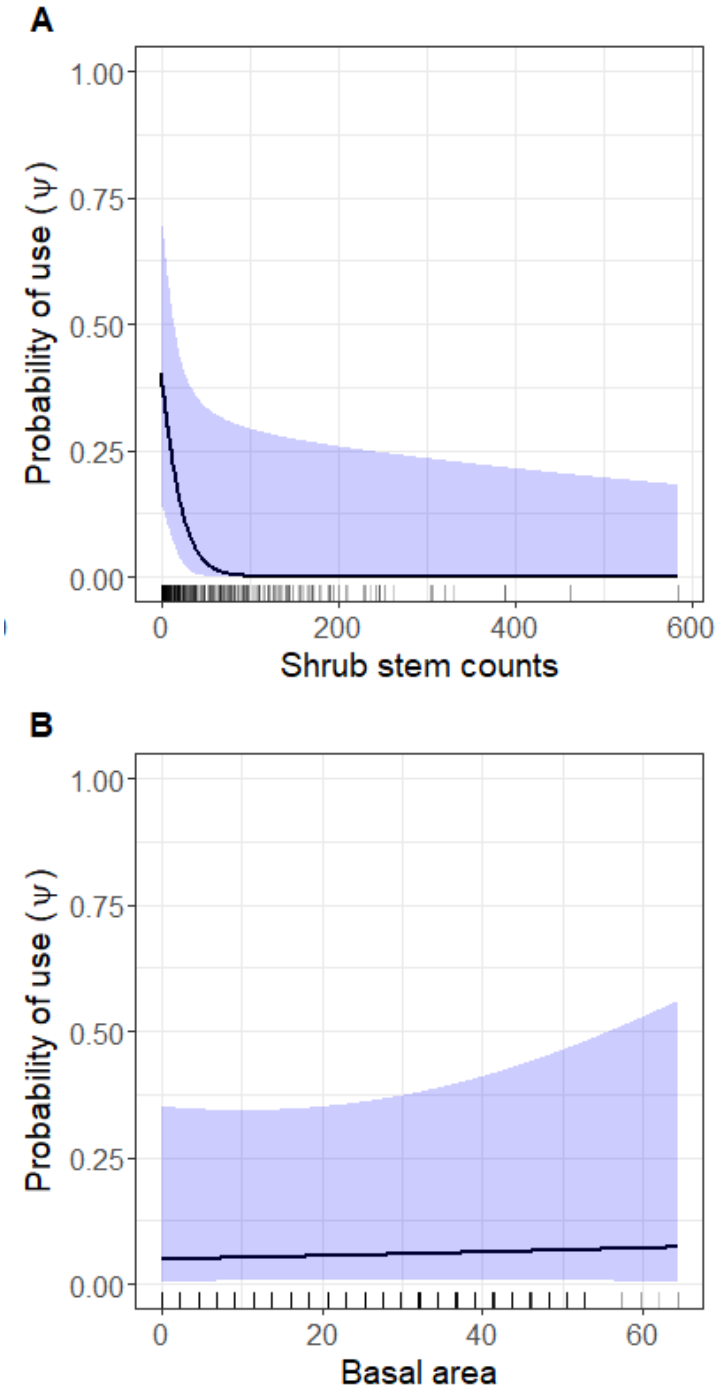

Figure 3.5: Martens had a higher probability of selecting areas with low shrub stem counts (marten3), however, basal area had a relatively weak effect on marten occupancy in this study (marten4).

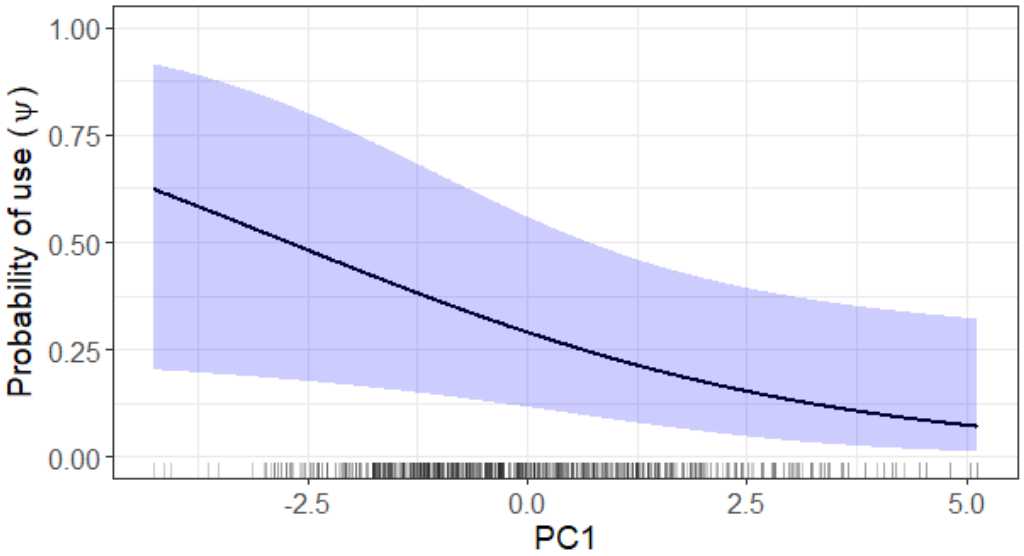

Figure 3.6: The top model for martens with principal components as predictors (marten8) indicated a strong positive relationship with PC1, suggesting that martens select against areas with high shrub stems counts, and are more likely to occupy areas with higher coniferous basal area and canopy closure, although this is not as strong of a relationship.

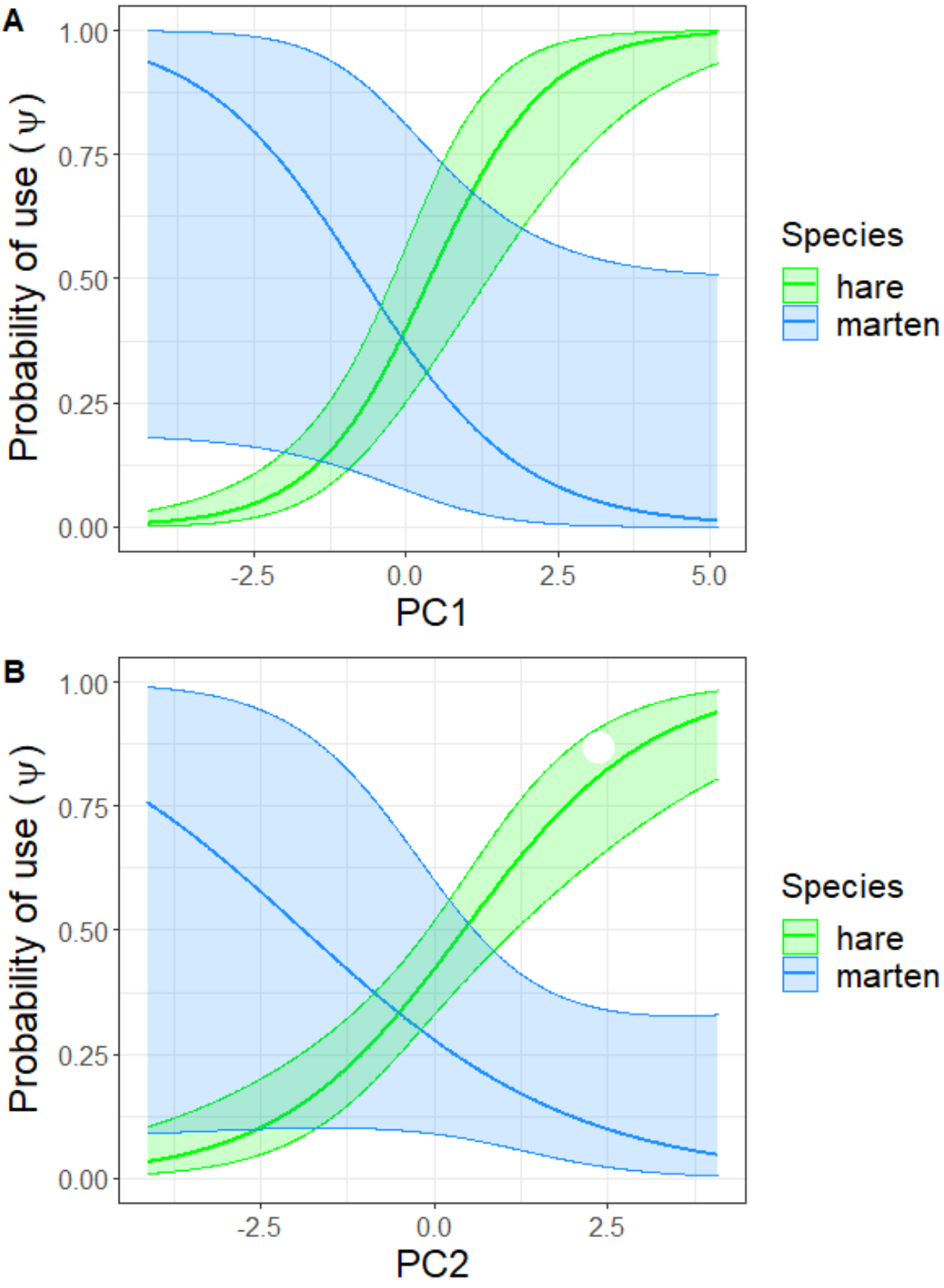

Figure 3.7: The visual-exploratory analysis indicated that the greatest habitat use overlap was where PC1 was approximately 0 and where PC2 was slightly negative, however, there was high uncertainty in these estimates.

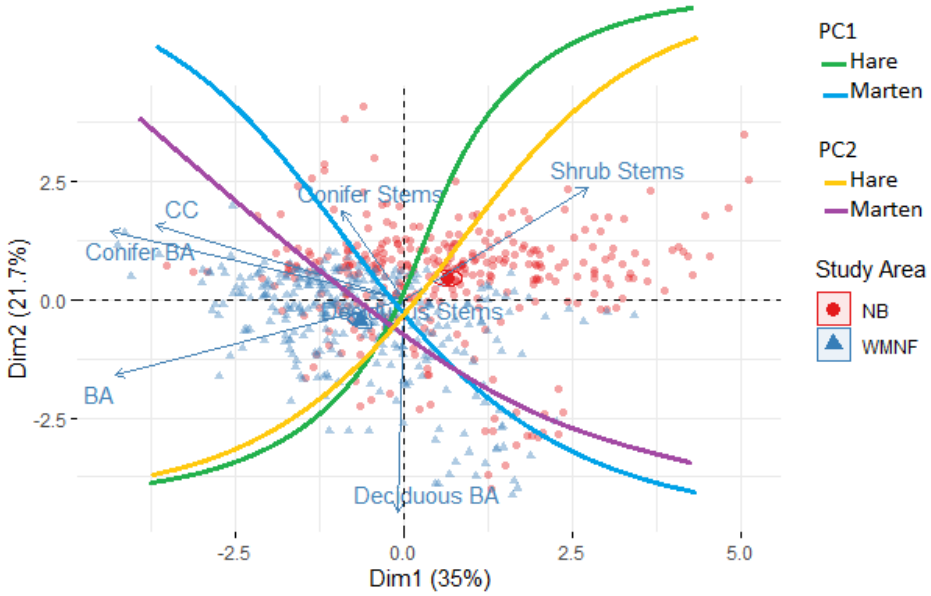

Figure 3.8: Biplot with PC1 and PC2 (from Chapter 2) and multidimensional space associated with deciduous stem counts. The multivariate intersection of the fitted occupancy lines where PC1 and PC2 cross, suggest that areas with higher deciduous stem counts were the forest structure variable associated with the highest overlap in habitat use at finer spatial scales for hares and martens.

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CHAPTER 4 – General Conclusions and the Importance of Identifying Key Forest Structure Characteristics for Species of Interest

Wildlife management is often funded by traditional methods: sales of fishing and hunting licenses, and funds from the Pittman-Robertson Act, which utilizes an excise tax on firearms and ammunition to provide Federal aid to States for wildlife management and restoration (Bechtel and Maestas 2007; Jacobson et al. 2007). These sources of funding are diminishing due to the declining number of sportsmen taking part in hunting, trapping and angling (Jacobson et al. 2007). Securing adequate funding for wildlife management has become increasingly difficult, making the execution of a cost-effective management plan with the highest probability of successcrucial. Correctly identifying key forest structure characteristics and interpreting habitat preferences of target species is imperative for the success of costly programs, such as species reintroductions and habitat restoration. Learning from past successes and failures can be utilized to implement the correct wildlife action plan for the future of keystone and umbrella species such as snowshoe hares (*Lepus americanus*) and American martens (*Martes americana*) that profoundly influence community dynamics.

Historical and Current Distribution of Martens in the Northeastern U.S. and Reintroduction Efforts

Marten populations were historically distributed throughout the boreal and conifer dominated forests of North America; however, they were extirpated from most of their southern ranges beginning in the 1600s due to unregulated fur harvesting and deforestation through agricultural expansion (Gibilisco 1994). These historical areas ranged west to Alaska, east to Newfoundland, north to the arctic tree line, and south to West Virginia (Krohn 2012).

Martens in New Hampshire-were prized and exploited for their fur once the American beaver (*Castor canadensis*) became scarce (Marshall 1951; Silver 1957). Their numbers steadily decreased, and in 1935, the marten trapping season was closed (Silver 1957). There were incidental reports of martens in the Connecticut Lakes Region and the White Mountain National Forest (WMNF) throughout the 1950s and in 1953, two martens were captured from Algonquin Provincial Park, Ontario, Canada, and released in the Second College Grant, located in eastern Coos County, New Hampshire (Silver 1957). A second reintroduction was attempted in 1975 by the United States Forest Service (USFS) with 29 martens released near the Wild River in Shelburne. However, the success of the reintroductions was uncertain due to limited data collection following the releases (Kelly et al. 2009).

Since the 1950s, the marten population in New Hampshire has recovered and was taken off the state list of threatened species in 2017 (NHFG 2017). Kelly (2005) analyzed reliable records of marten occurrences via visual observation, snow track surveys, road kills, trapper bycatch and live-trapping data and found that the

Connecticut Lakes region contained 57% of all records. This region has long winters with deep snow which provides martens with a refugia despite extensive timber harvesting. Further analysis via live-trapping suggested that marten densities may be highest in the Connecticut Lakes region, with potential in high elevation areas further south such as the White Mountain National Forest (WMNF) (Kelly 2005). A recent study confirmed that the WMNF is, in fact, a density hotspot, suggesting that the WMNF is a core habitat with potential to become a source population (Drummey 2021). The WMNF is a large contiguous land area occupying the northcentral part of New Hampshire, with forest structure characteristics that support both hares and martens. Although both species are present, hares occur at lower abundances due to the advanced successional growth stage and minimal forest openings associated with early-successional patches of vegetation that hares prefer. A source population for martens could lead to successful dispersal into the surrounding region if resource managers work to maintain a stable prey base (hares) and create forest corridors that connect large, contiguous habitats. Hares are an important prey item for martens, but also benefit a variety of wildlife due to their keystone characteristics. The current population density of martens in New Hampshire is estimated to be between 1,286 and 2,061 individuals (Drummey 2021).

Martens in Vermont are classified as endangered by the Vermont Fish and Wildlife Department (VFWD) and in 1989, VFWD coordinated with the U.S. Forest Service (USFS) to implement a recovery plan (DiStefano et al. 1990; Moruzzi et al. 2003). Their objective was to establish two populations greater than 300 individuals with the goal of changing their legal status from endangered to protected furbearer (DiStefano et al. 1990). The two release sites were 650-785 m in elevation to limit potential encounters with fisher (*Pekania pennanti*), and spruce and fir were the predominant species with incidental occurrences of northern hardwoods (Royer 1992; Moruzzi et al. 2003). Post-release monitoring over several years suggested that reintroduction efforts ultimately failed; detections via snow tracking, camera traps and radio-telemetry indicated that most individuals dispersed or could not be detected (Moruzzi et al. 2003). Reasons for failure typically involve an inadequate population size, single release efforts, dissimilar habitats from capture to release, trapping mortality, habitat fragmentation, lack of contiguous forest and interspecific competition (e.g., fishers) (Slough 1994; Trombulak and Royar 2001; Moruzzi et al. 2003; Carroll 2007). However, none of these were believed to be the cause of failure, and further investigation of landscape versus stand scale attributes may reveal the importance of identifying key forest structure characteristics between capture and release sites (Chapin et al. 1998; Hargis et al. 1999; Moruzzi et al. 2003). Further, recent genetic analysis suggests that individuals discovered in southern Vermont since 2010 may have originated from Maine, which was the primary source population of the reintroduction, although there is high uncertainty since these martens may have also originated from a relict population (Aylward et al. 2019). The martens discovered in

northeastern Vermont originated from an expanding New Hampshire population, which is indicated by their distinct genetic structure (Aylward et al. 2019).

Reintroduction efforts have varied success; however, they are of great importance to restore the ecological balance of an anthropocentric world. Genetic diversity is also key to a population's persistence and a significant conservation concern that allows for evolution through adaptation and the continued existence of organisms in a changing environment (Frankham 1996). Therefore, if reintroduction programs are to be successful, the importance of combining genetically diverse populations into the appropriate habitat to maximize allelic diversity cannot be overstated (Swanson et al. 2006). Natural resource managers must consider all factors, aside from key forest structure characteristics and habitat restoration that may potentially impact the success of reintroductions. Otherwise, populations that are limited may experience bottlenecks and local extinction due to the lack of gene flow (Frankham 1996). For example, Swanson et al. (2006) tested for bottlenecks in a small, reintroduced marten population located in Michigan by examining the rapid loss of rare alleles compared to other alleles, an effective method for bottleneck testing in small, reintroduced populations. Small populations are particularly susceptible to genetic drift, which results in the rapid loss of alleles inversely proportional to population size (Wright 1969). The source population of the martens released in the Vermont reintroduction were from Maine and New York, separated by less than 400 miles. The martens studied by Swanson et al. (2006) were from British Columbia and Michigan and separated by a considerably larger distance. There was high allelic diversity and no evidence of bottleneck in the Michigan population. Thus, factors such as these, including the particular landscape that source populations have adapted to, may highly influence the outcome of reintroductions.

Future Management

Climate change is currently inducing a warmer environment and hares and martens in the northeastern U.S. are expected to decline as a result of increased seasonal temperatures (Carroll 2007; WAP 2015; Zimova et al. 2019). Martens are morphologically adapted to traverse deep snow and persist in cold environments (Krohn et al. 2004) and hares have similar morphological adaptations, but they also rely on coat color for protection from predators (Hodges 2000). Camouflage mismatch in hares as a result of decreased snow duration, could have profound negative effects on their abundance and distribution (Zimova et al. 2019). Despite these global threats, forests need to be managed for the future with the consideration of effective patch size to secure a strong marten presence within the landscape, but also managed for hares, which serve as an important prey base. Advancing technology is developing new approaches to identify where management needs to occur, with the greatest probability of success.

Light Detection and Ranging (LiDAR) utilizes a laser to sample 3-dimensional objects (Fekety et al. 2019). It is an active remote-sensing technology that is highly accurate and may offer more efficient methods for vegetation surveys and collecting forest structure data compared to traditional, labor-intensive methods. A laser pulse is emitted toward the ground from a LiDAR device carried by an aircraft or drone. The laser reflection is returned to a sensor on the aircraft or drone and the position of the object that caused the laser reflection is accurately calculated by a combination of computations (Fekety et al. 2019). Both horizontal and vertical information can be provided by LiDAR remote sensing depending on the type of LiDAR system utilized and its configuration (Lim et al. 2003). The key habitat features for hares and martens measured by traditional forest structure sampling could be detected by the advancing technology of LiDAR, with the objective to understand the relationship between pellet density, vegetation structure and LiDAR signatures. Remote areas could be efficiently sampled with LiDAR on a large scale with high precision to determine current landscape condition and identify where management needs to occur. For example, few studies have attempted to measure coarse woody debris (CWD) volume, due to the tedious and labor-intensive task that is often associated with rugged terrain (Queiroz et al. 2020). Bryophytes tend to obscure logs of older decay, especially in the high elevation areas of the northeastern U.S., making it difficult to accurately detect and measure. Queiroz et al. (2020) revealed that CWD can be accurately detected and measured using a combination of optical imagery and multispectral aerial LiDAR. LiDAR may also quantify the concept of moderate in terms of optimal disturbance size, which could potentially guide foresters in their decisions regarding patch size and scale when implementing traditional timber harvesting strategies combined with ecological forestry. This technology in the sky may be the future of elegantly connecting the bridge between wildlife and forest management.

Habitat fragmentation is an ongoing threat to wildlife and not all species can successfully adapt to a rapidly changing environment. Contiguous forests are diminishing at an alarming rate due to the pressures of an expanding urban society, fueled by a growing human population and their economic demands (Litvaitis 2003; Lorimer and White 2003). Habitat connectivity between extensively forested regions in the northeastern U.S. is lacking. State and Federal agencies would have to work diligently with private and commercial landowners to implement new ideas, such as creating connecting corridors of desired habitat, if we want species like hares to persist and martens to fully recover in their southern range limits. LiDAR technology will continue to develop and may be implemented to detect potential corridors with key forest structure characteristics from source populations to link larger contiguous habitats. If corridors that link core populations can be created and effectively managed for hares and martens, the results could potentially increase overall biodiversity due to the keystone role of hares and ecological umbrella created by

martens. Although these efforts would take years, the reward would be invaluable for conservation.

Our study indicates that hares and martens can successfully coexist in areas characterized by a broad spectrum of forest characteristics within a common forest matrix. Martens selected against areas with high stem counts (specifically, shrub stems), however, a moderate abundance of deciduous stems were associated with the habitat use overlap of both species. The co-occurrence of hares and martens in these areas reinforces the importance of evaluating microhabitats on a much finer spatial scale. Although these areas were not abundant, they are unique in their potential to increase biodiversity and it is well established that both keystone and umbrella species have their place within the ecosystem to maintain optimum forest health. Future studies may wish to evaluate the role of seedlings when counting stems, a detail that is often overlooked. Regenerating patch size within an older matrix of forest may also have an influence on hares and habitat use and was not examined in this study. Assessing patch size with LiDAR may give further insight on occupancy. Analyzing the size-class of trees within forested stands may also indicate other factors that influence occupancy. Lastly, examining small patches within the WMNF where small-scale disturbances are evident may determine how these hotspots influence biodiversity and if the Intermediate Disturbance Hypothesis is scale dependent (*sensu* Connell 1978). Documenting and evaluating the habitat use overlap of species with different habitat preferences is challenging, however, it provides valuable insight for the future management of species that were once considered too different to coexist within the same forest matrix.

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