UNDERSTANDING ECOLOGICAL RELATIONSHIPS OF SNOWSHOE HARE (*LEPUS AMERICANUS*) IN THE 1836 TREATY CEDED TERRITORY OF MICHIGAN IN THE CONTEXT OF ADAPTIVE MANAGEMENT

By

Eric Michael Clark

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ABSTRACT

This dissertation is an applied research study focused on the identification and implementation of quantitative wildlife assessment techniques as part of a robust adaptive management framework for hemiboreal forest communities within the 1836 Treaty Ceded Territory, with snowshoe hares as a focus. Based on the Sault Tribe Wildlife Programs assessment of research needs regarding snowshoe hare (*Lepus Americanus*) and climate change, the following chapters seek to evaluate approaches to these programmatic research priorities with a focus on using state-space modeling frameworks that rely on software that is easily accessible to agency staff. These models focus on understanding the relationships between landscape patterns, climate dynamics, and snowshoe hare population performance. In Chapter one, I developed a model that evaluates coarse-scale relationships between snowshoe hare occupancy, bioclimatic variables, and landcover composition and configurations. In Chapter two, I implemented a spatial capture-recapture model for snowshoe hares on the east zone of the Hiawatha National Forest which was parameterized using landscape-scale forest composition and configuration metrics. In Chapter Three, in collaboration with the United States Geological Survey, we conducted a serosurey and implemented a prevalence model that was parameterized with individual snowshoe hare characteristics and ecological land type.

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INTRODUCTION

Hemiboreal Forest Relations and Waabooz

The Great Lakes Anishinaabeg (*the people* of the Three Fires Confederacy: Ojibway, Odawa, and Bodewadmi) migrated from the east coast of North America to the Great Lakes Region following a prophecy, which instructed them to move to the place where food grows on the water (Benton-Banai 1979). This westward movement of Anishinaabeg through the Great Lakes Basin followed the southern periphery of the boreal forest biome (referred to as hemiboreal region by western scientists), allowing the people to maintain relationships with plant, animal, and other relatives associated with this region through space and time. Great Lakes Anishinaabeg have been shaped by and have reciprocally shaped these landscapes through intense engagement with the land and co-creation of hemiboreal ecosystems therein. The land, waters, plants, wildlife, and other relatives provide critical foods, medicines, and ongoing instruction to the Anishinaabeg for living a good life. The Anishinaabeg influence the land and other relatives by following their teachings and working with the seasons and manidoog (*spirits*) of the land and waters, including widespread active practices with ishkode (*fire*) that have supported a wide range of fire-dependent ecosystem types, essential for Anishinaabe bimaadiziwin (*life*) (Clark 2021, Clark et al. 2022). The Great Lakes landscape was collaboratively maintained in a heterogenous network of fire-prone early successional and old growth forests with diverse understories and well-developed super canopies (Comer et al. 1995, Meunier et al. 2019, Sutheimer et al. 2021).

Defined by dominance of cold-tolerant tree species (e.g., balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), red pine (*Pinus resinosa*)) that co-occur with cold-intolerant species (e.g., northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), yellow birch (*Betula alleghaniensis*)), the hemiboreal region is found at the ecotone between temperate and boreal forest biomes(Brandt 2009.) Many of the plant and animal relatives that depend on these co-created ecosystems exist at the southern extent of their range in this region (e.g., waabizheshi (American marten; *Martes americana*), snowshoe hare; *Lepus americanus*), and Giizhik (northern white cedar; *Thuja occidentalis*)). These relatives, including Waabooz (snowshoe hare), are critical for the maintenance and renewal of Anishinaabe lifeways.

Globally the boreal/hemiboreal zone is warming faster than any other region (0.5° C per decade), causing novel impacts to vegetation communities (Gauthier et al. 2014). Predicted species responses to these warming trends are complex and occur unevenly due to climatic and biotic interactions, suggesting that priority effects (i.e., effect of the order and timing of species/community assemblages on ecosystem structure and function), and edaphic (soil-related) and anthropogenic (human-related) factors play an important role in vegetation response to climate (Beauregard and De Blois 2014, Boisvert-Marsh et al. 2014, 2019, Evans and Brown 2017, Solarik et al. 2020). The past few centuries of settler-colonial influence within the Great Lakes hemiboreal region introduced a legacy of intensive forest management focused on timber production, wildlife management focused on promoting herbivores, and fire suppression in fire-prone ecosystems.

One relative who is a particularly prominent actor in Anishinaabe creation stories and ongoing lifeways, and that is endemic to the hemiboreal region in North America, is Waabooz. The Anishinabeg maintain kinship relations with Waabooz, and members of the Sault Ste. Marie Tribe of Chippewa Indians rely on relationships with Waabooz for important subsistence and ceremonial practices that demonstrate the intersection of essential ecological and cultural relationships. Annually, Sault Tribe members harvest between 900-1800 snowshoe hares (Figure I.1) within the 1836 Treaty Ceded Territory in Michigan (Figure I.2). For over a decade, Sault Tribe members have consistently expressed concerns about Waabooz population resilience and habitat conditions resulting from settler-colonial forest management practices, changing climate, and associated declines in harvest (Sault Tribe Wildlife Program, unpublished data). Importance of Waabooz to Anishinaabe culture has an obvious connection to ecological roles that snowshoe hare play in hemiboreal ecosystems. Many species, including humans, rely on snowshoe hare for food especially lynx (*Lynx canadensis*), coyotes (*Canis latrans*), fishers (*Pekania pennanti*), American black bears (*Ursus americanus*), barred owls (*Strix varia*), ravens (*Corvus corax*), and red squirrels (*Tamiasciurus hudsonicus*) (Murray 2003) that occur in the hemiboreal regions of the 1836 Treaty Ceded Territory.

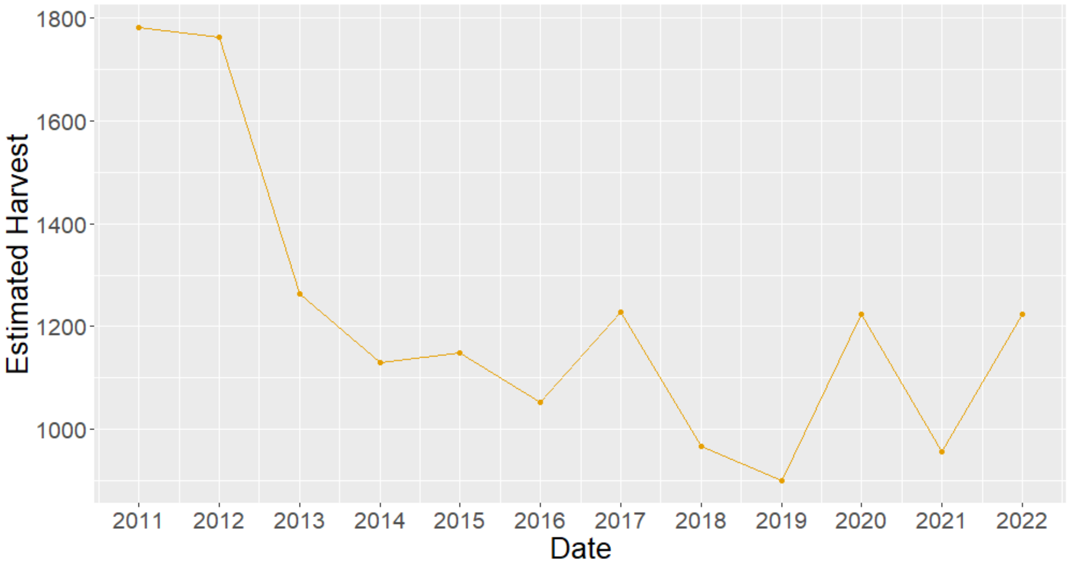

Figure I.1. Estimated snowshoe hare harvests by Sault Tribe hunters in the 1836 Treaty Ceded Territory from 2012-2021.

In 2015, in collaboration with a panel of experts from state, federal, and tribal agencies and universities, the Sault Tribe Wildlife Program conducted a Climate Change Vulnerability Assessment for snowshoe hares in the 1836 Treaty Ceded Territory and an assessment of research needs (Sault Tribe Wildlife Program, unpublished report). The Sault Tribe Wildlife Program adapted the U.S. Forest Service Rocky Mountain Research Station’s System for Assessing the Vulnerability of Species (SAVS) process, which involves evaluating species based on 22 criteria within four categories: biotic interactions, phenology, physiologic interactions, and habitat interactions (Bagne et al. 2011) This assessment suggested that snowshoe hare habitat resilience was a major source of vulnerability (Wonch et al. 2015). Specifically, availability, distribution, connectivity, specific habitat components (e.g., dense forest regeneration, thick cover), and transitional habitat types were identified by the panel as points of concern. Wonch et al. (2015) also identified potential detrimental physiological changes linked to climate change that could potentially be mitigated through provision of high-quality habitat. The assessment results suggested that snowshoe hare vulnerability to climate change was compounded by high levels of uncertainty about snowshoe hare distribution, population health issues, and magnitude and effects of climate dynamics (Wonch et. al. 2015).

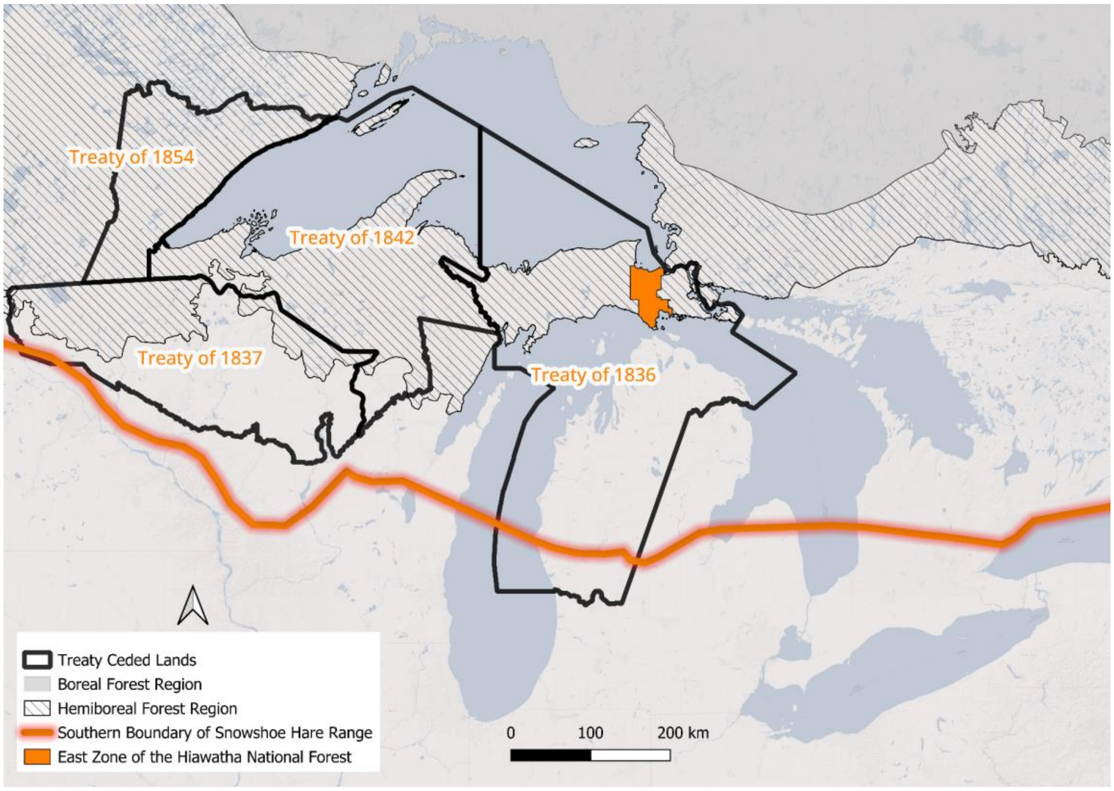

Figure I.2. The 1836 Treaty Ceded Territory and other Anishinaabe Treaty Ceded Lands (black lines) in the Great Lakes Region, USA, the East Unit of the Hiawatha National Forest (orange polygon), Hemiboreal Forest Biome (gray hashed lines), Boreal Forest Biome (dark gray), and snowshoe hare southern range boundary (orange line). Source: Ceded Territory Sault Tribe Wildlife Program, boreal/hemiboreal biomes (Brandt 2009), HIF Boundary USFS, snowshoe hare range (ICUN Red List, 2019).

Importance of forest structure and composition, and effects of forest and fire management, have been demonstrated for snowshoe hares at multiple scales across the North American hemiboreal and boreal forest zones. Many studies found that complex within-patch forest structure positively effects snowshoe hare survival and habitat use (Keith et al. 2011, Berg et al. 2012a, Fuller and Harrison 2013, Holbrook et al. 2017, Wilson et al. 2019). At landscape scales, composition and configuration of habitat patches have impacts on snowshoe hare distribution (Lewis et al. 2011, Sultaire et al. 2016a, 2022, Holbrook et al. 2017, Gigliotti et al. 2018, Wilson et al. 2023). Researchers also demonstrated that snowshoe hares increase habitat use in areas where dense early successional forest regeneration exists following timber harvest or fire (Homyack et al. 2007, St-Laurent et al. 2008, Berg et al. 2012, Thornton et al. 2012, Ivan et al. 2014, Holbrook et al. 2017). For example, Jacqmain *et al.* (2007) documented that subsistence harvest of snowshoe hares by First Nations members recovered 13-27 years after clearcutting black spruce forest when regeneration was >4m tall and tree stocking was >6,300 stems/ha. Additionally, positive associations between post-fire habitat use by hares and recovery and in some cases enhancement of forest structure and composition in conifer (e.g., spruce sp.) and aspen-dominated systems is well documented (Wolff 1980, Stephenson 1985, Paragi et al. 1997, Cheng et al. 2011, Berg et al. 2012, Strong and Jung 2012, Hutchen 2017, Olnes et al. 2019).

Sault Tribe in the Management Context

The Sault Ste. Marie Tribe of Chippewa Indians (Sault Tribe) is the most populous federally recognized Tribe east of the Mississippi River, with over 53,000 members. Sault Tribe is a signatory to the Treaty of 1836 at Washington where the Anishinaabeg ceded approximately 56,000 km^2 (1836 Treaty Ceded Territory) in return for goods and guaranteed education for future generations while retaining all usual rights of occupancy on unsettled lands (Figure I.2). Since that time, Sault Tribe members have continued to hunt, fish, trap, gather, and invoke other rights of occupancy across the 1836 Treaty Ceded Territory, as essential practices in Anishinaabe mino-bimaadiziwin, or living a good Anishinaabe life.

Due to widespread colonial-settler land dispossession practices and a unique federal recognition history, the Sault Tribe has a small land base (~20 km^2). As a result, almost all Sault Tribe treaty harvest of plants and animals occurs on public lands and waters within the 1836 Treaty Ceded Territory. Sault Tribe's harvest is managed collaboratively with four other 1836 Treaty signatory Tribes (Bay Mills Indian Community, Grand Traverse Band of Ottawa and Chippewa Indians, Little River Band of Ottawa Indians, and Little Traverse Bays Bands of Odawa Indians, under the umbrella of the Chippewa Ottawa Resource Authority), the United States, and the State of Michigan. These entities currently operate under the 2007 Inland Consent Decree (2007 ICD), which guides contemporary intergovernmental processes to manage harvests of fish, wildlife, and plants, including allocation and regulations (United States v. State of Michigan 1979). In addition, the five 1836 Treaty signatory Tribes have a Memorandum of Understanding with the United States Forest Service, enacted in 2006 (USFS - Chippewa Ottawa Resource Authority Tribes 2006), that guides subsistence and ceremonial harvests on the Hiawatha and Huron-Manistee National Forests, which comprise about 5,200 km^2 of the Ceded Territory.

Adaptive Co-Management of Treaty Resources on the Hiawatha National Forest

In a 2012 survey of the Sault Tribe Membership (Sault Tribe Wildlife Program, unpublished report), over 50% of Sault Tribe members identified National Forests as the most important lands for tribal member harvest, despite only accounting for 30% of the 1836 Ceded Territory landscape. The Hiawatha National Forest (HIF) is in the Hemiboreal sub-zone of the 1836 Treaty Ceded Territory (Brandt 2009). The HIF has a complex mix of fire-prone ecosystems and expansive lowland conifer systems that are home to rare and culturally important plants and animals (USFS 2006).

The Sault Tribe asserts that along with rights to harvest plants and animals codified within the 2007 ICD and the tribal, federal, and state governments have reciprocal responsibilities to those plants and animals and the larger ecological systems where they live and interact. As such, the 2007 ICD codifies the rights of the five Tribes to engage in restoration and reclamation activities within the 1836

Treaty Ceded Territory. In addition to this provision, the 2006 USFS MOU and other federal legislation and policies (e.g., Tribal Forest Protection Act, Joint Secretariat order #3403, Executive Office of the President Memorandum on Tribal Consultation and strengthening Nation to Nation relationships) bear specific provisions for Tribal co-management, co-stewardship, and elevated engagement, including incorporation of Indigenous knowledges in federal land management processes.

In 2023, the Sault Tribe executed a Tribal Forest Protection Act (TFPA) agreement with the Hiawatha National Forest, titled “Advancing Co-Stewardship of Federal Lands and Demonstrating Relational Engagement in Remnant Boreal Forests in the EUP: Engaging Anishinaabe and Western Sciences in Building Resilience in Remnant Boreal Forest Ecological Systems”. Led by the Sault Tribe Wildlife Program, this agreement focused on building ecological resilience in remnant boreal forest ecosystems within the HIF by developing adaptive management frameworks. Under this agreement, the Sault Tribe Wildlife Program and HIF collaboratively develop adaptive management frameworks that demonstrate a meaningful implementation of the Joint Secretariat Order #3403 (USDA & USDOI Secretaries 2021).

The 2023 TFPA agreement was the culmination of over a decade of collaboration between the Sault Tribe Wildlife Program and HIF. Together, the Tribe and National Forest jointly led adaptive management projects focused on: 1) understanding hemiboreal ecosystem function; 2) applied fire, silviculture, and wildlife management techniques; and 3) tribally led co-management and co-stewardship of federal lands within the 1836 Treaty Ceded Territory. The Sault Tribe Wildlife Program funded >20 grant projects through the Great Lakes Restoration Initiative –Bureau of Indian Affairs (BIA) Distinct Tribal Program, BIA - Tribal Resilience Program, BIA-Forestry, and United States Fish and Wildlife Service Tribal Wildlife Grant Program all of which were aimed at collecting ecological data to inform adaptive management processes in hemiboreal forest ecosystems, specifically on the HIF.

Adaptive management frameworks provide useful decision analytics when working in systems with varying amounts of control, uncertainty, and diverse understandings related to management issues (Williams et al. 2009, Gregory et al. 2012, Rist et al. 2013). Hence, adaptive management is an effective process for understanding ecological responses to fire and silvicultural management in the hemiboreal zone. Adaptive management seeks to reduce uncertainty in the management system through implementation of models to forecast and evaluate ecological responses to a suite of management alternatives (Williams and Brown 2012). The Sault Tribe Wildlife Program pursues adaptive management that is driven by Anishinaabe giikendaasowin, living knowledges within the Sault Tribe membership, per a Strategic Plan (Sault Tribe Wildlife Program unpublished report). Anishinaabe-led adaptive management requires ongoing engagement of, and program accountability to, Sault Tribe members, including: 1) community-based discussions that center and engage Anishinaabe giikendaasowin, values, and observations; 2) building collective understandings of, and theories on, ecosystems and ecosystem processes; 3) developing and implementing strategies; 4) observing and interpreting results; and 5) thinking about ways to move forward with lessons learned on behalf of current and future generations.

Anishinaabe giikendaasowin is inherently adaptive and well-suited to drive adaptive management frameworks. One pillar of adaptive management and structured decision-making is stakeholder engagement - not just in understanding issues, but in developing management actions and assessments, interpreting results, and then adaptively developing new strategies (Gregory et al. 2012, Williams and Brown 2012). Anishinaabe-led adaptive management moves beyond this conception of stakeholder engagement, recognizing Anishinaabe and other ecological community members (e.g., wildlife, plants, fire) as leaders in the process, with more authorities and responsibilities than "stakeholders."

National Forests are specifically mandated to emphasize restoration and resilience of natural resources against climate change, ensuring ecological, social, and economic sustainability in National

Forest management plans (USDA 2017). The selected alternative must prioritize transparency, collaboration, and public participation (USDA 2017). This planning rule centers an all-encompassing "all-lands approach" while remaining feasible and within the agency's capabilities. While the 2012 Planning Rule provides a consistent planning framework for all USFS lands, it also emphasizes the need for plans to adapt to unique needs of each National Forest System area, balancing local and overarching objectives. While adaptive management and tribal engagement in decision-making processes, and use of scientific information is mandated by the 2012 Planning Rule, examples of projects that incorporate these components are rare (Bormann et al. 2007). Implementation of adaptive management is often hampered by lack of expertise in decision science (Rist et al. 2013).

Ecological models, which integrate western statistical and Anishinaabe giikendaasowin-based knowledges are fundamental to Sault Tribe Wildlife Program adaptive management frameworks and as such, lie at the center of the TFPA agreement. These models serve as the basis for evidence-based decision-making in dynamic and uncertain contexts. Within adaptive management, the emphasis is on iterative learning and modifying strategies based on observed outcomes. These integrated ecological models are instrumental in deciphering relationships, projecting results, and handling uncertainties (Williams et al. 2009). They assimilate extensive datasets from monitoring endeavors, aiding managers in comprehending intricate ecological systems and the influence of various human activities. As management strategies are executed, feedback in the form of new data serves to refine these models, resulting in enhanced predictions and more enlightened decisions (Williams et al. 2009). Fundamentally, the use of Western statistics and Anishinaabe knowledges within ecological modeling transforms adaptive management into a structured, cyclical learning paradigm, where each phase augments our understanding and bolsters efficacy of interventions.

One example of an Adaptive Co-Management Framework is the Sault Tribe – Hiawatha National Forest Inter-Agency Ishkode (fire) Stewardship Plan (Ishkode Framework) (Sault Tribe Wildlife Program

2022). This framework has three components, the Inter-Agency Ishkode Stewardship Plan, a Tribal Community Engagement Assessment and Strategy (TCEAS), and an Ecological Assessment and Monitoring Strategy (EAMS). This framework was developed following the principles of adaptive management as advanced in the Department of Interior's Adaptive Management Technical Guide (Williams et al. 2009) and has use of Anishinaabe and Western sciences as a central tenet. Using TCEAS and EAMS, the Ishkode Framework applies ecological models for key species and develops predicted responses to prescribed fire within proposed treatment areas.

Dissertation Format

The Dissertation that follows is intended to be an applied research study focused on the identification and implementation of quantitative wildlife assessment techniques as part of an adaptive management framework for fire-dependent hemiboreal forest communities within the 1836 Treaty Ceded Territory, with snowshoe hares as a focal outcome. I demonstrate how outputs from analytical tools can be used by scientific staff within management agencies in support of adaptive management. I also evaluated landscape pattern (i.e., habitat patch composition and configuration) on snowshoe hare density and intentionally focused on scale of data inputs. Climate data sources (WorldClim 2 and SNODAS) were chosen with respect to spatial and temporal resolutions of ecological processes being evaluated, reliability of the data, and ease of replication. The analyses within, where possible, use rigorous model selection processes and evaluation of model fit. I adapted Zuur et al.'s (2010) protocol for data exploration to avoid common statistical problems for the analyses in each chapter.

Chapter 1 seeks to address uncertainty in our understanding of landscape scale climate-habitat-snowshoe hare interactions, specifically factors identified in the Sault Tribe Wildlife Program's 2015 Snowshoe Hare Climate Change Vulnerability Assessment (Wonch et al. 2015). I developed a model that explains climate and habitat drivers of snowshoe hare occupancy across Michigan. I used remote sensing-based climate and landcover composition and configuration covariates to inform occupancy and site-level data on snowshoe hare occupancy from Burt et. al (2017). The Burt et al. (2017) data included information from tribal hunters in identifying potential survey sites for hares, thus incorporating Indigenous knowledges (albeit at a relatively simplistic level) into the process. I expanded upon the Burt et al. (2017) work by explicitly incorporating detection probability, gridded climate data, and forest and climate covariates in a suite of competing Bayesian occupancy models.

In chapter 2, I developed a spatial capture-recapture model that portrays the association between landcover composition and configuration and snowshoe hare density for the east zone of the Hiawatha National Forest. Here, a robust estimate of snowshoe hare density could form the basis for an objective function (e.g., increase snowshoe hare density by implementing prescribed fire) in an adaptive management framework. Using stratified spatially balanced random sampling and spatial mark-recapture models, I produced a spatially explicit prediction of snowshoe hare density and demonstrated how these models can be used to provide baseline ecological information for key species to evaluate alternative habitat prescriptions under adaptive management frameworks (Figure I.3).

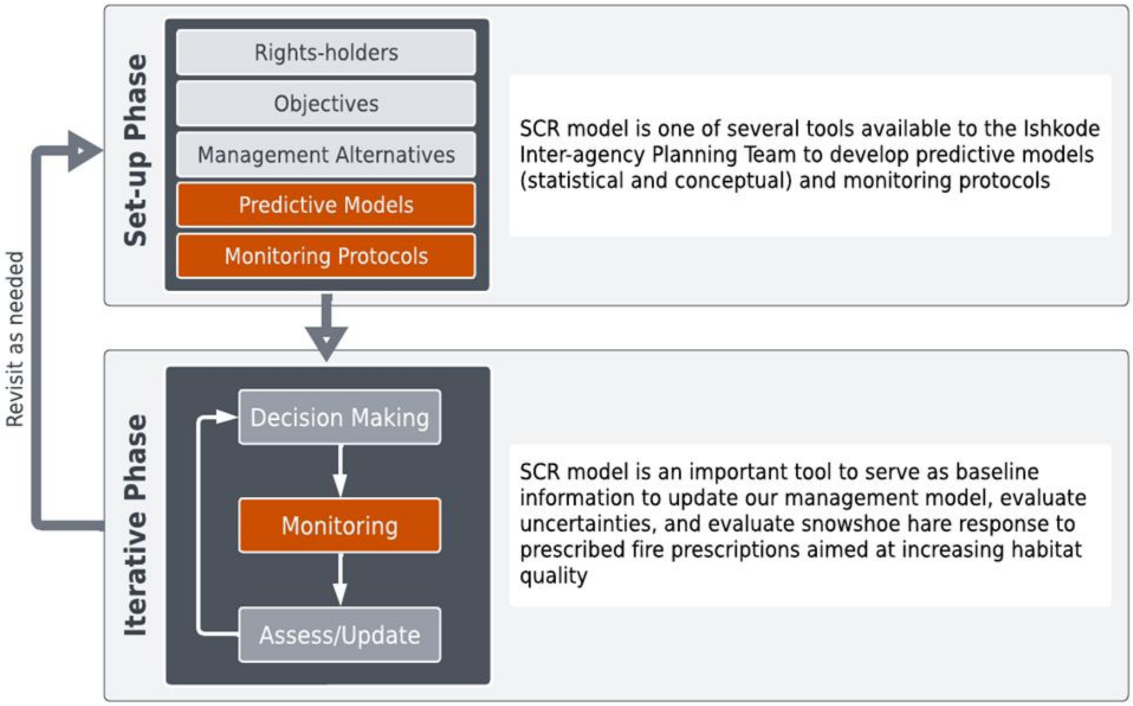

Figure I.3. Adaptive Management Process as, presented in (Gregory et al. 2012), highlights stages in both the set-up and iterative phases of the cycle where SCR models (Chapter 2) will be used in the Ishkode Project.

In chapter 3, in collaboration with the United States Geological Survey – National Wildlife Health Center, I coordinated a serosurvey for arboviruses in snowshoe hare on the HIF. This chapter addresses an uncertainty identified in the 2015 Snowshoe Hare Climate Change Vulnerability Assessment regarding impacts of diseases on snowshoe hare populations. In this chapter, (already published with colleagues) we evaluated exposure rate of several mosquito born viruses in snowshoe hare (Jamestown Canyon virus, Silverwater virus, Lacrosse encephalitis virus, West Nile Virus, *Borrelia burgdorferi*, Powassan virus, and *Francisella tularensis*) and evaluated the relationship between snowshoe hare virus, individual hare traits, and ecological land type on the east zone of the HIF.

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CHAPTER 1: ASSESSING THE RELATIONSHIPS BETWEEN LANDSCAPE SCALE FOREST PATTERNS, CLIMATE, AND SNOWSHOE HARE OCCUPANCY

Introduction

Waabooz (snowshoe hare; *Lepus americanus*) are endemic to North America and depend on hemiboreal forest ecosystems within the Great Lakes Region. These forest ecosystems are characterized by mixed conifer and deciduous trees, with deep snows, cold winters, and mild summer temperatures, to which snowshoe hare are well adapted (Murray 2003). Anishinaabe members of the Sault Ste. Marie Tribe of Chippewa Indians maintain kin relationships with Waabooz; Sault Tribe members rely on Waabooz for essential subsistence and ceremonial practices, within foundational, inter-generational ecological and cultural relationships. Annually, Sault Tribe members harvest between 900-1800 snowshoe hares within the 1836 Treaty Ceded Territory, an area for which the Tribe retains treaty-reserved rights and responsibilities (unpublished Sault Tribe Wildlife Program Harvest Data).

Within the 1836 Treaty Ceded Territory, the Hemiboreal forest ecosystems occur at the southern-most extent of snowshoe hare range (Figure 1.1). Defined by dominance of cold-tolerant boreal tree species (e.g., balsam fir (*Abies balsamea*), paper birch (*Betula papyrifera*), red pine (*Pinus resinosa*), and American elm (*Ulmus americana*)) that co-occur with more cold-intolerant temperate species (e.g., northern red oak (*Quercus rubra*), red maple (*Acer rubrum*), green ash (*Fraxinus pennsylvanica*), and yellow birch (*Betula alleghaniensis*)), the hemiboreal region is the ecotone between temperate and boreal forest biomes (Brandt 2009). Globally the boreal/hemiboreal zone is warming faster than any other (0.5° C per decade) causing novel impacts to forest vegetation communities (Gauthier et al. 2014). Predicted species responses to these warming trends are complex and occur unevenly across space due to climatic and biotic interactions(Evans and Brown 2017). For instance, Boisvert- Marsh et. al. (2014) demonstrated that <50% of species they examined exhibited expected distributional shifts due to climate change, which suggests that priority effects and edaphic and anthropogenic factors play an important role in vegetation response to climate (Beauregard and De

Blois 2014, Boisvert-Marsh et al. 2019, Solarik et al. 2020). In the hemiboreal region within the 1836 Treaty Ceded Territory, there is a legacy of intensive forest management focused on timber production, wildlife management focused on promoting herbivores (e.g., white-tail deer (*Odocoileus virginianus*)), and a long history (i.e. ~120 years) of fire suppression in fire-prone ecosystems.

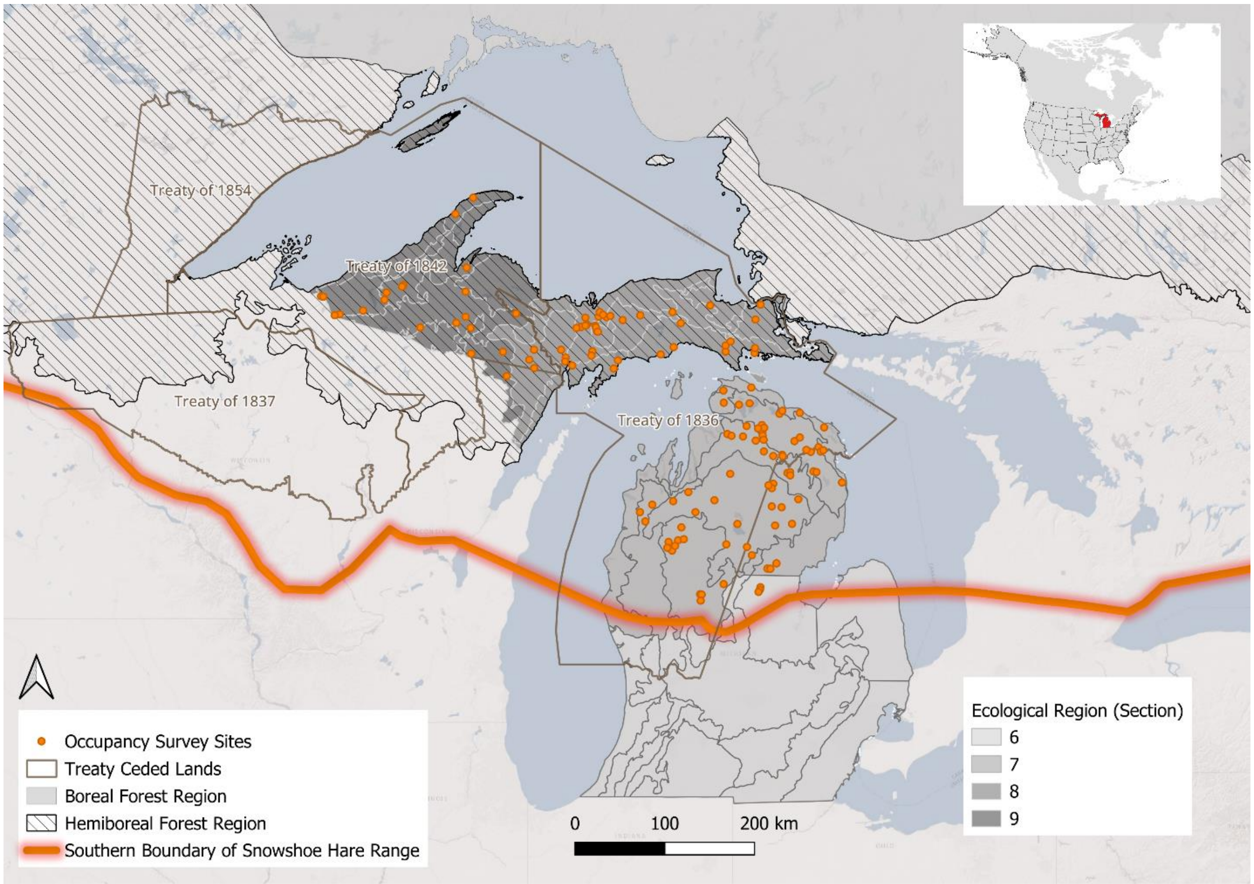

Figure 1.1. Study areas with Ecological Regions depicted from light to dark gray, and Ecological Sub-Sub Regions depicted as outlines only (Albert 1995). Snowshoe hare occupancy and site-level vegetation sampling locations from 2013 are shown as orange points. The southern extent of snowshoe hare range is depicted in orange data source: (IUCN (International Union for Conservation of Nature) 2019).

For over 15 years, Sault Tribe members have consistently expressed concerns to the Sault Ste. Marie Tribe of Chippewa Indians Wildlife Program about declines in Waabooz population resilience and associated habitat conditions as a result of settler-colonial forest management practices and changing climate dynamics (Sault Tribe Wildlife Program 2022). Associations between geographic distributions of snowshoe hares and a variety of climate and habitat conditions in the Great Lakes Region are well documented (Sultaire et al. 2016a,b, 2022, Burt et al. 2017, Wilson et al. 2023). The geographic range of snowshoe hares has been contracting northward along the discontinuous trailing edge of the boreal forest biome (Burt et al. 2017, Sultaire et al. 2022). The causes of this range contraction include both direct and indirect processes. Decreased snow depths and seasonal duration of snow cover increase predation rates (Peers 2017, Wilson et al. 2019, Peers et al. 2020, Majchrzak et al. 2022), and physiological stresses due to increasing seasonal temperatures have been documented (Meslow and Keith 1971, Kielland et al. 2010). Indirect causes may include habitat change due to competitive exclusion of boreal plant species across the hemiboreal region as a result of complex interactions between anthropogenic disturbance and climate dynamics (Brice et al. 2020, Collier et al. 2022, Soubeyrand et al. 2023). These studies offer important insights, yet the Sault Ste. Marie Tribe of Chippewa Indians sought to address uncertainty in understanding landscape-scale climate-habitat-snowshoe hare interactions. In response to these concerns, the Sault Ste. Marie of Chippewa Indians Wildlife Program initiated a climate change vulnerability assessment in collaboration with experts from state, federal, and tribal agencies, and universities (Wonch et al. 2015). The assessment suggested that snowshoe hares are highly vulnerable to climate change, and this vulnerability is compounded by high uncertainty regarding snowshoe hare distribution, population health, and magnitude and effects of climate dynamics (Wonch et al. 2015).

Working with the Sault Ste. Marie Tribe of Chippewa Indians Wildlife Program and other partners, Burt et. al. (2017) examined the association between climate variables and snowshoe hare occupancy within northern Michigan. My study improves on previous uses of Burt et. al.'s (2017) analysis by developing Bayesian occupancy models that examine forest composition, configuration, and climate patterns while explicitly dealing with detection probability in a space-for-time substitution framework (Lele et al. 2012, Charbonnel et al. 2014, Peach et al. 2017). I developed this analysis with easily repeatable methodologies, using open source and freely available data, statistical methods that require minimal custom coding, and grain sizes of remotely sensed datasets that deliberately align. I intended to collate this set of tools to evaluate snowshoe hare distribution from Bayesian and frequentist methods to maximize efficiency and flexibility in the modeling process in support of an adaptive management framework (Sault Tribe Wildlife Program 2022). Beyond the flexibility of these mixed models, Bayesian analyses have several advantages in management contexts, such as reliability, accuracy, and intuitive results interpretation (Makowski et al. 2019).

Methods

Study Area

This study occurred in the northern Lower and Upper Peninsulas of Michigan (Figure 1.1), a landscape dominated by forested ecosystems with approximately 1,8210 km^2 of state, federal, and tribal forest lands. The study area spans the boundaries of the 1836 Treaty Ceded Territory with smaller portions in the 1842 and 1819 Treaty Ceded Territories (Figure 1.1). The landscape represents a gradient from the temperate forest biome in the south to the hemiboreal region in the north, where Brandt (2009) depicts the dividing line (tension line) as the north shores of Lakes Huron and Michigan. Across the study area, temperature and precipitation patterns have been rapidly altered from the historic range of variability. Average annual temperatures increased 2.3°F (1.3°C) between 1951 and 2017 in the Great Lakes region, with an additional 3°F to 6°F (1.7°C to 3.3°C) projected by mid-century (GLISA 2023). These temperature increases have predominantly occurred during the winter (Melillo et al. 2014). Mean annual precipitation across this area increased by 14% over this same period, with increasingly wetter winters and springs projected into the future (Melillo et al. 2014).

Data Collection

Snowshoe hare occupancy and site-level vegetation data were collected in 2013 (Burt et al. 2017) (Figure 1.1), with site selection based on local knowledge of historical snowshoe hare occurrences from natural resource professionals and tribal hunters. Data were collected using a single-visit sampling design (Burt et al. 2016) with winter snow track counts conducted along nine parallel 125m transects separated by 75m and centered on study site centroids (Burt et al. 2017). For each transect, the presence/absence of snowshoe hare and predator tracks were recorded. Surveys were conducted 12-72 hours after fresh snowfall to allow tracks to accumulate (Burt et al. 2016). Vegetation structure and composition data were collected along each transect at the time of occupancy surveys. Conifer and deciduous tree stem counts were collected using 2m-wide and 4m-long belt transects, and horizontal cover was recorded from three height classes (<0.5 m, 0.51-1.0 m, and 1.1-1.5 m) using a Robel Pole (Robel et al. 1970) at the location of the first snowshoe hare detection along a transect, or in the case of no detections, at a random point along the transect (Burt et al. 2017). For modeling, I calculated the mean horizontal cover index for each transect taking the mean values from all three height classes.

I derived climate variables from down-scaled 1-kilometer gridded datasets, including average annual snow depth from 2004-2020 (SNODAS: (National Operational Hydrologic Remote Sensing Center 2004) all 19 WorldClim 2 bioclimatic variables for the years 1970-2013 (Fick and Hijmans 2017). This time frame corresponded to the temporal extent of historical snowshoe hare occupancy information collected via interviews (Burt et al. 2017)and represents a meaningful period to measure climate change. I extracted climate variables for each study site using the Raster Package (Hijmans 2019) in R (R Development Core Team 2018). A 1km^2 area surrounding surveyed sites is larger (100ha) than the average hare home range (23 ha) and this represents an area influencing home range placement. I extracted landcover variables from the Coastal Change Analysis Program data produced by the National Oceanic and Atmospheric Administration (National Oceanic and Atmospheric Administration 2016). I used the landscapemetrics package in R to calculate landscape composition and configuration (Hesselbarth et al. 2019) and FRAGSTATS metrics (McGarigal et al. 2012) for each sampling site. I calculated percentage of the landscape within one kilometer of the sampling site for 7 undeveloped land cover classes (deciduous forest, evergreen forest, mixed forest, scrub/shrub, palustrine forested wetland, palustrine scrub/shrub wetland, and palustrine emergent wetland). All developed land cover types were masked from the analysis. I also compiled six landscape-level pattern metrics within one kilometer of each site, including split, division, edge density, interspersion and juxtaposition index, Simpson's Diversity Index, and Shannon's Diversity Index (McGarigal et al. 2012). I also assigned each sampling site to the Section and Sub-sub section levels of Albert's (1995) Regional Landscape Ecosystems of Michigan spatial dataset. Ecological regions represent generally homogenous geophysical conditions that affect vegetation establishment, growth, and disturbance regimes (Albert 1995).

Data Analysis

I ran single-season occupancy models with the R package unmarked (Fiske and Chandler 2011) and performed the final model selection with the R package UBMS (Kellner et al. 2022). I estimated snowshoe hare occupancy and its relationship to forest composition, landscape configuration, and climate trends using a Bayesian framework and fit a latent state logistic regression model using Markov-chain Monte Carlo (MCMC) methods implemented in package UBMS software (Kellner et al. 2022). The detection sub-model was parameterized using transect-level vegetation data and the presence of predator tracks (Burt et al. 2017). The occupancy sub-model was parameterized using 35 climate and landcover covariates derived from remotely sensed and other spatial data sources (Appendix A, Table A.1).

The default vague priors in UBMS were used for all models (Kellner et al. 2022) and I ran 4 parallel Markov chains with 3000 iterations. Model convergence checks were based on the Rhat statistic and a visual examination of trace plots. I calculated the Mackenzie and Bailey Goodness of Fit statistic and posterior predictive p-value to evaluate model fit (MacKenzie and Bailey, 2004). I generated 95% and 50% Bayesian Credible Intervals (BCI), to evaluate the significance of covariate effects (Makowski et al. 2019). I considered a covariate strongly supported if the 95% BCI did not overlap zero and moderately supported if the 50% BCI did not overlap zero (Nguyen et al. 2022).

I used the UBMS package's standard model selection tools that employs leave-one-out cross-validation based on evaluation of expected log pairwise predictive density (elpd) (Kellner et al. 2022). I also evaluated each model by comparing fit using predictive p-values. To select candidate model sets, I first fit the detection sub-model using the ecological region as a random effect. After selecting the pooling variable that best described latent variation in the detection model, I fit univariate models while holding the occupancy sub-model at the null (intercept only) for each site-level variable. I fit all combinations of my top-performing detection covariates with the ecological region as a random effect. I selected all covariates that performed better than the null model to formulate my candidate detection model set.

I adapted the above approach for the occupancy sub-model. In this case, I first evaluated random effects structures. I fit univariate models for landscape composition, landscape configuration, and climate variables while holding the detection model with the top-ranking random effect. I again used the evaluation elpd metrics to select the top variable from all three categories to create the candidate occupancy model set. Finally, I compared all combinations of the candidate detection and occupancy sub-models and selected the top full model, again based on elpd metrics. I also dropped candidate models that had non-significant parameters (i.e. 95% BCI overlapping zero). In the results, I only describe the final stage of the model section process for those models that performed better than the null model.

Results

Snow Track Surveys, Detection, and Occupancy Sub-Model Variables

Of the 117 sites sampled (9 transects each), I documented 343 transect-level detections with an average of 2.9 detections per site and 72 sites with at least one transect-level detection (Figure 1.2). The comparison of random effects variables on the detection sub-model determined that Ecoregion Sub-Subsection performed the best (Appendix A, Figure A.1). The top detection sub-models included two covariates: conifer stem density (0 to 16 stems/transect; mean = 2.36) and horizontal cover (0 to 10; mean = 1.70) (Table 1.1).

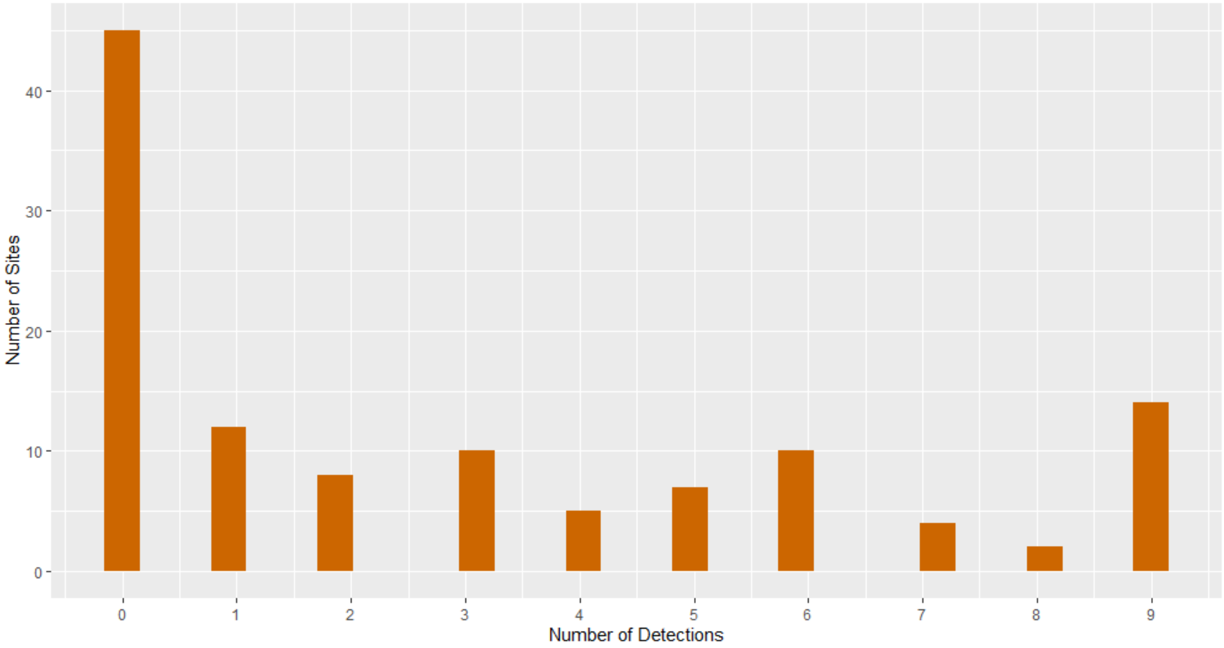

Figure 1.2. Number of sites (n=117) with zero to 9 transect level detections of snowshoe hares from Burt et. al. 2016 in the northern Lower and Upper Peninsulas of Michigan, 2013.

Table 1.1. Global Model variable set for modeling occupancy for snowshoe hares in the northern Lower and Upper Peninsulas of Michigan, 2013.

Sub-Model	Variable	Description	Range (mean)
θ	SD	Annual mean snow depth (SnoDAS)	23.0-174.4 (98.3)
	AMT	Annual Mean Temperature (Bio1)	3.4-7.5 (5.8)
	MTWQ	Mean Temperature of Warmest Quarter (BIO10)	16.0-19.4 (17.9)
	PFW	Percentage of Forested Wetland (CCAP Class 13)	0.0-90.9 (30.3)
	SDI	Simpson Diversity Index of (CCAP Landcover)	0.03-0.82(0.61)
ρ	CSD	Conifer stem density (stems/$8m^2$).	0.0-32 (2.4)
	HCI	Horizontal Cover Index (1-10 integers)	0-10 (1.7)
	ESS	Ecoregion sub-sub section[1]	20 Levels

1. Albert, D. A. 1995. Regional Landscape Ecosystems of Michigan, Minnesota, and Wisconsin: A Working Map and Classification (Fourth Revision: July 1994).

I fit 20 climate models and the top-performing covariates were Annual Mean Temperature AMT), Snow Depth (SD), and Mean Temperature of the Warmest Quarter (MTWQ) (Table 1.1 & Table 1.2). I also fit 8 landscape configuration covariates and only Simpson's Diversity Index (SDI) performed better than the null model (Table 1.2) and I fit 8 landscape composition covariates, three of which performed better than the null model including Percent Forested Wetland (PFW), Percent Deciduous Forest (PDF), and Percent Scrub-Shrub (PSS) (Table 1.2).

Model Selection

The combined candidate model set selection included four models that performed better than the null model (Table 1.3) and had no non-significant parameters (Table 1.4). The top model showed a strong negative effect for MTWQ (95% BCI [-1.38, -0.30]) and a strong positive effect of PFW (95% BCI [0.08,1.07]) on snowshoe hare occupancy (Table 1.4). As site-level PFW increased from 0 to 91%, snowshoe hare occupancy probability increased from ~0.5 to ~0.85 (Figure 1.4). As site-level MTWG increased from 16 to 19 °C, snowshoe hare occupancy probability decreased from ~0.95 to ~0.25 (Figure 1.5). I found a strong positive effect for CSD (95% BCI [0.24, 0.57]), HCI (95% BCI [0.46, 0.83]), and ESS as a random effect (95% BCI [0.78, 1.95]) on snowshoe hare detection probability (Table 1.4). As CSD increased from 0 to 32 stems/8m2, snowshoe detection increased from ~0.35 to ~0.95 (Figure 1.6), and as horizontal cover index increased from 0 (no cover) to 10 (full cover), snowshoe hare detection increased from ~0.35 to ~0.85 (Figure 1.7). Visual inspection of the model trace plots and Rhat (Rhat ~ 1) indicated that model chains were adequately mixed, and the Mackenzie-Bailey Goodness of Fit test (Posterior Predictive P = 0.246) suggested that this model had adequate fit (Figure 1.8).

Table 1.2. Candidate model sets for snowshoe hare occupancy in the northern Lower and Upper Peninsulas of Michigan in 2013.

Sub-Model	Candidate Model Structure
θ	~ MTWQ + SDI + PFW
	~ SD + SDI + PFW
	~ AMT + SDI + PFW
	~ MTWQ + PFW
	~ SD + PFW
	~ AMT+ PFW
	~ MTWQ
	~ SD
	~ AMT
	~ PFW
ρ	~ (1|ESS) + CSD~1
	~ (1|ESS) + HCI ~1
	~ (1|ESS) + CSD + HCI~1

Table 1.3. Full Model Ranking.

Model Structure	elpd	nparam	elpd_diff	se_diff	weight
~ (1|ESS) + CSD + HCI ~ MTWQ + PFW	-470.66	49.61	0	0	0.46
~ (1|ESS) + CSD + HCI ~ AMT + PFW	-470.97	50.57	-0.31	1.38	0.24
~ (1|ESS) + CSD + HCI ~ SD + PFW	-472.05	51.27	-1.39	2.63	0.12
~ (1|ESS) + CSD + HCI ~ PFW	-474.55	52.96	-3.89	3.53	0.12
~ (1|ESS) ~ (.)	-520.14	50.2	-49.48	11.39	0.07

Table 1.4. Top Model.

Model Structure: ~ (1 | ESS) + scale (CSD) + scale (HCI) ~ scale (MTWQ) + scale (PFW)						
Occupancy (logit-scale):	Estimate	SD	2.50%	97.50%	n_eff	Rhat
(Intercept)	0.776	0.235	0.3373	1.258	5179	1
scale (MTWQ)	-0.837	0.274	-1.3849	-0.304	5321	1
scale (PFW)	0.552	0.251	0.0851	1.068	6200	1
Detection (logit-scale):	Estimate	SD	2.50%	97.50%	n_eff	Rhat
(Intercept)	-0.0357	0.316	-0.695	0.567	786	1.01
scale (CSD)	0.4297	0.0988	0.235	0.623	6983	1
scale (HCI)	0.6381	0.093	0.462	0.826	6363	1
sigma[1|ESS]	1.246	0.296	0.778	1.949	2623	1

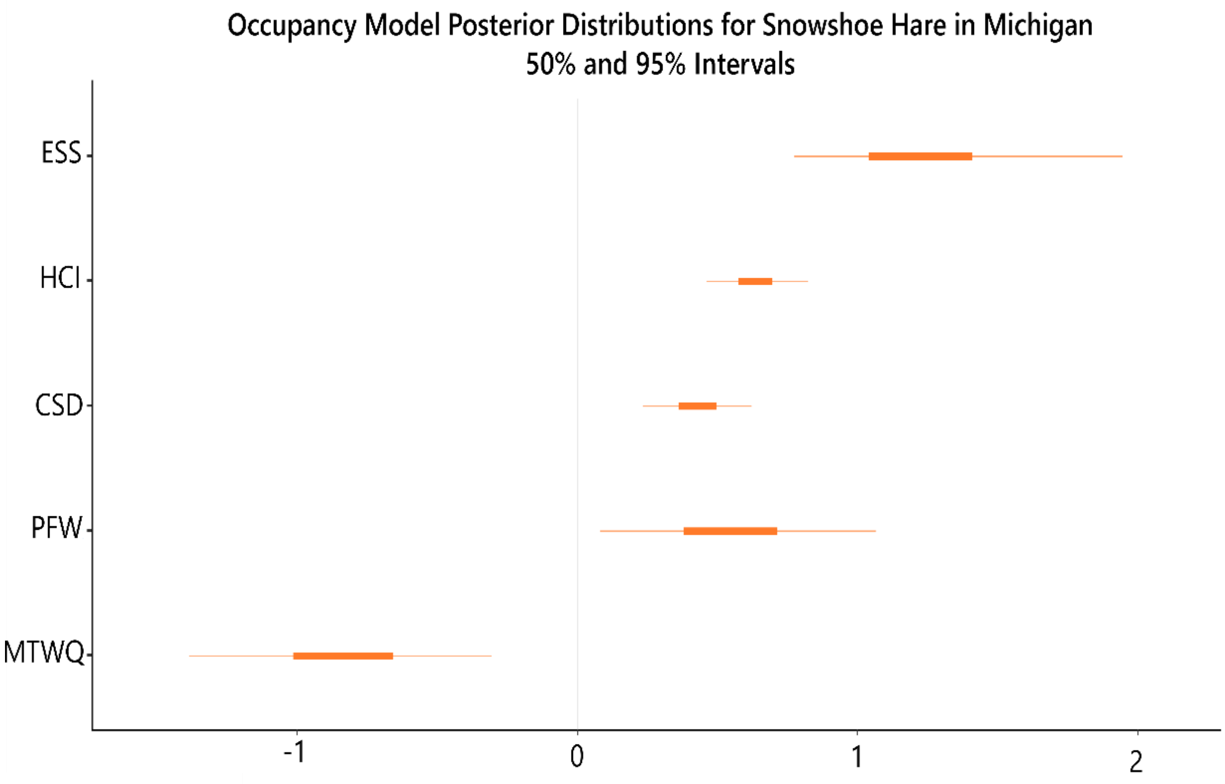

Figure 1.3. Posterior model distributions for response variables for snowshoe hare occupancy model in Michigan.

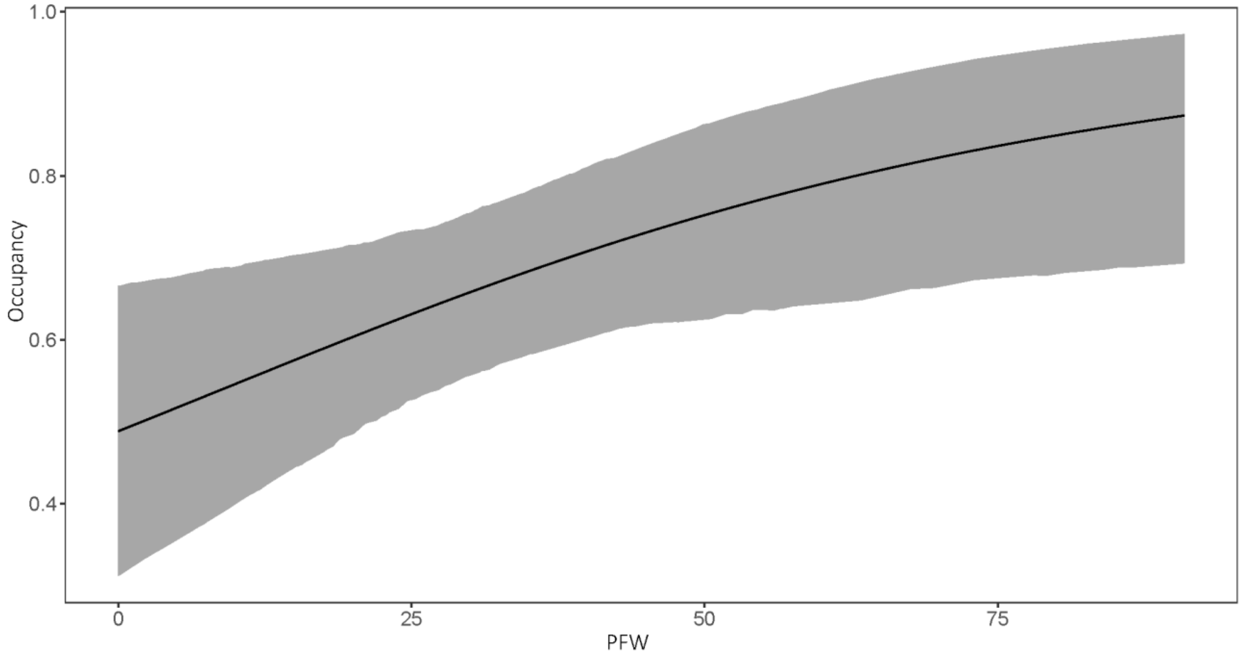

Figure 1.4. Marginal effect of percentage of forested wetlands with 1km of the study site (PFW) on the occupancy of snowshoe hare in the northern Lower and upper Peninsula of Michigan.

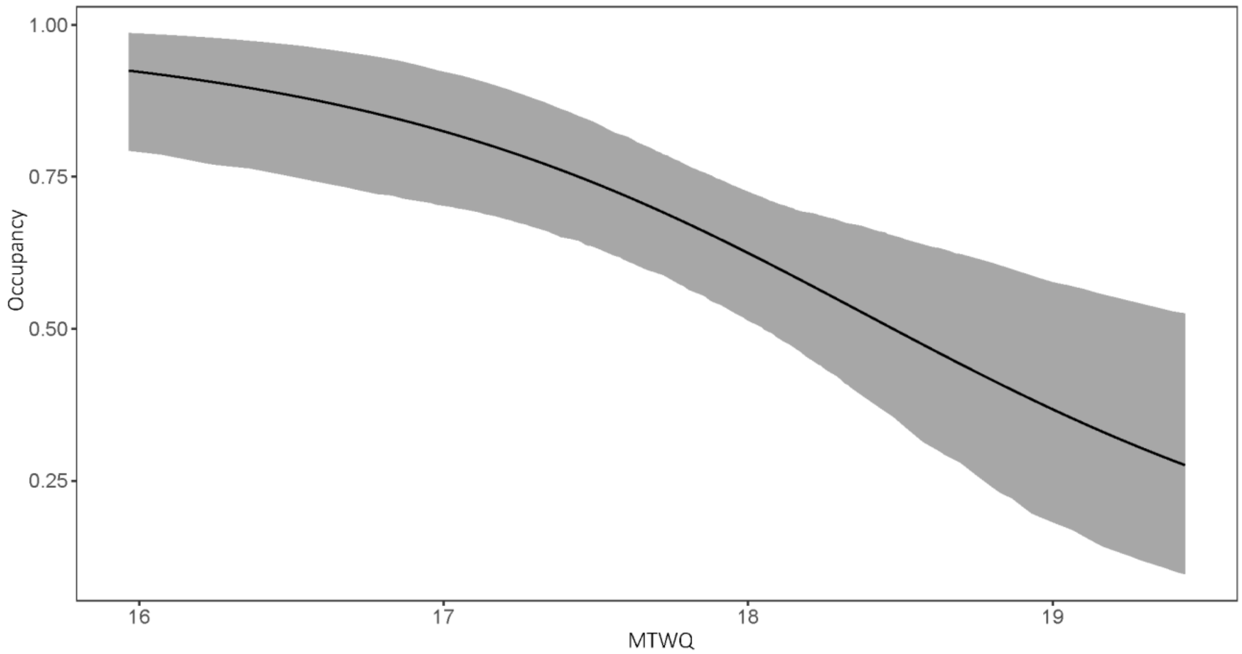

Figure 1.5. Marginal effect of the mean temperature of the warmest quarter of the year (MTWQ) on the occupancy of snowshoe hare in the northern Lower and upper Peninsula of Michigan.

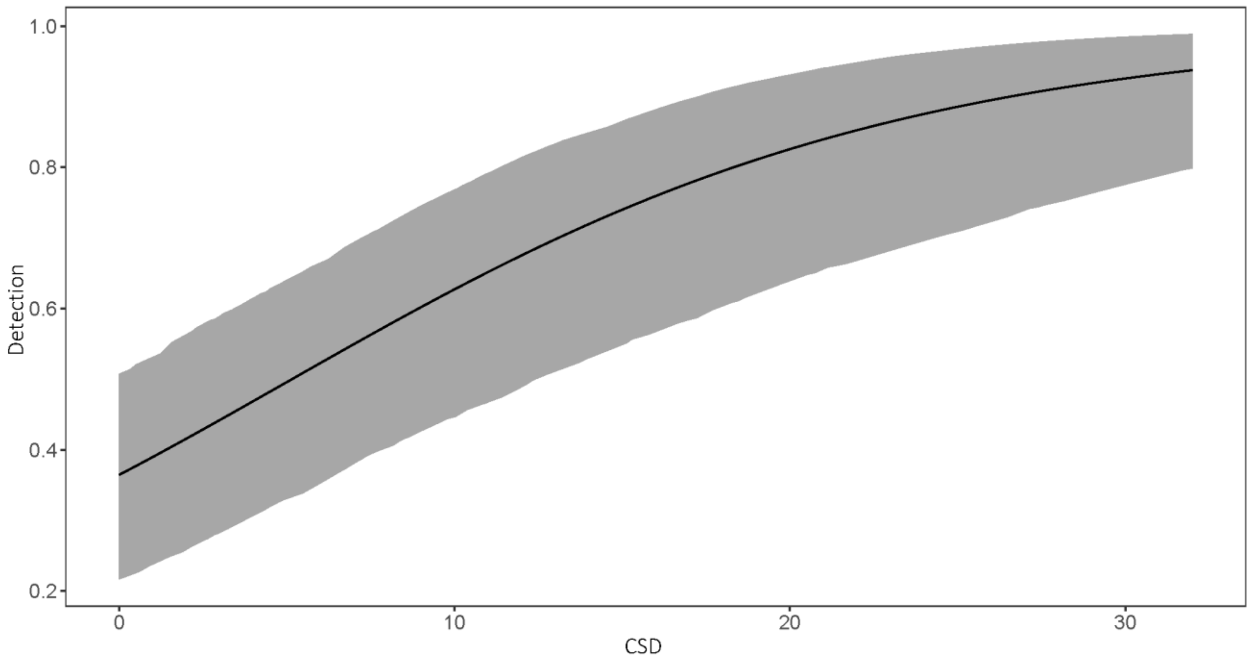

Figure 1.6. Marginal Effects of conifer stem density on snowshoe hare detection probability in the northern Lower and upper Peninsula of Michigan.

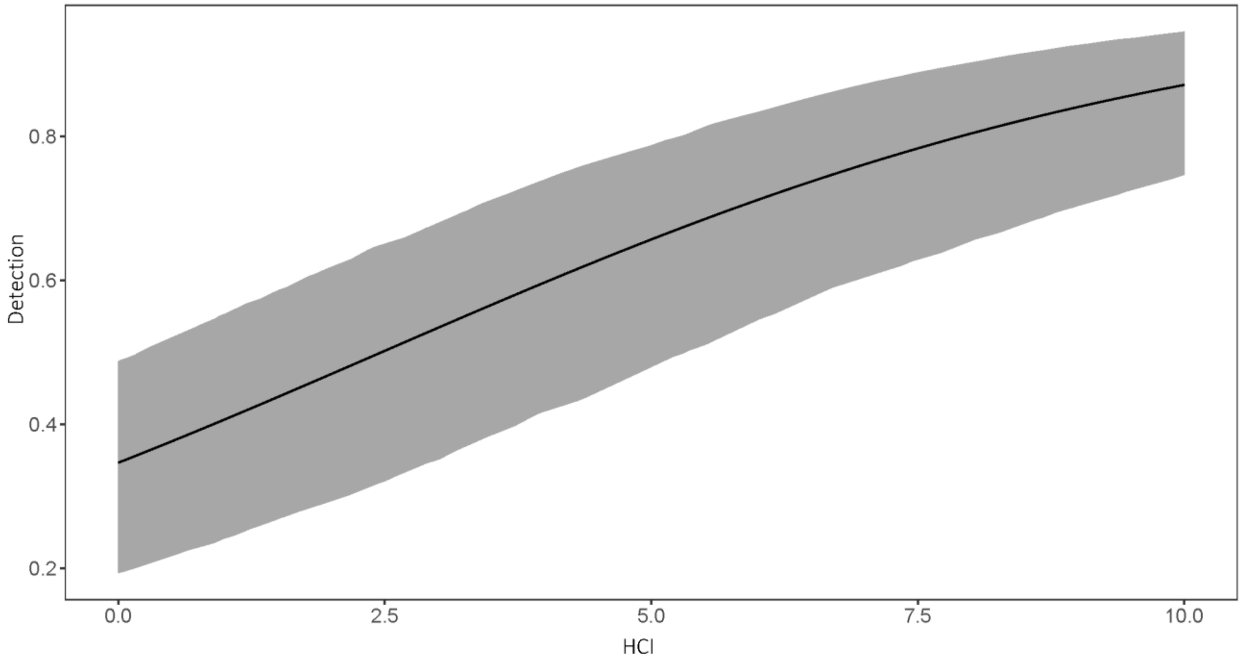

Figure 1.7. Marginal Effects of the horizontal cover index on snowshoe hare detection probability in the northern Lower and upper Peninsula of Michigan.

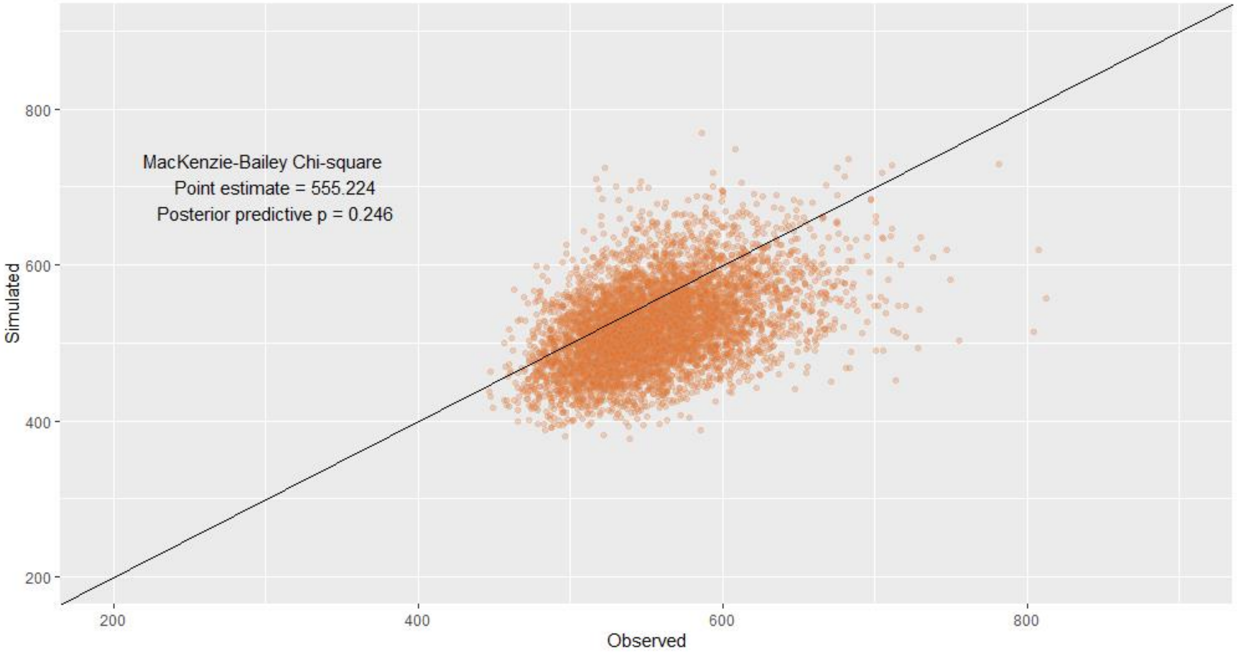

Figure 1.8. Mackenzie-Bailey Fit Statistic and posterior predictive p value demonstrating adequate fit.

Discussion

Consistent with other studies on snowshoe hare – environment relationships, I found that temperature, landcover composition, and winter precipitation influenced snowshoe hare occupancy probability during winter across broad spatial extents (Sultaire et al. 2016*a*, 2016*b*, 2022, Burt et al. 2017, Wilson et al. 2023), and that vegetation composition and structure are important considerations for snowshoe hare detection (Burt et al. 2017). These detection covariates presumably represent the chances of a hare depositing a track on a transect, and not the ability of surveyors to accurately identify and detect tracks (Burt et. al. 2017). The novel contribution of this work stems from my assessment of landcover covariates around sampled locations, offering insights into the effects of the configuration and composition of habitat patched on snowshoe hare occurrence.

I found that snowshoe hare occupancy probability increased as proportion of forested wetlands within one kilometer of study sites increased. Forested wetlands in northern Michigan represent three broad types: 1) depressional wetlands resulting from glacial activity or prehistoric sand dune geomorphology (e.g., northern hardwood swamp, poor conifer swamp,), 2) areas associated with headwater streams and groundwater discharge (e.g., hardwood-conifer swamp, rich conifer swamp, rich tamarack swamp), and 2) riparian wetlands associated with floodplains of rivers and streams that traverse the state (e.g., floodplain forest, northern shrub thicket; (Kost et al. 2007)). Vegetation in these wetlands ranges from emergent herbaceous marsh to scrub-shrub (e.g., willow (*Salix* spp.), alder (*Alnus* spp.)) to heavily forested (e.g., mixed conifer swamps [white cedar (*Thuja occidentalis*); balsam fir (*Abies balsamifera*); black spruce (*Picea mariana*), hemlock (*Tsuga canadensis*) and water tolerant hardwoods (e.g., some ashes (*Fraxinus* spp.). Radio telemetry data from northern Michigan indicate that hares use these wetland types throughout the year (Sault Ste. Marie Tribe Wildlife Program, unpublished data), but heavily use scrub-shrub forested environs in winter. The scrub-shrub cover type offers abundant vertical and horizontal cover (and associated browse), and hares tend to contract their home ranges in these areas during winter (Sault Tribe Wildlife Program, unpublished data). Hares also use densely regenerating conifers in uplands (e.g., young jack pine (*Pinus banksiana*), early successional deciduous species (e.g., aspen (*Populus* spp.), and multi-storied dense mixed mature forest types (e.g., northern hardwoods with balsam fir and hemlock in the understory). Hence, although hares will use a variety of dense cover types during winter, forested wetlands with dense understories potentially play a critical role for conserving hares.

In Michigan, conifer-dominated forested wetlands are vulnerable to altered climate dynamics. Under multiple climate projection scenarios, black spruce, white spruce, northern white cedar, balsam fir, paper birch (*Betula papyrifera*), tamarack (*Larix occidentalis*), and quaking aspen (*P. tremuloides*) are projected to significantly decrease in by mid-century (Stephen Handler et al. 2014) Ecological systems that support these tree species are important to snowshoe hares, providing vital escape cover, forage, and connectivity among populations (Lewis et al. 2011, Thornton et al. 2013, Sultaire et al. 2016*b*) Many of the conifer-dominated forest wetlands in northern Michigan are considered remnants of boreal forest communities to the north and like MTWQ, exhibit a latitudinal gradient with increase dominance in the north (Figure 1.10). In areas south of the hemiboreal tension line, these forested wetlands may currently be serving as climate refugia for species such as snowshoe hare. Competitive exclusion as a driver of conversion from boreal tree to temperate forest tree species assemblages is documented (Frelich et al. 2021, Soubeyrand et al. 2023). Forest dynamics models suggest that conversion of boreal forest communities to more temperate forest communities will occur in the future (Stephen Handler et al. 2014). Related declines in hemiboreal forest communities within northern Michigan may be particularly impactful for snowshoe hares and the Sault Tribe Anishinaabeg, whose relationships with hares are centered in, and often confined to, the 1836 Treaty Ceded Territory (Figure 1.1).

In addition to changes in forest composition and habitat provision, snowshoe hares are vulnerable to physiological responses from altered climate dynamics (Mills et al., 2013, Zimova et al. 2014; Zimova et al. 2016). My study suggests that the mean temperature of the warmest quarter (MTWQ) at survey sites has an inverse association with snowshoe hare occupancy in Michigan. The mechanisms that limit hare occupancy across the temperate-hemiboreal transition in Michigan relative to warming temperatures remains unknown. There is a clear latitudinal gradient, from north to south, in MTWQ across this study area (Figure 1.9). Other studies demonstrated temperature extremes as drivers of snowshoe hare distribution at large spatial extents (Sultaire et al. 2016*a*, 2022, Sirén et al. 2021). These studies also demonstrated the complexities of direct and indirect relationships in bioclimatic systems that impact climate vulnerable species like snowshoe hares. The MTWQ variable highlights the importance of relationships between summer temperature in snowshoe hare occurrence at the southern extent of their range. My study suggests that conifer dominated wetlands with complex understory vegetation structure provide climate refugia for hares, and research suggests that managing for high quality habitat can alleviate climate-related stressors (Wilson et al. 2019). Given projected increases in future temperatures and changes in precipitation patterns, future studies may address relationships among snowshoe hare lifecycles, local habitat characteristics (including forested wetland cover, conifer stem densities and horizontal cover), and seasonal temperature and precipitation patterns.

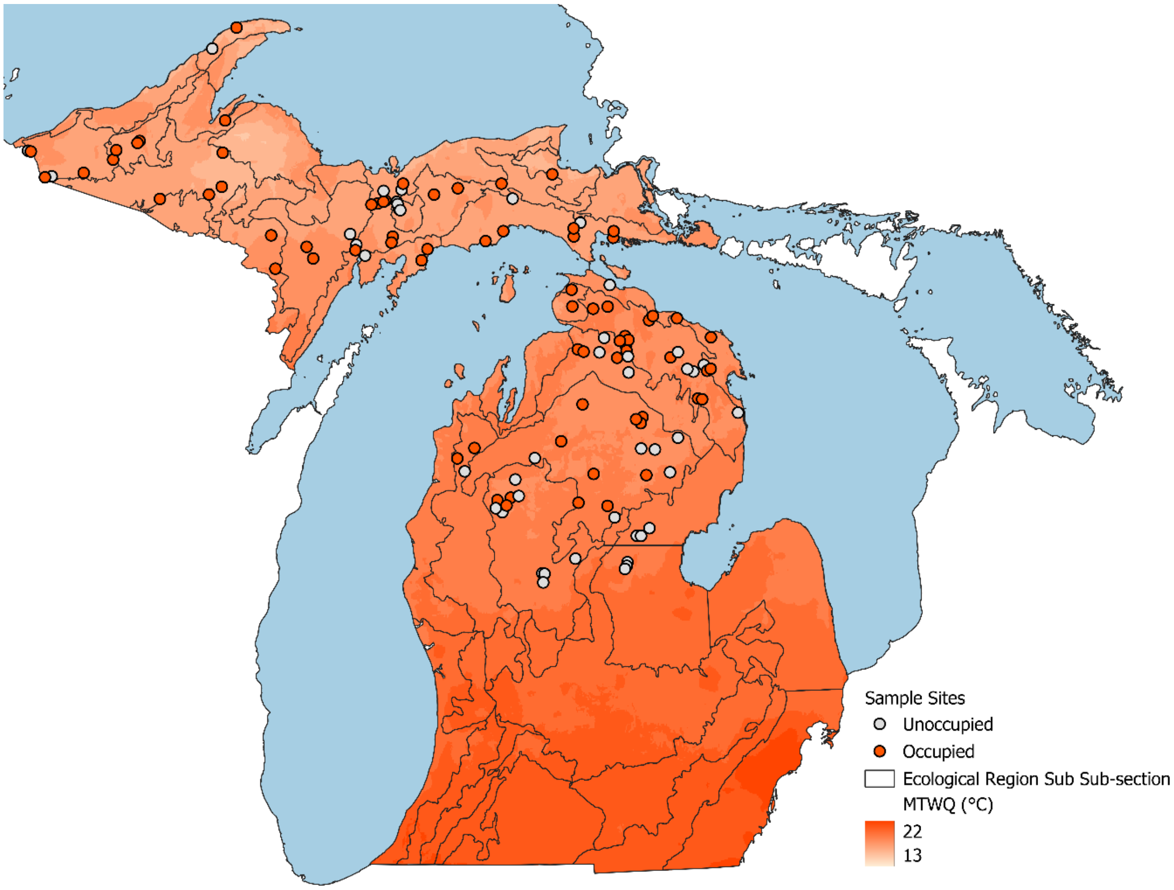

Figure 1.9. The mean temperature of the warmest quarter and snowshoe hare sampling site across Michigan.

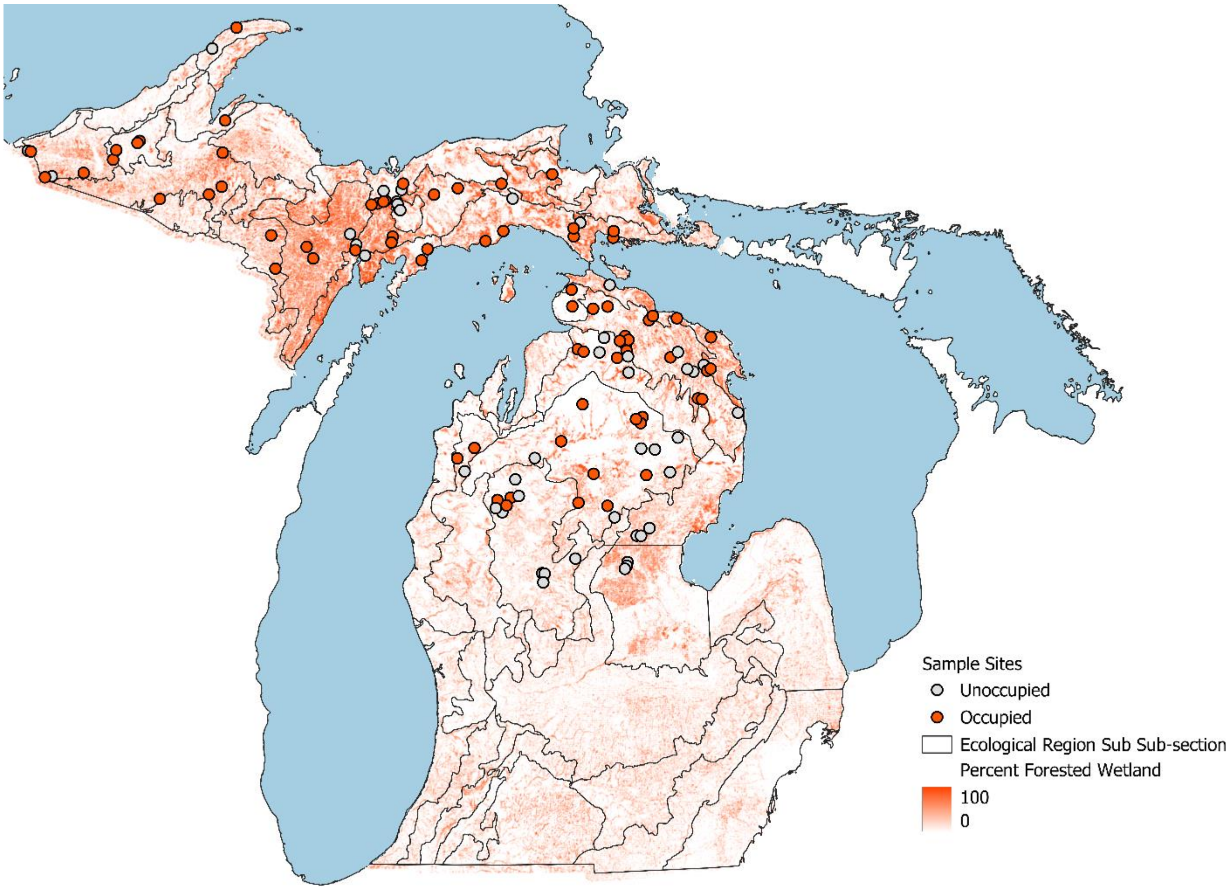

Figure 1.10. The Percentage of Forest Wetland within 1 km^2 and snowshoe hare sampling site across Michigan.

Models developed through this study improved our understanding of snowshoe hare occupancy in northern Michigan, yet several aspects of the dataset and modeling process may be improved. Unmodeled spatial heterogeneity in the detection process exists, and spatial covariation among transects (that were deemed as spatial replicates) potentially confounds the detection model. Furthermore, I note that site selection was not random, but rather weighted to historical knowledge of snowshoe hare occurrences in support of a different project objective (Burt et al. 2017). Future studies of the relationships between landscape-scale snowshoe hare occupancy could be improved by conducting multiple visits and using a more rigorous approach to the spatial distribution of sampling locations (Bailey et al., 2007, Pacifici et al. 2016, Steenweg et al. 2018), especially in locations where snowshoe hares are projected to become increasingly rare on the landscape.

Conclusion

Waabooz (snowshoe hare) are closely tied to hemiboreal forest ecosystems within the Great Lakes Region, and the Anishinaabeg who share these lands and waters. Anishinaabe members of the Sault Ste. Marie Tribe of Chippewa Indians rely on Waabooz for subsistence, ceremony, and in maintaining Anishinaabe ways of life. The Sault Tribe of Chippewa Indians Wildlife Program seeks to understand and address the needs of snowshoe hare within the 1836 Treaty Ceded Territory, to foster resilience among Waabooz populations and to ensure that tribal members can maintain their essential relationships with Waabooz in future generations. My study indicates that hemiboreal forested wetlands play an important role in broad-scale occupancy for hares and hence, should be a conservation priority.

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APPENDIX A: SUPPLEMENTAL MATERIALS

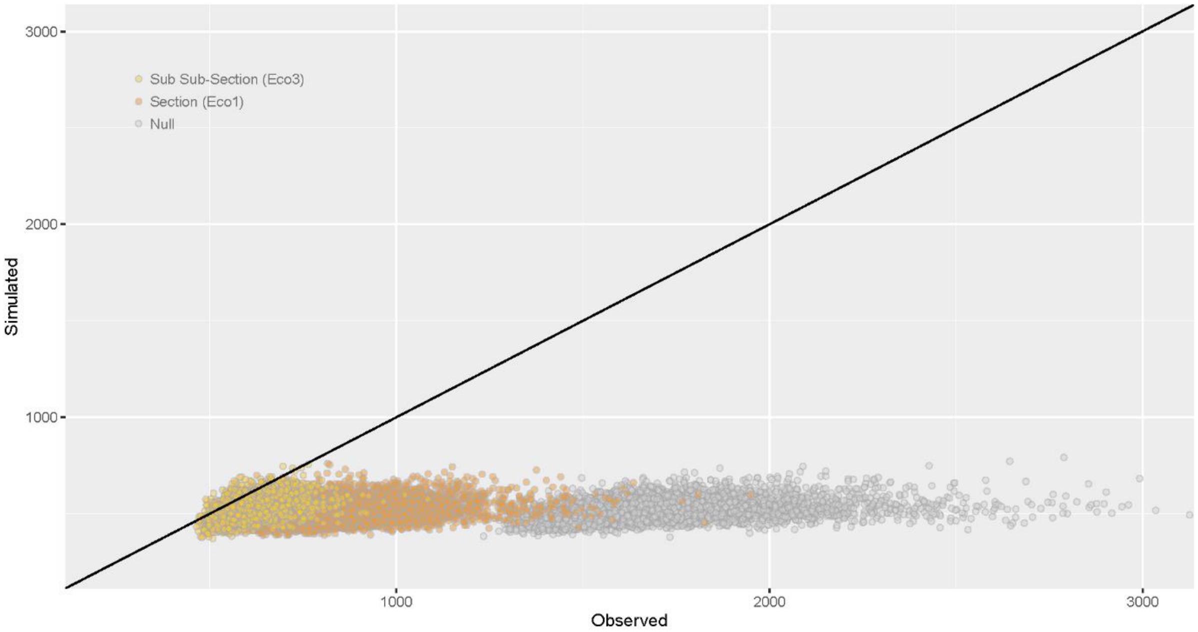

Figure A.1. Detection model fit evaluation using the posterior predictive check with three levels of ecological regions (Albert 1995) and peninsula (Upper vs. Lower Peninsula of Michigan). Null model is represented here in light gray, light orange is Eco3 (sub-sub section), and dark orange is Eco1 (subsection). All models used the null occupancy sub-model (intercept only). This figure was produced by extracting values from “gof” function in UBMS (Kellner 2021) using the default 6000 samples and plotting them together in ggPlot2 (Wickham 2016).

Table A.1. Variables initially explored to model snowshoe hare occupancy in the norther Lower and Upper Peninsulas of Michigan, USA, 2016.

Sub-model	Type	Variable	Description
θ	Climate	AMT	Annual Mean Temperature
		MDR	Mean Diurnal Range
		Iso	Isothermality (BIO2/BIO7) (×100)
		TS	Temperature Seasonality (standard deviation ×100)
		MTWM	Maximum temperature of the warmest month
		MTCM	Minimum Temperature of Coldest Month
		TAR	Temperature Annual Range (BIO5-BIO6)
		MTTQ	Mean Temperature of Wettest Quarter
		MTDQ	Mean Temperature of Driest Quarter
		MTWQ	Mean Temperature of Warmest Quarter
		MTCQ	Mean Temperature of Coldest Quarter
		AP	Annual Precipitation
		PWM	Precipitation of Wettest Month
		PDM	Precipitation of Driest Month
		PS	Precipitation Seasonality (Coefficient of Variation)
		PTQ	Precipitation of Wettest Quarter
		PDQ	Precipitation of Driest Quarter
		PWQ	Precipitation of Warmest Quarter
		PCQ	Precipitation of Coldest Quarter
		SD	Mean annual snow depth
ρ	Landscape Composition	PMF	Percent mixed forest within 1km
		PDF	Percent deciduous forest within 1km
		PCF	Percent evergreen forest within 1km
		PSS	Percent scrub/shrub land within 1km
		PFW	Percent palustrine forested wetland within 1km
		PSSW	Percent palustrine scrub/shrub wetland within 1km
		PEW	Percent emergent wetland within 1km
	Landscape Configuration	Split	Split
		DIV	Division
		ED	Edge density
		IJI	Interspersion and juxtaposition index
		SDI	Simpson's Diversity Index
		ShDI	Shannon's Diversity Index
	Site Level Vegetation	CSD	Conifer stem density
		DSD	Deciduous stem density
		HCI	Horizontal cover index
	Ecoregions	ES	Ecoregion section
		ESS	Ecoregion sub-sub section

CHAPTER 2: A SPATIALLY EXPLICIT DENSITY ESTIMATION FOR SNOWSHOE HARE (LEPUS AMERICANUS) ON THE EAST ZONE OF THE HIAWATHA NATIONAL FOREST

Introduction

In Anishinaabe creation stories and ongoing lifeways, one relative endemic to the hemiboreal region in North America is particularly prominent, Waabooz (snowshoe hare; *Lepus americanus*). The Anishinabeg maintain kinship relations with Waabooz for subsistence and ceremonial practices, demonstrating the intersection of essential ecological and cultural relationships. Annually, Sault Tribe members harvest between 900-1800 snowshoe hares within the 1836 Treaty Ceded Territory (unpublished Sault St. Marie Tribe of Chippewa Indians Harvest Data) (Figure 2.1), and Sault Tribe members have consistently expressed concerns about Waabooz population resilience and habitat conditions (Sault Tribe Wildlife Program 2022). Stimulated by tribal concerns over Waabooz, in 2015 the Sault Tribe Wildlife Program conducted a Climate Change Vulnerability Assessment (CCVA) and research needs assessment for snowshoe hares in the 1836 Treaty Ceded Territory (Wonch et. al 2015). The CCVA indicated that a potential, but uncertain, source of adaptive capacity for snowshoe hares relates to projected increases in wildland fire and associated habitat effects. Hence, the research needs assessment called for future investigations on the relationships between snowshoe hare habitat management prescriptions for silviculture and fire (Wonch et al. 2015).

Snowshoe hare associations with forest structure and composition and associated effects of forest and fire management occur at multiple scales across the North American hemiboreal and boreal zones. Within-stand forest structure is important to snowshoe hare survival, and habitat use has a positive relationship with increasing structural complexity of vegetation (Keith et al. 2011, Berg et al. 2012a, Fuller and Harrison 2013, Holbrook et al. 2017, Wilson et al. 2019). At landscape scales, the composition and configuration of habitat impact snowshoe hare distributions (Lewis et al. 2011, Sultaire et al. 2016a, 2022, Holbrook et al. 2017, Gigliotti et al. 2018, Wilson et al. 2023). Researchers have also demonstrated hare relationships with forest management practices, often highlighting higher snowshoe hare habitat use with dense early successional forest regeneration St-Laurent et al. 2008, Berg et al. 2012, Thornton et al. 2012, Ivan et al. 2014, Holbrook et al. 2017). Heterogenous early successional forest types resulting from wildland fire are important ecological systems for snowshoe hares across their range. The positive association between post-fire habitat use by hares is generally attributed to structural changes (e.g., higher stem counts, increased horizontal cover) in conifer (e.g., spruce sp.) and aspen-dominated systems as ecosystems recover (Wolff 1980, Stephenson 1985, Paragi et al. 1997, Cheng et al. 2011, Berg et al. 2012, Strong and Jung 2012, Hutchen 2017, Olnes et al. 2019).

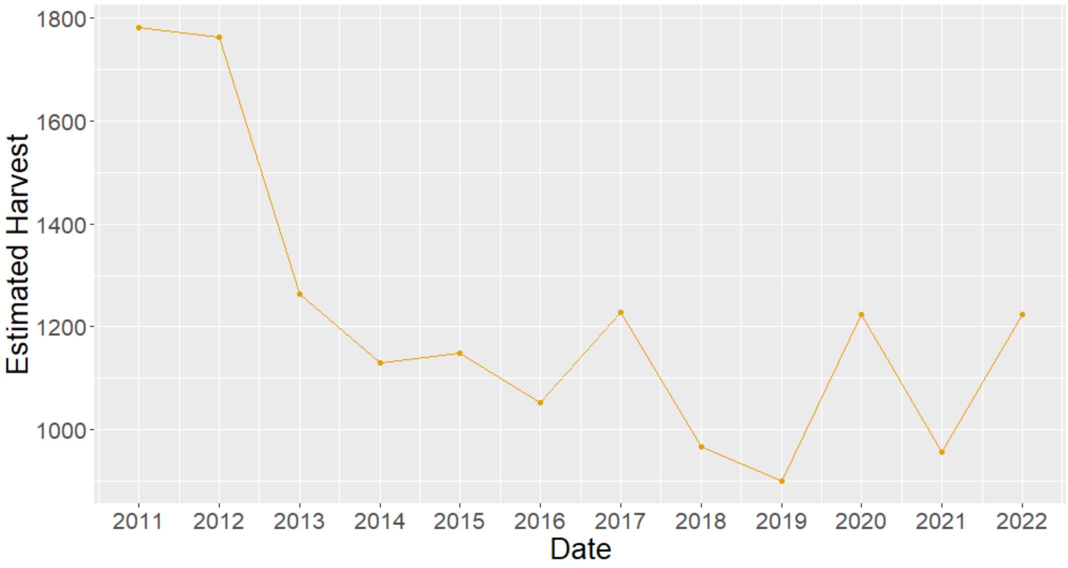

Figure 2.1. Estimated snowshoe hare harvests by Sault Tribe hunters in the 1836 Treaty Ceded Territory from 2011-2022.

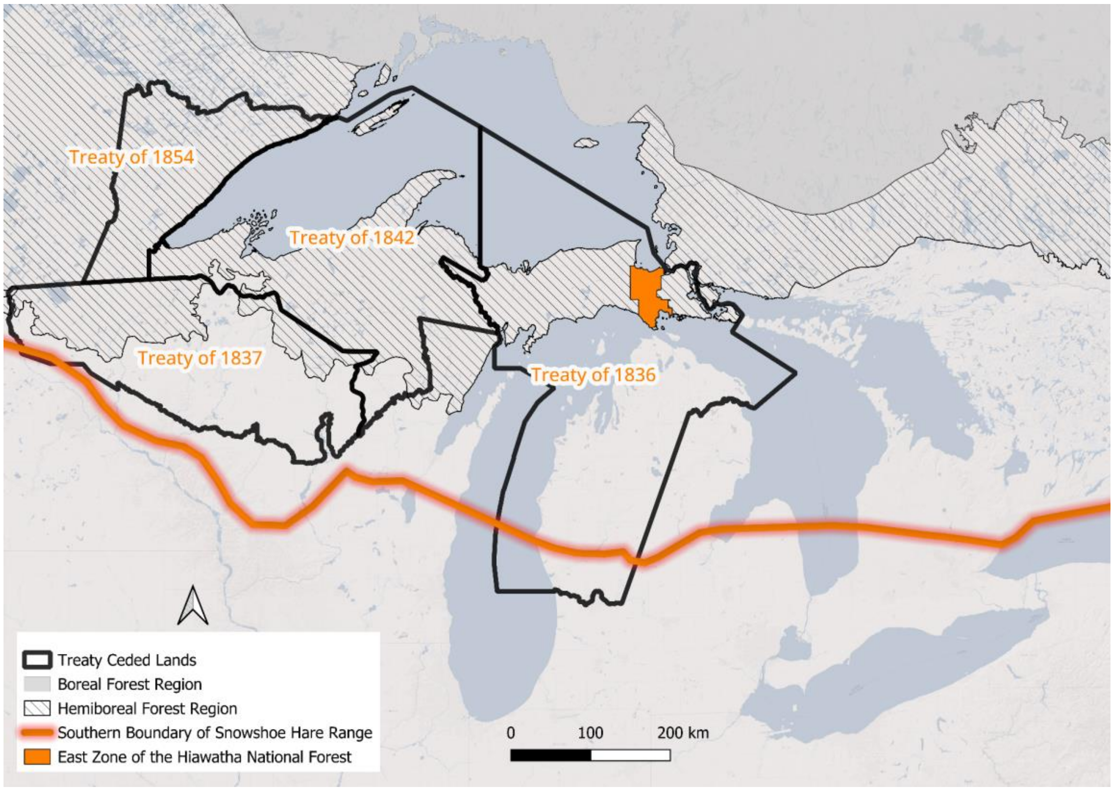

Figure 2.2. The 1836 Treaty Ceded Territory and other Anishinaabe Treaty Ceded Lands (black lines) in the Great Lakes Region, USA, the East Unit of the Hiawatha National Forest (orange polygon), Hemiboreal Forest Biome (gray hashed lines), Boreal Forest Biome (dark gray), and snowshoe hare southern range boundary (orange line). Source: Ceded Territory Sault Tribe Wildlife Program, boreal/hemiboreal biomes (Brandt 2009), HIF Boundary USFS, snowshoe hare range (ICUN Red List, 2019).

The southern distribution of snowshoe hares in the Great Lakes region generally corresponds to the hemiboreal forest zone (Brandt 2009), and ecosystems within this zone play an important role in hare occurrence and abundance (Sultaire et al. 2016*b*, 2022, Wilson et al. 2018). The Hiawatha National Forest is located in the hemiboreal sub-zone of the 1836 Treaty Ceded Territory (Brandt 2009) (Figure 2.2). Defined by dominance of cold-tolerant boreal tree species that co-occur with more cold-intolerant temperate tree species, the hemiboreal zone is the circumpolar ecotone between temperate and boreal forest biomes (Brandt 2009). Globally the boreal/hemiboreal zone is warming faster than any other zone (0.5°C per decade) resulting in novel impacts to forest vegetation communities (Gauthier et al. 2014). In the hemiboreal sub-zone across the 1836 Treaty Ceded Territory, there is a legacy of intensive forest management focused on timber production, wildlife management focused on promoting herbivores, such as white-tail deer, and a long history of fire suppression in fire-prone ecosystems. The Hiawatha National Forest alone has over 234,095 ha designated as suitable for timber harvest (U.S. Forest Service 2006), as well as, over 29,000 ha of fire-prone ecosystems where active fire suppression has occurred for over 100 years. To maintain and restore vital culturally important forest ecosystems in the Hiawatha National Forest, novel approaches to management are required to maintain remnant boreal forest ecosystems (Park et al. 2014).

Adaptive management is a form of structured decision-making appropriate when a reasonable amount of control, high levels of uncertainty, and a need for optimal decisions exist (Gregory et al., 2012),One example of a collaborative Adaptive Management Framework is the Sault Tribe – Hiawatha National Forest Inter-Agency Ishkode (fire) Stewardship Plan (Ishkode Framework) (Sault Tribe Wildlife Program 2022). This framework has three components, the Inter-Agency Ishkode Stewardship Plan, a Tribal Community Engagement Assessment and Strategy (TCEAS), and an Ecological Assessment and Monitoring Strategy (EAMS). This framework was developed following the principles of Adaptive Management as advanced in the Department of Interior's Adaptive Management Technical Guide (Williams et al. 2009) and has the engagement of Anishinaabe and western sciences as a central tenet.

A key step in the adaptive management learning cycle (Figure 2.3) is development of ecological forecasting models that allow managers to predict ecological responses to management actions, and provision of monitoring tools to evaluate those responses (Williams and Brown 2012). Using the TCEAS and the EAMS, the Ishkode Framework applies ecological models for key species and develops predicted responses to prescribed fire within treatment areas. Spatial capture-recapture models (SCR) can be an important analytical technique for adaptive management frameworks focused on achieving habitat-related objectives for focal wildlife species. SCR methods use information about the spatial location of individual encounters to make inferences on density (Royle and Young 2008) and can unify landscape and population ecology by allowing inference on second and third-order resource selection (Royle et al. 2017). Recently, tools have become available that allow wildlife researchers and managers to easily implement SCR methods without custom programming (i.e., R packages oSCR and SECR). These tools allow wildlife professionals to make spatially explicit predictions of animal density across a state space sampling area (Borchers and Efford 2008, Royle and Young 2008, Sutherland et al. 2019). With these easily implemented tools and robust guidance on sampling design (Sollmann et al. 2012), SCR methods are effective for pre-treatment monitoring, forecasting, and prescription evaluation under adaptive management frameworks.

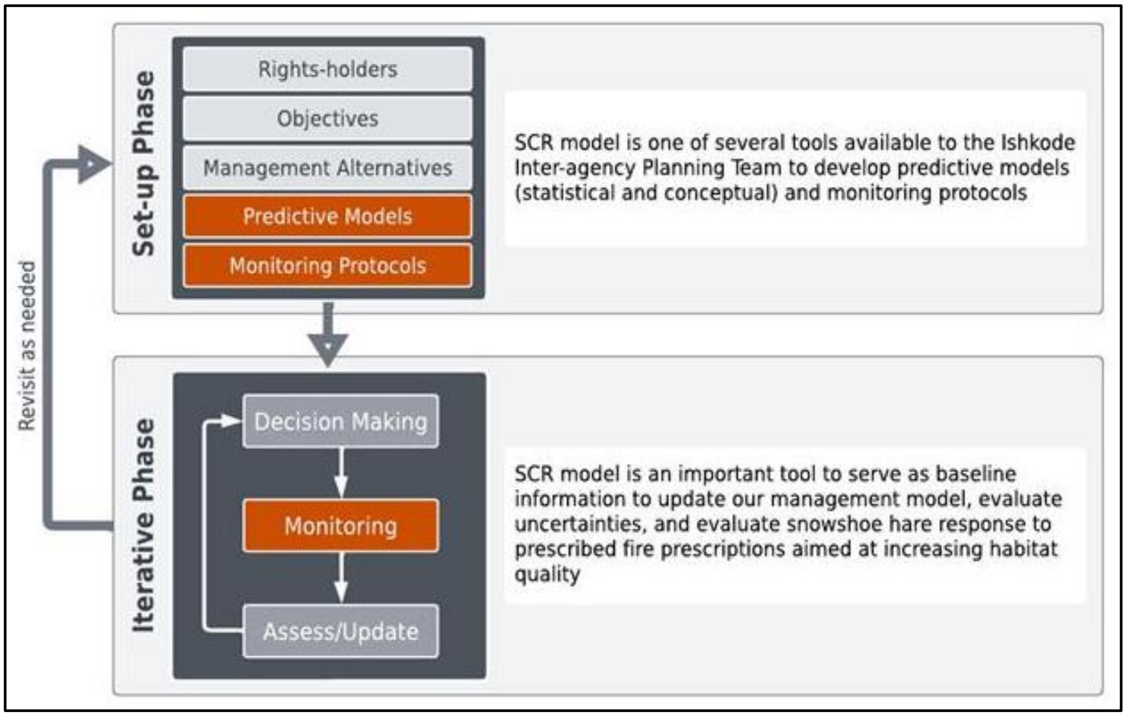

Figure 2.3. Adaptive management process (Williams and Brown 2012), highlights stages in both the set-up and iterative phases of the cycle where SCR models were used in the Ishkode Project.

The Ishkode Framework sets forth management and monitoring objectives that seek to increase the quality of snowshoe hare habitat in response to fire and silvicultural prescriptions. In 2023, the Sault Tribe Wildlife Program and Hiawatha National Forest completed pretreatment monitoring on approximately ~1,915 hectares known as the Betchler Marsh Burn Complex within the Ishkode Framework project area. This area contains a suite of silvicultural and prescribed fire management prescriptions with a variety of ecosystem and snowshoe hare-specific objectives (Figure 2.4).

Betchler Marsh Ecosystem Objectives

- Re-establish ishkode (fire) in Betchler Marsh.
- Maintain peatlands and open wetland character.
- Reduce black spruce woody encroachment.
- Create opportunities for cedar and hemlock regeneration and recruitment.
- Identify opportunities to protect and promote late seral forests at fine scales.
- Increase biological and structural diversity specifically in red pine plantations.
- Maintain high canopy closure and large wood debris recruitment in cold water streams.
- Engage Sault Tribe members in assessing plant response, habitat change, and other monitoring activities through site visits and harvest reports

Waabooz - Snowshoe Hare Habitat Management Objectives

Desired Outcomes: Increase and maintain quality and quantity of snowshoe hare habitat.

Strategies: Increase landscape heterogeneity, jack pine thickets, and the amount of woody understory for horizontal cover using fire.

Monitoring: Monitor for occupancy, abundance, and distribution. Engage Sault Tribe members in assessing habitat and population changes through site visits and harvest reporting.

Figure 2.4. Betchler Marsh ecosystem and Waabooz habitat management objectives from Sault Tribe – Hiawatha National Forest Inter-Agency Ishkode (fire) Stewardship Plan.

In this Chapter, I demonstrate how the Sault Tribe Wildlife Program is using snowshoe hare SCR models to analyze associations between landcover composition and configuration and snowshoe hare density for the East Zone of the Hiawatha National Forest. My hypotheses are informed by snowshoe hare habitat objectives in the Ishkode Framework (Figure 2.4). I hypothesize that snowshoe hare density will be positively associated with increased landscape heterogeneity (landcover composition and configuration as characterized by landscape pattern metrics) resulting from proposed prescribed fire in the project area. I also demonstrate how spatially explicit snowshoe hare density predictions can be used as important baseline information for silvicultural and fire prescriptions in the Betchler Marsh Burn Unit.

Methods

Study Area

This study occurred on the east side of the Hiawatha National Forest (362,320 ha) in the Upper Peninsula of Michigan. USA (UP) (Figure 2.2). Land cover in the eastern UP is primarily forested with most of the landscape in Federal and State ownerships (Mackinaw State Forest), and to a lesser extent private and commercial forests. The cities of Sault Ste. Marie and St. Ignace are proximate to the Hiawatha National Forest, with this part of the national forest spanning from the northern shores of Lakes Michigan and Huron to the southern shore of Lake Superior (Figure 2.5). Hares are generally patchily distributed and common in forested environs of the eastern UP, and likely occupied this landscape shortly after the last period of glaciation (~10,000 years ago; (Schaetzl 2001)).

Although primarily forested, the eastern UP is characterized by heterogeneous vegetation patches that exist on varying depths of glacial deposits (Michigan Natural Features Inventory 1998). Glacial landforms play an important role in vegetation composition, and range from sandy outwash plains, and thick moraines of glacial till, to exposed bedrock benches (Michigan Natural Features Inventory 1998). Proximity to the upper three Great Lakes influences regional climatic conditions, with large amounts of annual lake-effect snow exerting a controlling influence on the mosaic of soils and vegetation communities (Henne et al. 2007).

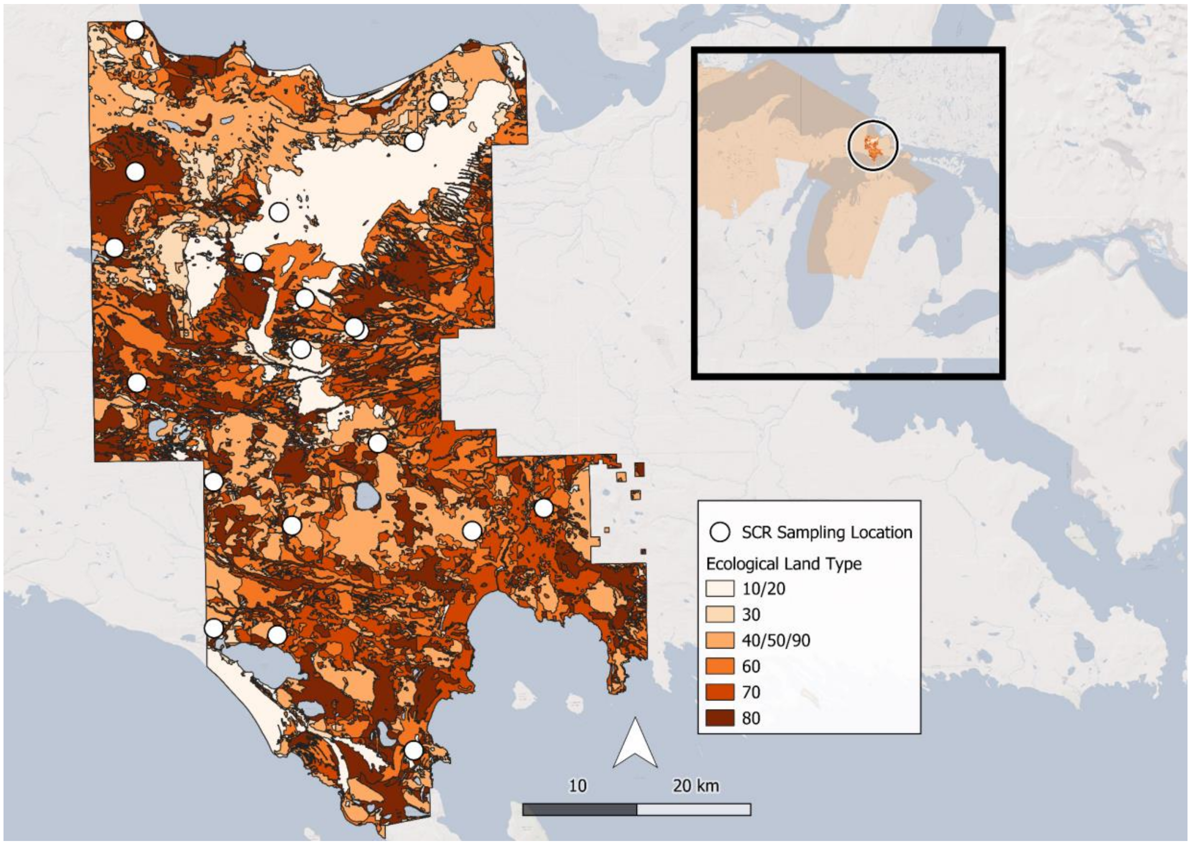

Figure 2.5. Snowshoe hare sampling sites on the east zone of the Hiawatha National Forest stratified by Ecological Land Type.

The Bechtler's Marsh Burn Complex is in the 2023 Inter-Agency Ishkode Management Plan that covers 30,102 hectares. This Burn Complex has 1,915 hectares of silvicultural and prescribed fire prescriptions at the implementation stage in 2023 (Figure 2.6). The Betchler's Marsh Burn Complex is a mix of upland conifer, primarily red pine (*Pinus resinosa*) plantations, and peatland complexes, with embedded patches of naturally regenerated late seral red, white (*Pinus strobus*), and jack pine (*Pinus banksiana*). There is a long history of Anishinaabe use of fire across this landscape with pre-European contact fire return intervals of 6-31 years (Sutheimer et al. 2021).

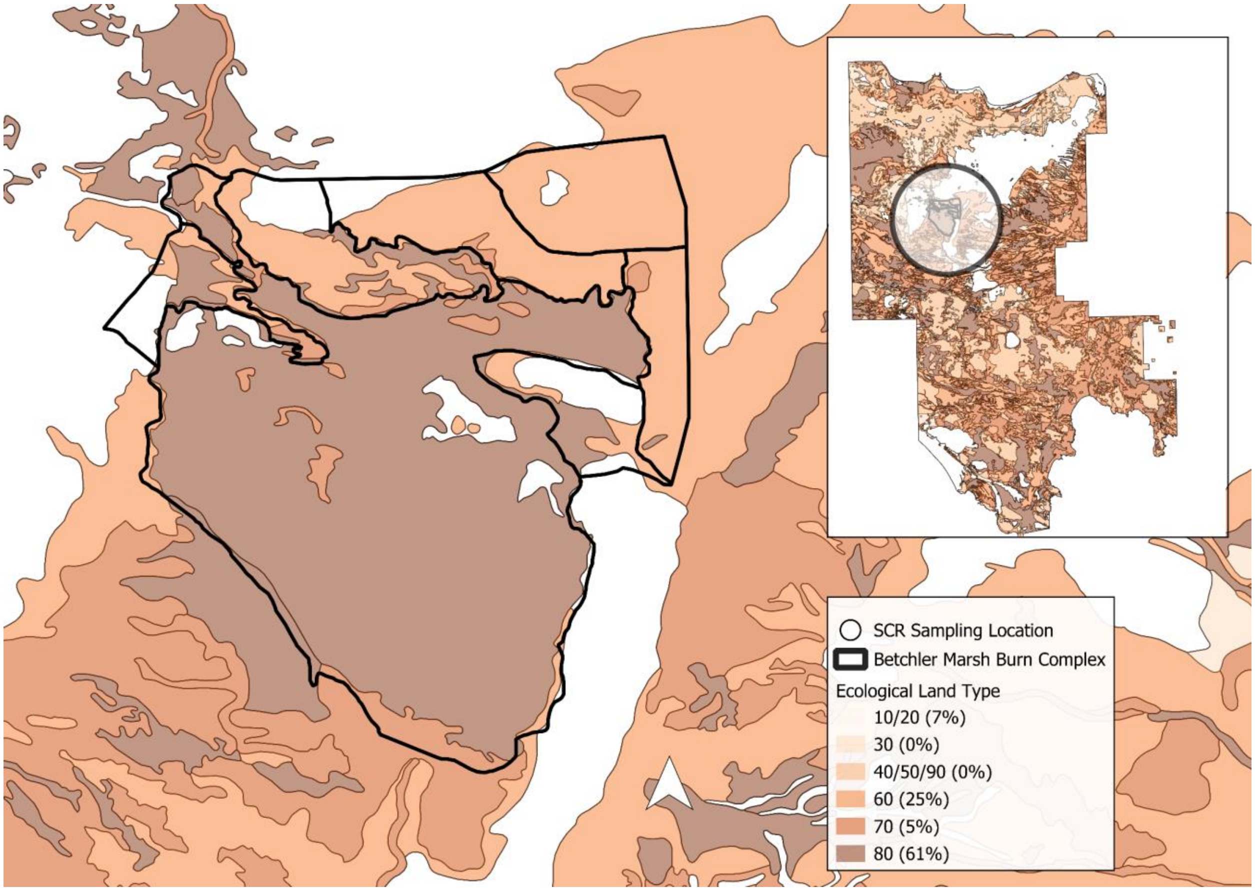

Figure 2.6. The Betchler Marsh Burn Complex on the Hiawatha National Forest. Ecological land types percentages are for the area within the boundaries of the complex.

The Betchler Marsh Land Type Association is defined by lowland outwash plains of sandy or sandy-skeletal soils (Silbernagel et al. 1997). Lowland shrubs and mixed non-forest wetlands are dominant. Wetlands occupy most of the area. Northern white cedar (*Thuja occidentalis*), black spruce (*Picea mariana*), hemlock (*Tsuga canadensis*), quaking aspen (*Populus tremuloides*), big tooth aspen (*Populus grandidentata*), red pine, white pine, and lowland hardwoods such as, black ash (*Fraxinus nigra*), dominate the area (Figure 2.7). There is historic and current use by Sault Tribe members for hunting and gathering.

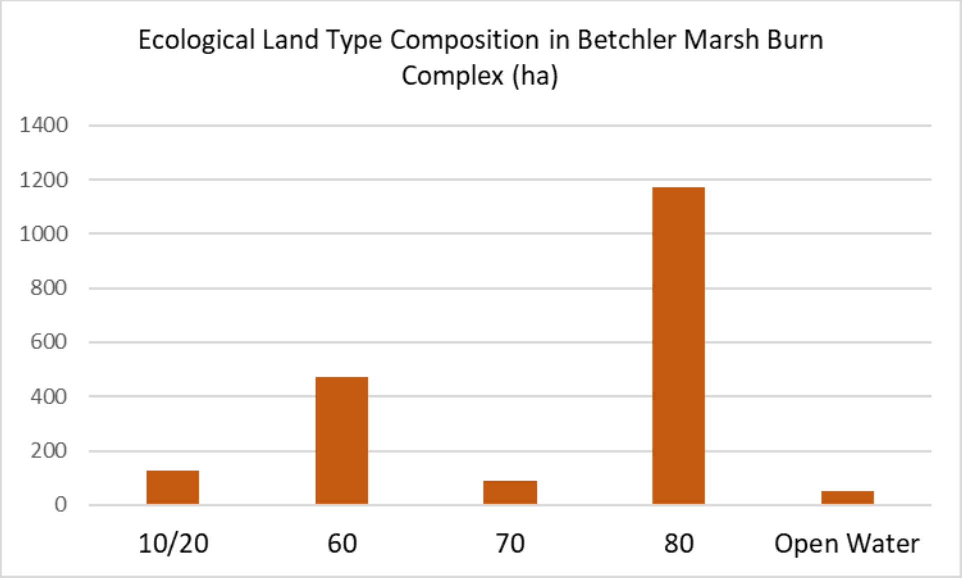

Figure 2.7. The composition of Ecological Land Types in the Betchler Marsh Burn Unit, area is in hectares.

Snowshoe Hare Live Trapping

I centered snowshoe hare trapping on a spatially balanced stratified random sample derived from generalized random tessellation sampling (GRTS) in the spsurvey package (Dumelle et al. 2021) in R. I stratified trapping sites based on Ecological Land Type (ELT), which classify landscapes based on geology, landform, soils, flora, and fauna (USDA Forest Service 2006) (Table 2.1, Figure 2.5**Error! Reference source not found.**). I selected 20 potential trapping sites and buffered each by 500 m. I removed portions of buffers that fell outside the focal ELT boundary, resulting in trapping areas between 20 and 78 hectares. I removed sites that were <20 ha in size from the sample and replaced those sites from the overdraw panel generated by the GRTS procedure. I then selected 30 random trap locations within each site that were a minimum of 18 m apart for a total of 600 trap locations across the study area (Figure 2.8).

Table 2.1. Ecological land type (ELT) groups in the Hiawatha National Forest, Upper Peninsula Michigan.

Ecological land type group	Description	Area in hectares (% study site)
10/20	Sandy outwash plains typically supporting jack pine or red pine. Fire is the major disturbance factor in these xeric ecosystems.	28,274 (14%)
30	Sandy outwash plains and morainal areas with a slightly higher productivity than ELT group 10, 20. ELT 30 typically supports red pine, mixed conifer, hemlock, or low-volume hardwood stands.	11,368 (6%)
40/50/90	Glacial moraines, pitted outwash, bedrock-controlled moraines, and areas where bedrock is close to the surface. Typically, these land types support northern hardwoods and have better-developed soils. Soil texture ranges from sand to silty clay loam.	44,642 (22%)
60	Land-type 60 encompasses the transition zone between dry uplands to true wetlands. ELT 60 often occurs at the edge of the outwash plains but includes the somewhat poorly drained soils on the clay plain landform. Vegetation is highly variable on ELT 60. In the historic condition, the 10/20, 30, and 60 ELTs were the heart of the white pine-hemlock forest type.	42,768 (21%)
70(A&B)	ELT 70A includes mineral soil wetlands supporting vegetation indicative of acid soil conditions. Black spruce, tamarack, and hemlock are common species on this land type. ELT 70B consists of mineral soil wetlands supporting vegetation indicative of higher pH (>5.5) or basic soil conditions. Cedar, mixed swamp conifers, tamarack, and balsam fir are typical of the vegetation on this land type.	32,288 (16%)
80(A&B)	ELT 80A consists of forested wetlands with more than 12 inches of wet, acidic (pH<5.5) organic soil. The forested areas of this ELT (80AF) typically support black spruce stands and to a lesser extent tamarack stands. ELT 80B consists of forested wetlands with more than 12 inches of wet, basic (pH > 5.5) organic soil. The forested areas of this ELT (ELT 80BF) typically supports northern white cedar stands, mixed swamp conifer stands and to a lesser extent tamarack and black ash stands.	39,245 (19%)

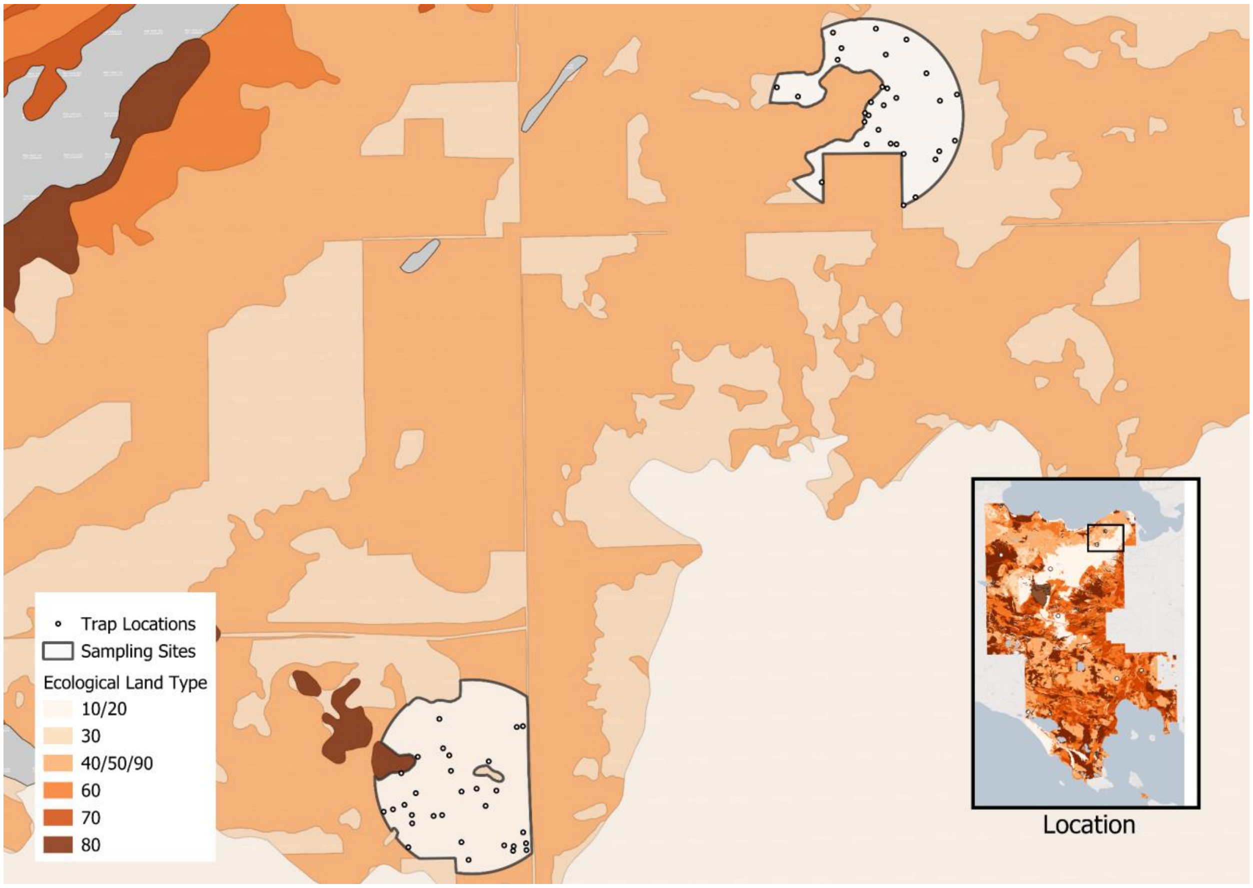

Figure 2.8. Detailed map of two snowshoe hare sampling locations in the east zone of the Hiawatha National Forest.

STWP personnel live-captured hares between June 2016 and September 2019 using Tomahawk traps (Tomahawk Live Traps, Hazelhurst, WI) baited with aspen bark boiled in cinnamon, alfalfa, and/or apples. Field crews transported hares to a mobile laboratory where they were briefly anesthetized with isoflurane, receiving an induction dose of 4% with oxygen flow at 3 liters per minute followed by a maintenance dose of 2-2.5% isoflurane. A blood sample (<1% body weight) was obtained from the saphenous vein for disease and parasite testing. Hares weighing at least 833 grams were fit with a 26 g VHF transmitter (Advanced Telemetry Solutions, Isanti, MN) and injected with a subcutaneous 16 mm Passive Integrated Transponder (BioMark, Boise, Idaho). Following recovery from anesthesia, hares were released at the point of capture. All animal procedures were developed with a consulting wildlife veterinarian, approved and conducted by staff of the STWP under the authority of section XXI of the 2007 Inland Consent Decree (US v Michigan 2007) and following animal handling guidelines of the American Society of Mammologists under the USGS NWHC ACUC protocol EP160819 (Sikes 2016).

Site-Level Vegetation Structure and Composition

At each trap location, field crews measured percent horizontal and vertical vegetation cover, as well as coniferous and deciduous stem densities. Field crews collected horizontal and vertical cover measures along four random azimuth bearings radiating from the trap and from 4m away using a moosehorn densitometer (Figure 2.9). For each horizontal cover height strata (i.e., 0.5 and 1.0 m above the ground), presence/absence of cover was recorded. I combined horizontal cover values for 0.5 meter and 1-meter data points resulting in 8 horizontal cover points per trap location and then calculated the percent horizontal cover by summing the present counts and dividing by 8. For vertical cover, field crews measured stem densities by functional types (i.e., conifer or deciduous (broadleaf)) using a 1x4 meter belt transect that extended west from the trap location (Figure 2.9).

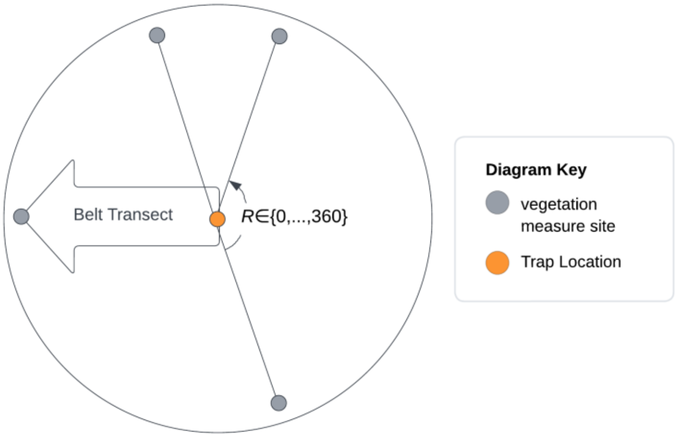

Figure 2.9. Diagram of vegetation measure (vertical and horizontal cover) in relation to each trap location for all 600 trap sites.

Landscape Composition and Configuration from Remotely-sensed Data

I extracted landcover-based variables around each trapping location using the 2016 Coastal Change Analysis Program data from the National Oceanic and Atmospheric Administration (Office of Coastal Management 2021). I first created univariate landcover data sets for 6 undeveloped landcover classes (Upland Coniferous Forest, Upland Deciduous Forest, Upland Mixed Forest, Upland Scrub-Shrub, Grassland, Forested Wetland, and Scrub-Shrub Wetland) and then calculated the percentage of each landcover class within 0.5 km in each 30-meter pixel using a roving window analysis. The output of this process was 6 continuous raster datasets (one for each landcover type) where each pixel was the percent of landcover within 0.5 kilometers. I next created continuous raster datasets for four Fragstats-based pattern metrics (interspersion-juxtaposition, percent adjacent land, and edge density) using the landscapemetrics package in R (Hesselbarth et al. 2019). Processing landscape variables as continuous gridded surfaces for the entire project area allowed for extraction of values for the SCR state space and aided in developing spatially explicit predictions of snowshoe hare density for the study area.

Data Analysis

I employed a spatial-capture recapture model using the package oSCR in R to analyze competing models for estimating snowshoe hare density (Royle and Converse 2014, Sutherland et al. 2019) SCR models leverage spatial information about the location of hare captures to infer the home range or activity center of each individual. These models assume each hare capture was a Bernoulli random variable with individual- and trap- specific detection probabilities. The detection probability p_{ij} of an individual i at trap j is assumed to decrease as distance (d_{ij}) from its activity center increases according to a detection function. I used the default half-normal detection function:

$$p_{ij} = p_0\, exp\left(-\frac{d_{ij}^2}{2\sigma^2}\right)$$

where p_0 is the probability of detecting an individual when the trap is at the geographic center of the range and sigma is the spatial parameter that controls the steepness of the detection decay. Given that trap locations were randomly allocated to sites drawn from a spatially random and balanced sample, I considered all sampling sites as a single capture session which allowed me to leverage spatial information about sigma across all sites. This also allowed me to incorporate sites with no captures into the density estimates.

I used a modified secondary candidate set/build-up model selection process to develop my global model (Morin et al. 2020). In this case, I fit all possible combinations of the detection sub-model then used a build-up process for the density sub-model. I initially ran univariate models for all configuration variables and those which were uncorrelated and within 10 AIC points of the top model moved forward in the analysis. I then repeated this process for the landscape composition variables. All model covariates were z-scaled in program R. I evaluated the resulting set of landscape composition and configuration covariates for correlation and removed one of the pairs with a Pearson's correlation coefficient ≥ 0.6. I present the top five ranked candidate models.

I produced a spatially explicit map of snowshoe hare density from my top model using the package oSCR for the Betchler Marsh Burn Complex. To forecast, snowshoe hare response to fire treatments, I simulated a projected landscape by reclassifying pixels classified as Upland Coniferous Forest to Grassland, Upland Mixed Forest, Upland Deciduous Forest, or Upland Scrub-Shrub with the Raster Package in R, using a simple unbalance random assignment. Finally, I replicated the process used to estimate the spatially-explicit snowshoe hare density estimate that involved recalculating Fragstats metrics, extracting values to each point in the state-space and estimating and producing a spatially explicit prediction density response based on the simulated landscape. To estimate pretreatment and posttreatment snowshoe hare densities, I used zonal analysis tools in ArcGIS to calculate the mean snowshoe hare densities for the Betchler Marsh Burn Complex.

Results

Snowshoe Hare Live Trapping and Site-Level Vegetation Variables

In 2016 and 2017, I recorded 2,400 trap nights and captured 66 individual hares. Field crews recaptured 6 of these individual a single time and one twice, hence recapture information was sparse. All 600 traps across trapping sites were operated for four nights. I recorded an average of 1.14 recaptures per site and 1.11 spatial recaptures (i.e., recaptures in a new trap). I observed a maximum daily movement of 75.7 m. Field crews completed 600 vegetation plots that included horizontal cover index (mean = 0.72; range = 0.00 – 1.00), vertical cover (mean = 0.82; range = 0.00 – 1.00)), conifer stem density (mean = 0.26 stems/m^2; range = 0.00 – 4.00)), and deciduous stem density (mean = 0.67 stems/m^2; range = 0.00 – 18.25) (Table 2.2).

Landscape Composition and Configuration

I sampled three landscape configuration metrics that included edge density (mean=153; range =10.36-357.1), Simpson diversity index (mean=0.53, range = 0.03-0.86), and interspersion-juxtaposition index (mean=44; range = 1 - 101). Similarly, I sampled eight landscape composition metrics that included percent of the landscape in upland conifer forest (mean=21.7; range = 0.0-98.3), upland mixed forest (mean=3.0; range = 0.0 – 18.5), upland deciduous forest (mean= 21.1; range = 0.0 – 97.4), upland shrub scrub (mean = 11.6; range = 0.0 - 98.1), shrub scrub wetland (mean = 10.0; range = 0.0 – 62.7), forested wetland (mean= 23.0; range = 0.0 – 97.4), and grassland (mean= 4.7; range = 0.0 – 72.8) (

Table 2.2).

Model Selection

Of the 24 candidate models (Table 2.3), two covariates consistently appeared in the top-ranked detection sub-model; coniferous stem density and deciduous stem density. Similarly, in the abundance sub-model, interspersion-juxtaposition Index (IJI), percent upland coniferous forest (pUCF), edge density (ED), and percent palustrine scrub-shrub wetland (pPSW) appeared in top-ranked models. All other covariates that appeared in the five top-ranked models were uninformative with 85% confidence intervals that overlapped 0 with p values >0.05 (Table 2.4).

Table 2.2. Global Model variable set for modeling snowshoe hare density on the East Zone of the Hiawatha National Forest, 2016-2017.

Sub-Model	Variable	Description	Range (mean)
density	pUCF	Percent Upland Conifer Forest contains areas dominated by trees generally greater than 5 meters tall and greater than 20 percent of total vegetation cover. More than 75 percent of the tree species maintain their leaves all year. Canopy is never without green foliage. (CCAP class 11)	0-98.3 (21.7)
	pPFW	Percent Palustrine Forested Wetland includes wetlands dominated by woody vegetation less than 5 meters in height. Total vegetation coverage is greater than 20 percent. Species present could be true shrubs, young trees and shrubs, or trees that are small or stunted due to environmental conditions. (CCAP class 15)	0.0-97.4 (22.8)
	pPSW	Percent Palustrine Scrub/Shrub Wetland includes wetlands dominated by woody vegetation less than 5 meters in height. Total vegetation coverage is greater than 20 percent. Species present could be true shrubs, young trees and shrubs, or trees that are small or stunted due to environmental conditions	0.0-62.7 (10.0)
	IJI	Interspersion and Juxtaposition index Fragstats Metric	0.0-99.9 (68.9)
	ED	Edge Density Fragstats metric	10.4-357.1 (153.1)
	SIDI	Shannon Diversity Index Fragstats metric	0.3-0.86 (0.53)
detection	CSD	Conifer stem density (stems/m^2).	0.0-4.0 (0.26)
	VCI	Vertical Cover Index (0-1)	0.0-1.0 (0.83)
	DSD	Deciduous stem density (stems/m^2).	0-18.8 (0.67)
	HCI	Horizontal Cover Index (0-1)	0.0-1.0 (0.72)

My top model accounted for 22% of the weight of evidence from the candidate model set and showed a positive association between coniferous stem density (85% CI = 0.09, 0.35) and deciduous stem density (85%CI=0.09, 0.35) and snowshoe hare detection (Table 2.5). As trap location-level deciduous stem density increased from 0 stems/m^2 to 12 stems/m^2, detection probability increased from ~0.04 to ~0.41 (Figure 2.10), and as trap site-level conifer stem density increased from 0 stem/m^2 to 7 stems/m^2, snowshoe hare detection probability increased from ~0.04 to ~0.17 (Figure 2.11). The top-ranked model portrayed a negative association between snowshoe hare density and pUCF (85% CI =

-.88, -0.2), and a positive association between IJI (85% CI = 0.17, 0.61), and pPSW (85% CI = 0.17, 0.52; Table 2.5). As trap location-level pUCF increased from 3% to 95%, snowshoe hare density decreased from ~0.60 hares/ha to ~0.08 hares/ha (Figure 2.12). As site-level IJI increased from 0 to 100, snowshoe hare density increased from ~0.05 to ~0.91 hares/ha (Figure 2.13). As trap location-level pPSW increased from 0.1% to 62%, snowshoe hare density increased from ~0.30 hares/ha to ~1.5 hares/ha (Figure 2.14). The top model produced a mean estimated snowshoe hare density of 0.52 hares/ha (85%CI = 0.21, 0.83).

Table 2.3. Candidate model sets for snowshoe hare density on the East Zone of the Hiawatha National Forest, 2016-2017.

Sub-Model	Candidate Model Structure
Density	~ ED + pUCF
	~ ED + pUCF + pPSW
	~ ED + pUCF + pPFW
	~ ED + pUSS + pUCF + pPSW
	~ IJI + pUCF
	~ IJI + ED + pUCF + pPSW
	~ SIDI + pUCF + pPSW
	~ SIDI + pUCF
Detection	~ VCI + DSD + CSD
	~ HCI + VCI + DSD + CSD
	~ DSD + CSD
	~ HCI + DSD + CSD

Table 2.4. Full Model Ranking describing the top five models ranked by AIC for snowshoe hares on the East Zone of the Hiawatha National Forest, 2016-2017.

	Model	logL	K	AIC	dAIC	weight	CumWt
1	D(~IJI + pUCF + pPSW) p(~DSD + CSD)	326.6	8	669.1	0.0	0.2	0.2
2	D(~IJI + ED + pUCF + pPSW) p(~DSD + CSD)	326.0	9	670.0	0.9	0.1	0.4
3	D(~ED + pUCF) p(~DSD + CSD)	328.2	7	670.4	1.3	0.1	0.5
4	D(~ED + pUCF) p(~VCI+ DSD+ CSD)	327.4	8	670.9	1.7	0.1	0.6
5	D(~ED + pUCF) p(~HCI + DSD + CSD)	328.2	8	672.4	3.3	0.0	0.6

Table 2.5. Top ranking model for snowshoe hare density on the East Zone of the Hiawatha National Forest, 2016-2017.

Model Structure: D(~IJI + pUCF + pPSW) p(~DSD + CSD) sig ~1

	Estimate	SE	15% CI	85% CI	z	P(>|z|)
d0.(Intercept)	-2.50	0.37	-3.04	-1.96	-6.72	0.00
IJI	0.39	0.15	0.17	0.61	2.59	0.01
pUCF	-0.54	0.24	-0.88	-0.20	-2.28	0.02
pPSW	0.32	0.14	0.13	0.52	2.36	0.02
sig.(Intercept)	3.89	0.17	3.64	4.14	22.47	0.00
p0.(Intercept)	-3.12	0.41	-3.70	-2.53	-7.66	0.00
DSD	0.22	0.09	0.09	0.35	2.42	0.02
CSD	0.22	0.09	0.09	0.35	2.42	0.02

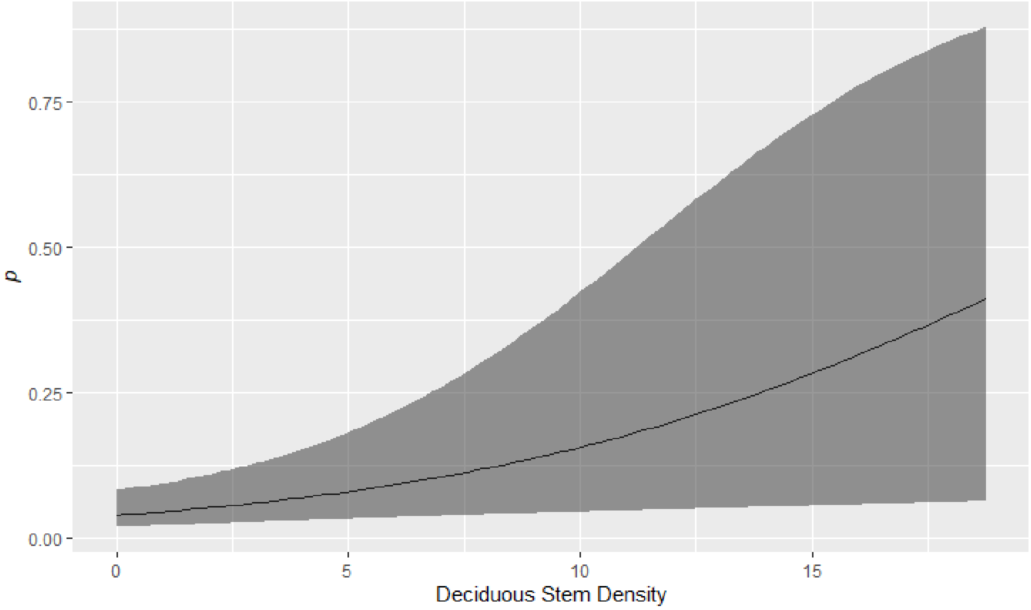

Figure 2.10. The effect of Deciduous Stem Density on the detection probability of snowshoe hare on the Hiawatha National Forest, 2016-2017.

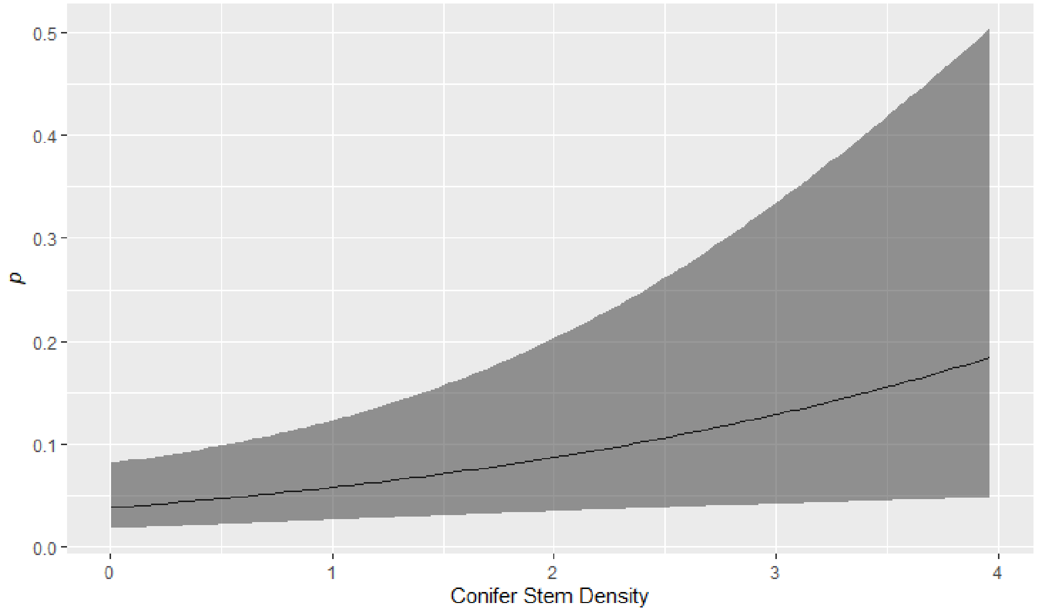

Figure 2.11. The effect of Conifer Stem Density on the detection probability of snowshoe hare on the Hiawatha National Forest, 2016-2017.

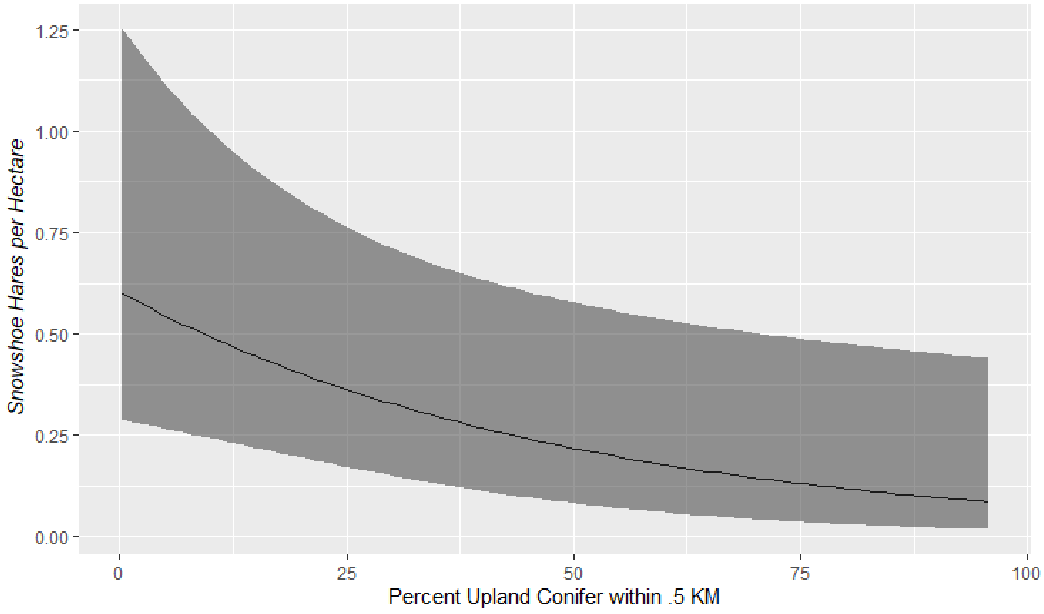

Figure 2.12. The effect of Percent Upland Coniferous Forest on the density of snowshoe hare on the Hiawatha National Forest, 2016-2017.

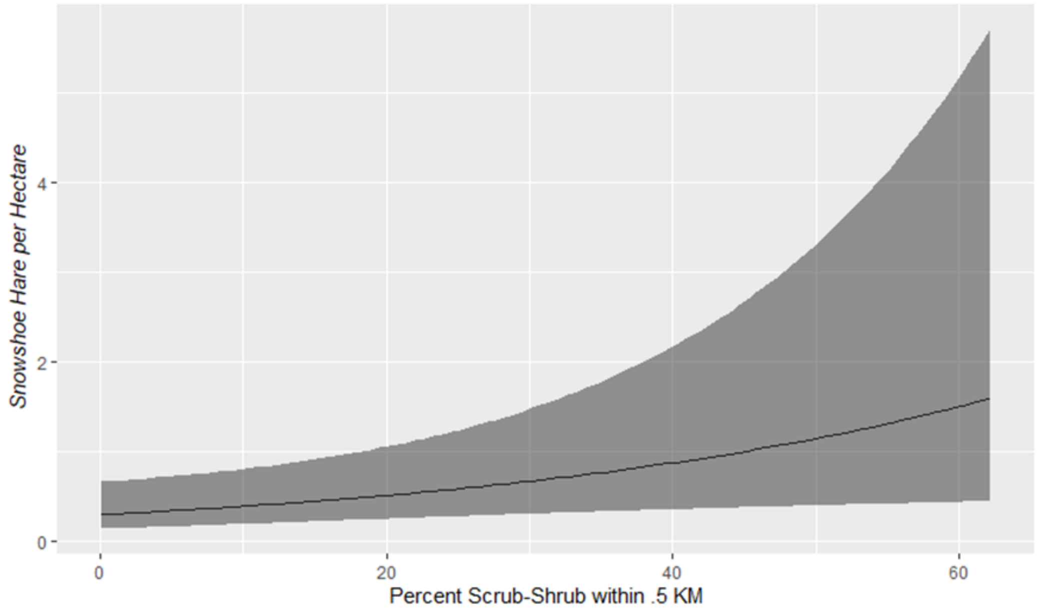

Figure 2.13.The effect of Percent Palustrine Scrub-Shrub Wetland on the density of snowshoe hare on the Hiawatha National Forest, 2016-2017.

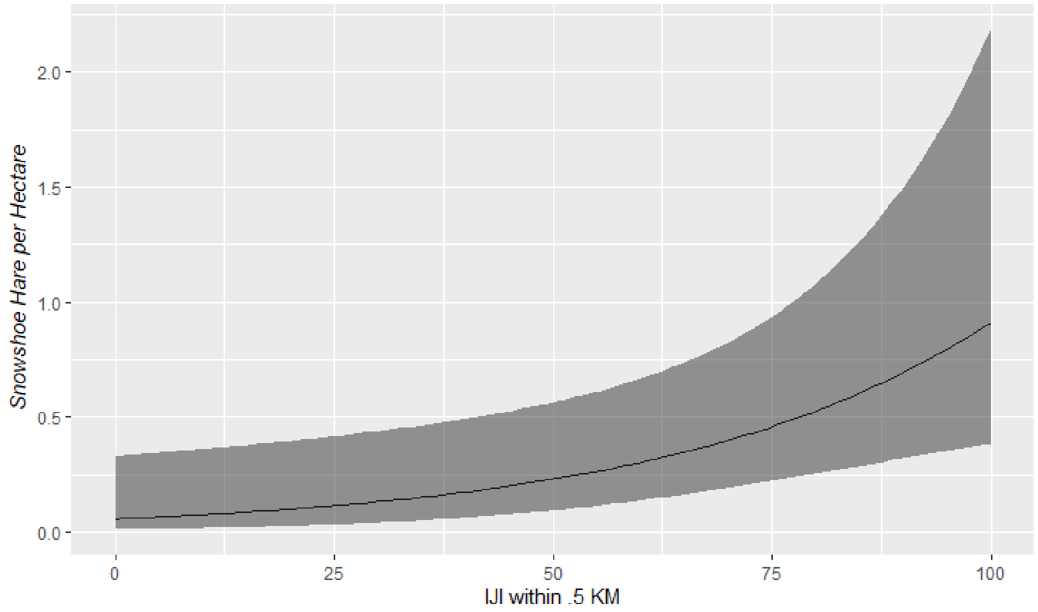

Figure 2.14. The effect of the Interspersion-Juxtaposition Index on the density of snowshoe hare on the Hiawatha National Forest, 2016-2017.

Betchler Marsh Burn Complex

The simulated random landscape reduced the amount of upland coniferous forest (-297 ha) and increased the amount grassland (+68 ha), upland deciduous forest (+75 ha), upland mixed forest (+76 ha), and upland scrub/shrub (+79 ha) across the Betchler Marsh Burn Complex (Figure 2.15 & Figure 2.16). In the Betchler Marsh Burn Complex, estimated pre-treatment snowshoe hare density was 0.73 hares per hectare; predicted post-treatment density was 0.76 hares per hectare. There was a noticeable change in the geographic distribution of estimated hare densities pre- and post-treatment (Figure 2.18 & Figure 2.19).

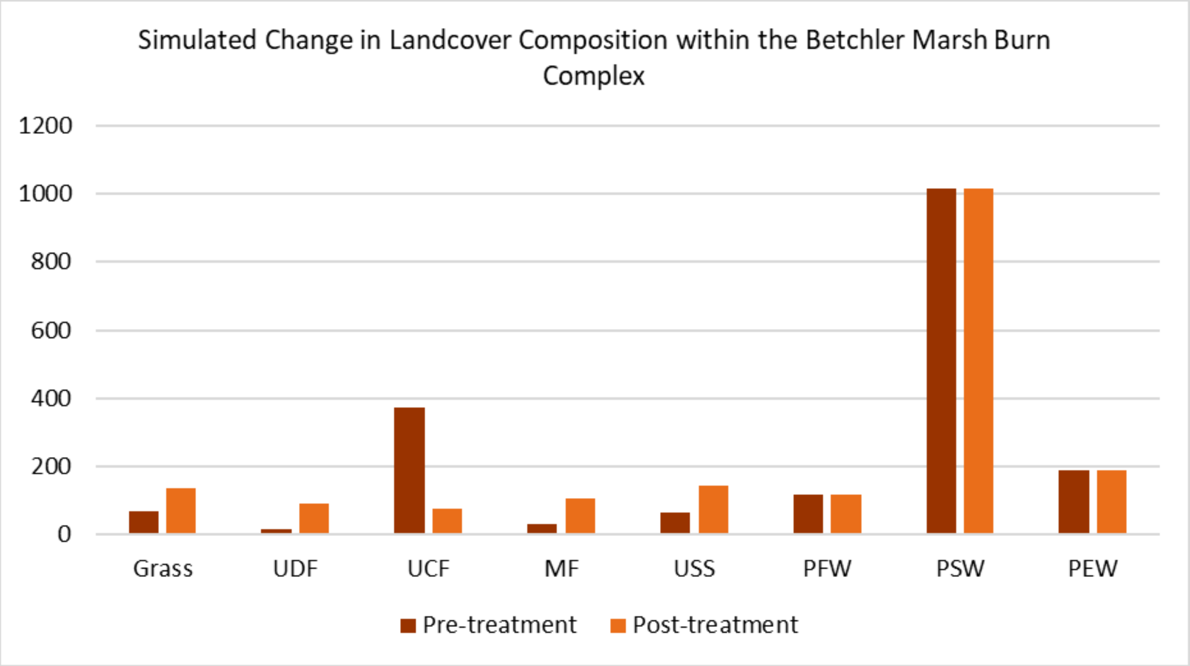

Figure 2.15. Pre/Post treatment composition of landcover classes based on simulated landscape (Grass = Grassland, UDF= Upland Deciduous Forest, UCF=Upland Conifer Forest, MX= Upland Mixed Forest, USS=Upland Scrub/Shrub, PFW=Palustrine Forested Wetland, PSW=Palustrine Scrub/Shrub Wetland, PEW=Palustrine Emergent Wetland).

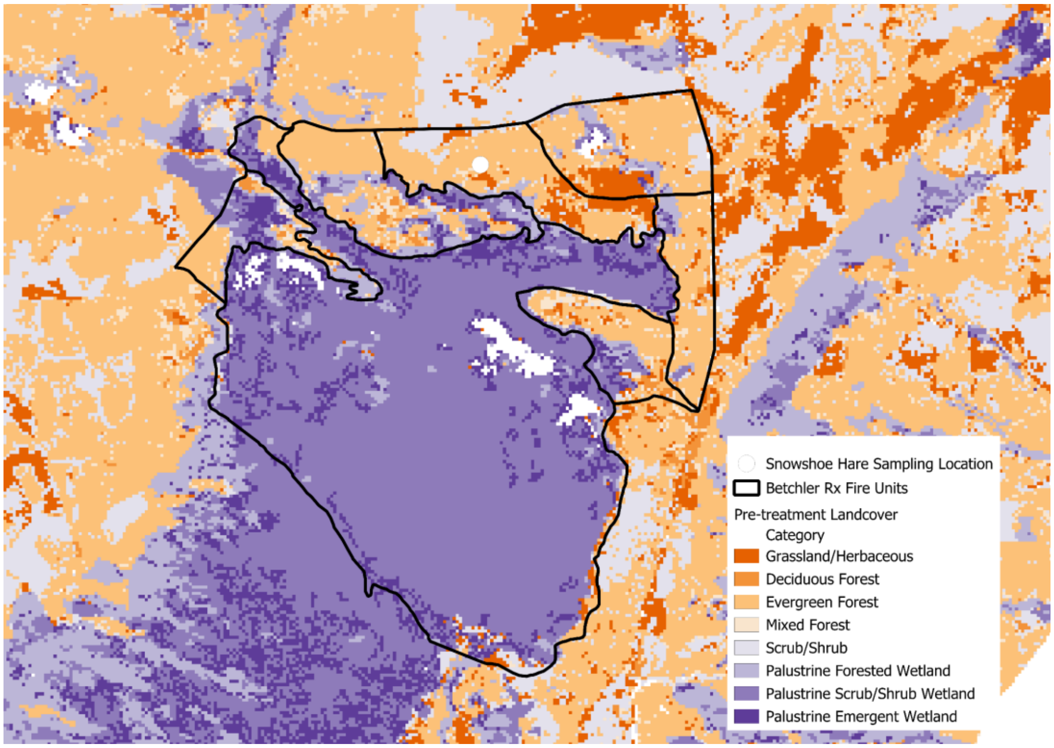

Figure 2.16. Pre-treatment landcover across the Betchler Marsh Burn Complex.

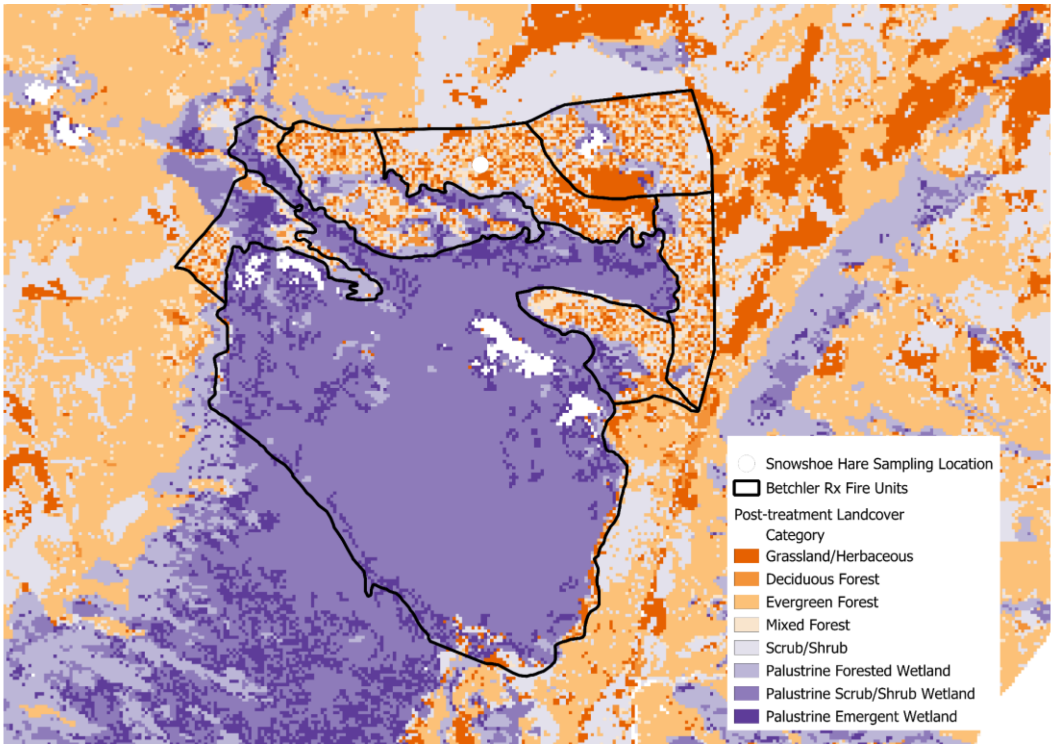

Figure 2.17. Pre-treatment landcover across the Betchler Marsh Burn Complex.

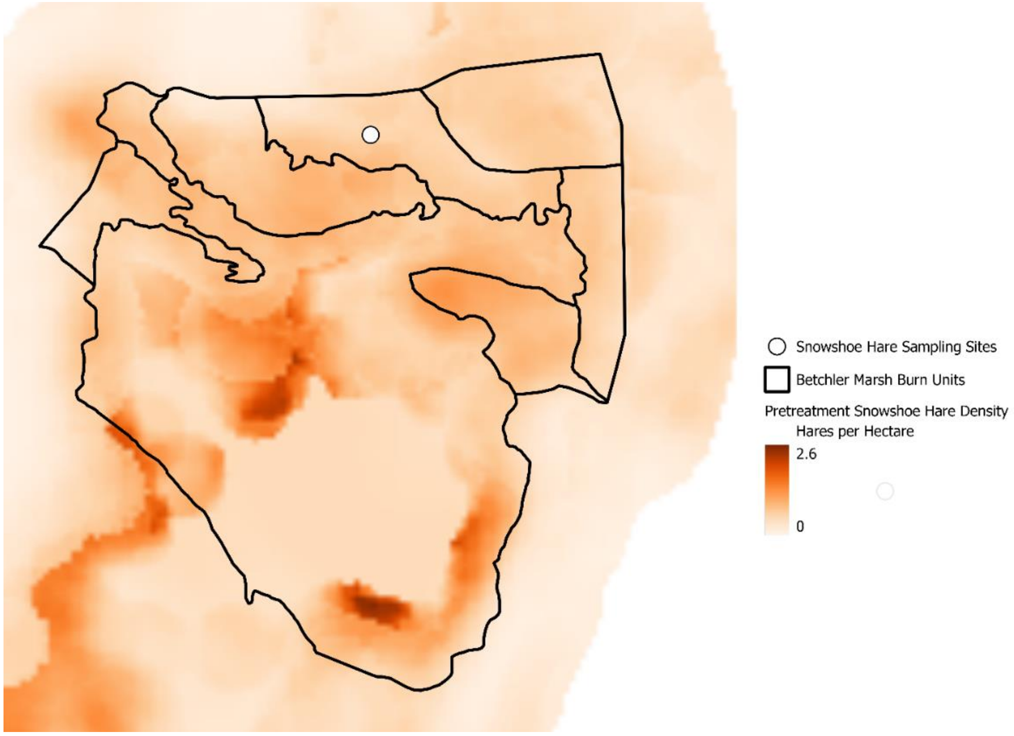

Figure 2.18. Estimated Snowshoe Hare Density in the Betchler Marsh Burn Complex on the Hiawatha National Forest.

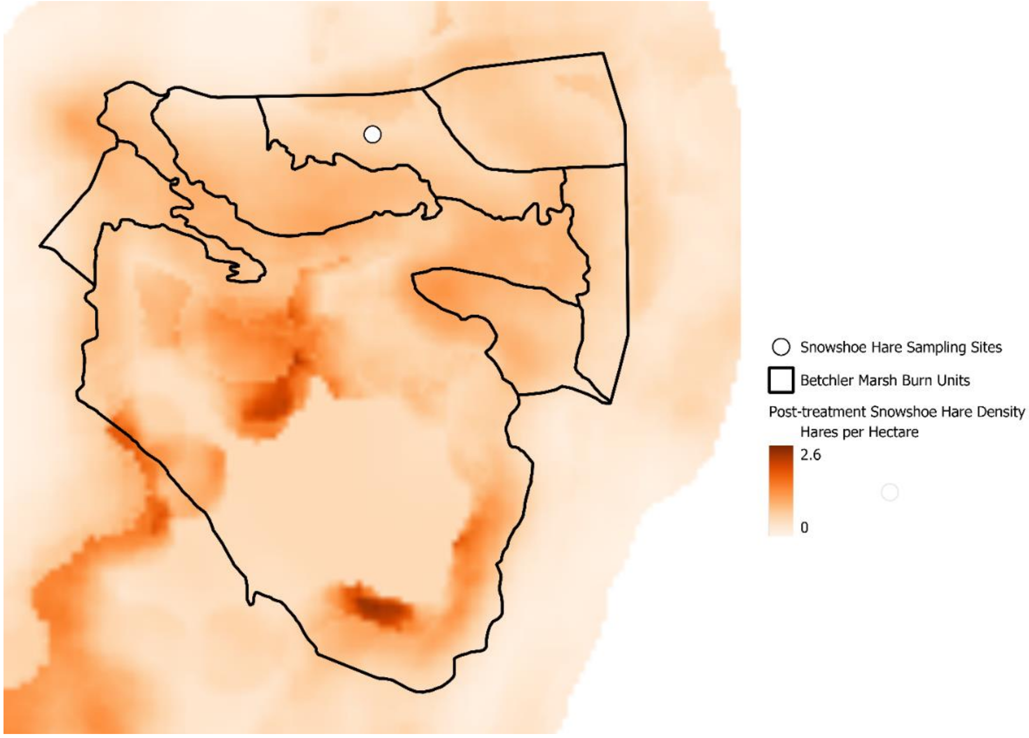

Figure 2.19. Estimated Snowshoe Hare Density in the Betchler Marsh Burn Complex on the Hiawatha National Forest.

Discussion

Influential variables in my snowshoe hare model are generally aligned with documented habitat associations. The positive relationship between snowshoe hare detectability and dense understory vegetation cover is known (Thornton et al. 2013, Ivan et al. 2014), as is the positive relationship of detection probability to localized snowshoe hare abundance (Murray 2003). I found that the IJI, pUCF, and pPSW within 0.5 km^2 of trap locations were important correlates of snowshoe hare densities across the East Zone of the Hiawatha National Forest. Dense understory vegetation is often associated with soft edges or ecotones between vegetation cover types, hence the positive association between hare density and IJI is not surprising. The pUCF class is described as "vegetation over 5 meters tall and > 75% coniferous trees, and is often dominated by mature red pine and jack pine plantations" (Office of Coastal Management 2021). Closed canopy red and jack pine plantations tend to have low levels of understory structural and biological complexity (Gachet et al. 2007, Park and Carpenter 2015), andknowing that hare density positively associates with understory vegetation thickness (Ivan et al. 2014), the negative relationship between pUCF and snowshoe hare density in the study is explainable. Artificially regenerated (i.e., plantations) upland conifers are a tension point between natural resources stakeholders that emphasize wood production and associated revenue, and stakeholders or tribal members that place greater value on ecological and cultural outcomes. The adaptive management framework and associated analytical and forecasting tools offers a means for consideration of these contrasting value systems.

Snowshoe hares have a strong affinity for scrub/shrub wetland ecosystems (Wolff 1980, Jacqmain et al. 2007, Keith et al. 2011, Wilson et al. 2019). On the East Zone of the Hiawatha National Forest, ecological land types 70 and 80 which support scrub/shrub wetland landcover types account for over 35% (over 61,000 ha) of the total landscape. Given the dependence of scrub/shrub wetland on water balance this cover type will likely be impacted by altered temperature and precipitation dynamics due to climate change (Mitsch and Hernandez 2013). My model results draw attention to this cover type as an important management consideration to support persistence of snowshoe hares and overall resilience of this important ecological system.

My analysis provides reasonable snowshoe hare density estimates (mean = 0.52 hares/ha, 85% CI=0.21,0.83) given other estimates of snowshoe hare density. In Michigan, Linden et. al. (2011), estimated snowshoe hare densities ranged from <0.07-0.75 hares/ha. In Washington, mean snowshoe hare densities of 0.82 hare/ha were documented (Lewis et al. 2011), and densities between 0.0-4.21 hares/ha were documented in the northern Rocky Mountains (Holbrook et al. 2017). Consistent with other studies on the trailing edge of snowshoe hare range, density estimates from this study are low compared to those from core range of the boreal forest biome to the north, where densities have been documented in excess of 6 hares/ha (Kielland et al. 2010).

To meet the objectives of the 2012 USFS Planning Rule and Joint Secretariat Order #3403, it is critical that the Hiawatha National Forest (and other national forests in the U.S.) build capacity to implement adaptive management frameworks as a routine part of land management practices. This is particularly important as the Hiawatha National Forest (for example) embarks on updating their 2006 Forest Plan (U.S. Forest Service 2006). Updated national forest plans should include integration of tribal needs and concerns to comply with current federal policies. Adaptive management frameworks, centered on tribal perspectives that honor community knowledge and tribal science as part of decision analytics are needed to implement the Forest Service’s trust responsibility of protecting habitats and species critical to Sault Tribe (and other Anishinabeg) lifeways (Rist et al. 2013). I demonstrated that modeling and forecasting elements of the adaptive management process can be informed with field data collected by tribal natural resource departments combined with existing quantitative tools that provide spatially explicit estimates of animal populations (in this case, snowshoe hares). Estimates of snowshoe hare density that I produced serve as existing baselines for evaluation of management alternatives. It is important to note, in the case of the Betchler Marsh Burn Complex analysis, the projected change in density in approximately +3% and this SCR model alone would not be able to detect this change. This has highlighted the need for multiple metrics to evaluate adaptive management decisions and helps to frame monitoring objectives and techniques moving forward.

Conclusion

The Hiawatha National Forest is home to more rare and sensitive species than any other National Forest in Region 9 of the Forest Service, and many of those species are documented as occurring only on the Hiawatha National Forest (U.S. Forest Service 2006). As the most populous tribe in the eastern United States (~53,000 members), the Sault Tribe issues over 55,000 permits to hunt, fish, gather, and trap across the 5,584,661 ha 1836 Treaty Ceded Territory. Forested ecosystems that support harvest of these plants and animals are inextricably linked to lifeways of Sault Tribe members and for many of those species, the Hiawatha National Forest represents an opportunity to demonstrate use of adaptive management as a way to fuse Anishinaabe and western sciences to build resilient systems.

I focused on SCR model outputs for providing important baseline information about snowshoe hares and landcover patterns that directly relate to applied habitat management. The ability to produce empirically derived spatially explicit population density predictions is a powerful tool for adaptive management frameworks, such as the Ishkode Framework. This SCR model, along with a suite of others, forms the analytical backdrop on which alternative habitat management prescriptions are written and outcomes of proposed actions are forecasted. This is a key process in the adaptive management cycle that will allow decision-makers from the Sault Tribe Wildlife Program and Hiawatha National Forest to reduce uncertainty in ecosystem responses to fire by iteratively updating our conceptual and statistical models based on pre/post treatment assessment.

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CHAPTER 3: SEROLOGIC SURVEY OF SELECTED ARTHROPOD BORNE PATHOGENS IN FREE-RANGING SNOWSHOE HARES (LEPUS AMERICANUS) CAPTURED IN NORTHERN MICHIGAN, USA

Status: Published.

In collaboration with the United States Geological Survey – National Wildlife Health Center, I coordinated a serosurvey for arboviruses in snowshoe hare on the HIF. In this study, we evaluated exposure rate of several mosquito born viruses in snowshoe hare (Jamestown Canyon virus, Silverwater virus, Lacrosse encephalitis virus, West Nile Virus, *Borrelia burgdorferi*, Powassan virus, and *Francisella tularensis*) and evaluated the relationship between snowshoe hare virus, individual hare traits, and ecological land type on the east zone of the HIF. In this study, I contributed equally to my NWHC Colleagues. I was responsible sample design, data collection, and leading prevalence modeling and NWHC conducted and reported the serosurvey.

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CONCLUSION

Waabooz plays an important role in the Sault Tribe and Anishinaabe lifeways. Given their importance, the Sault Ste. Marie Tribe of Chippewa Indians Wildlife Program has invested considerable resources to, not only understand their vulnerability to climate at coarse scales, has sought to work with federal partners to understand the impact of silvicultural and prescribed fire treatments.

In Chapter 1, I demonstrate associations between climate and forest patterns at landscape scales. This study aligns with others from the Great Lakes Region however it does not make inferences about the ecological mechanisms that drive these associations. Research into climate and forest pattern-driven mechanisms of snowshoe hare decline in the 1836 Treaty Ceded Territory is an important area for future research. Similarly, in Chapter 2, at finer scales, I demonstrate that forest patterns impact snowshoe hare densities on the Hiawatha National Forest. Yet, again, this does not infer causation. Here again, this highlights the need to develop a mechanistic understanding of snowshoe hare population performance and the relationship to silvicultural and fire management regimes.

Adaptive management as a framework is an important tool for decision-making in the context of forest, fire, and wildlife management. This study demonstrates some of the challenges associated with the implementation of effective analytical tools to predict the response of species, in this case, snowshoe hare, to complex silviculture and fire prescriptions. These challenges highlight the need for multiple analytical tools to evaluate adaptive management prescriptions.