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EFFECTS OF DISSIMILAR SILVICULTURAL TECHNIQUES ON SMALL MAMMAL COMMUNITIES IN MICHIGAN'S UPPER PENINUSLA

By

Breanna R. Gusick

A THESIS

Submitted in partial fulfillment of the requirements for the degree of

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In Forest Ecology and Management

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This thesis has been approved in partial fulfillment of the requirements for the Degree of MASTER OF SCIENCE in Forest Ecology and Management.

College of Forest Resources and Environmental Science

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College Dean: *Andrew J. Storer*

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Author Contribution Statement

This thesis includes data in Chapter 2, which I collected within the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED), wherein, small mammal communities were sampled across a variety of silvicultural canopy regeneration methods and site preparations during a single-season. Additionally, I collected fecal and ectoparasite samples from captured small mammals; these samples were transported for long-term storage and future analysis in Dr. Kristin Brzeski's eDNA lab.

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Abstract

Small mammal populations, and predators reliant upon them as food resources, are often challenged by conflicting objectives of timber production and maintenance of quality habitat. With over 70% of the landscape forested, and nearly one-third of the land privately owned, Michigan's Upper Peninsula (UP) is a matrix of independent management strategies. To assess the effects of various silvicultural regeneration methods on small mammal populations in the Upper Peninsula, we trapped small mammals in experimental silviculture plots, whereby treatments varied by regeneration method (amount of residual canopy cover) and site preparation (i.e., control, tip-up, and scarification), and deer exclosures. We used capture data from experimental treatments to estimate small mammal species richness and variation in community structure. Our results suggest that increased canopy cover, two years post-harvest, resulted in decreased small mammal species richness and greater variability in community structure. Conversely, small mammal communities varied marginally across site preparations, while mid-canopy retention strategies resulted in more stable communities, possibly mitigating short-term site preparation disturbance. I recommend maximizing biodiversity at the regional scale by incorporating mid-canopy retention methods, which retain approximately 30 – 60% canopy cover, with tip-ups as CWD to provide suitable habitat heterogeneity and food resources, as the core prescription to maintain stable small mammal communities upon which mesopredator populations depend. Ultimately, our results can be applied to larger spatial scales, with potential to influence wildlife and timber management across the northern hardwood bioregion.

1 Introduction

Encompassing eight US states and one Canadian province, the Great Lakes Region boarders the five Great Lakes, providing 84% of North America's and 21% of the world's surface fresh water (U.S.EPA, 2021). Brimming with natural resources of timber, minerals, wildlife, and natural beauty – and benefitting from the ease of transportation – the Great Lakes Region quickly became an economic-hub (Beeton, 2022). Rapid colonization of the region converted pre-settlement hemlock-white pine-northern hardwood forests into sugar maple-types by extensive selective logging, wherein, landscapes were further altered by slash and burn fires, destroying pine seed trees and seedlings and converting timber production to pulp-oriented industries (Whitney, 1987). Though widespread habitat degradation by human disturbance has forever changed the region's landscapes, timber harvesting still remains an economically important industry.

Revered for its forested landscapes and rich natural history, Michigan's Upper Peninsula (UP) has been shaped by human disturbances. During the early- to mid-1800s, early records estimate that nearly 95% of Michigan was forested (Matson et al., 2013). Vast forests across the UP provided habitat for economically important furbearing species, while iron ore and copper were discovered by settlers of European heritage (Hamel et al., 2013; Matson et al., 2013). Following the diminishment of furbearer populations, due to unregulated trapping, intensive mining of iron ore and copper ignited across the Keweenaw Peninsula in the 1840s, resulting in increased settlement in the area (Hamel et al., 2013; Matson et al., 2013). Increased demand for timber as wood fuel and for home construction, in-hand with forest clearing for crops and railroad construction, decimated UP forests by the late-1800s (Matson et al., 2013). Such disturbances caused severe droughts and fires across the peninsula, degrading land and water quality, leading to the loss of many aquatic and terrestrial species (Matson et al., 2013). Given the mismanagement of the state's forests, mineral wealth, and wildlife, in 1902, Michigan's government intervened to reduce exploitation of its natural resources (Matson et al., 2013), shifting towards more sustainable practices (Hamel et al., 2013).

More than a century later, forested-land in Michigan has increased more than two-million acres since the 1980 inventory, with approximately 95% (19.3 million acres) designated as 'timberland' for timber production (Pugh, 2018). In 2015, Leefers (2017) reported that 5.9% of the manufacturing jobs in Michigan were within forest product industries, producing a direct output of over $6 billon, with nearly one-third of these jobs across the Keweenaw Peninsula. The UP comprises only 29% of the state, yet 45% of Michigan's forests are estimated to exist across the peninsula (Pugh, 2018). The UP's uniqueness is furthered, in that, approximately 44% of the forested landscape is privately owned, while only about 38% is owned by the State of Michigan, USDA Forest Service, and other public groups combined (Pugh, 2018), resulting in conflicting management strategies; hence, forest management throughout the UP and North America has shifted towards ecological-focused timber harvest practices by emulating historic natural disturbance regimes through natural disturbance-based management (NDBM), promoting biodiversity and sustainability (Bengtsson et al., 2000; Kern et al., 2014, 2019). By fostering sustainability and resiliency through implementation of differing silvicultural harvest techniques, we can ensure continued ecosystem function and subsequent services.

Infinitely complex and sensitive, trophic cascades within forested ecosystems are altered by both natural and anthropogenic disturbances (Carey et al., 1999; Dunham, 2008). Forest-dwelling organisms respond variably to differing timber harvest practices, including the magnitude and time since the disturbance (Paillet et al., 2010). For example, Marshall (2000) suggests extending crop rotations and/or implementing shelterwood canopy regenerations (lower-intensity harvests) with extended rotations, to minimize impacts on soil biota. Additionally, Mushinski et al. (2018) observed significantly different soil fungi communities and functional guild abundance at the surface-soil level, but no overall difference below 30 cm within highly intensive forest-floor treatments. Furthermore, a novel multi-trophic study by Laigle et al. (2021) observed short-term forest-soil community composition to be influenced by bottom-up effects in relation to harvest intensity. Forest harvest impacts complex above- and below-ground interactions by causing short- and long-term disruption to food and habitat availability for ground-dwelling organisms, in-turn, affecting functional guilds important to forested ecosystem function and productivity (Dunham, 2008; Mushinski et al., 2018).

Within forested ecosystems, forest-dwelling small mammals comprise important functional guilds, providing ecological services (Lacher Jr. et al., 2019; McShea, 2000). For example, small mammals of the Great Lakes Region provide beneficial services including; seed dispersion (Kellner et al., 2016; Vander Wall et al., 2005), fungal dispersion (Pyare & Longland, 2001, 2002), soil aeration (Hole, 1981), pest-control (Larsen et al., 2018), and prey-sources (Fryxell et al., 1999). Additionally, habitat quality may be assessed through observation of small mammal diversity and abundance (McLaren et al., 1998; Pearce & Venier, 2005). On the other hand, small mammals may also prove detrimental to habitat and/or human well-being as seed (Kellner et al., 2016) and nest predators (Schmidt et al., 2001, 2008), or zoonotic hosts (Ostfeld & Keesing, 2000; Roy-Dufresne et al., 2013). For example, *Peromyscus* species (i.e., white-footed and deer mice) across the region are often associated with high-intensity oak (*Quercus* spp.) regeneration sites and observed predators of gypsy moth pupae (*Lymantria dispar*), which cause high mortality of oak trees through defoliation (Larsen et al., 2018). Conversely, the presence of white-footed mice (*P. leucopus*), in response to successful mast production, leads to increased acorn (Kellner et al., 2016; McShea, 2000) and incidental ground- and low-nesting bird predation (Schmidt et al., 2001, 2008). Furthermore, presence of white-footed mice may lead to increased public health concerns, as a principal reservoir for Lyme disease, spreading rapidly throughout the Great Lakes Region, United States, and into Canada in recent decades (Ostfeld & Keesing, 2000; Roy-Dufresne et al., 2013).

Silviculture is the synthesis of art and science to maintain the diverse needs and values of societies and individuals reliant upon sustainable forest and woodlots (FSM, 2014, p. 17). Thus, to ensure continued ecosystem services and public health well-being, forest managers should incorporate silvicultural techniques which promote habitat heterogeneity and support biodiversity (Bengtsson et al., 2000; Kern et al., 2019; Smith et al., 2011) by applying differing silvicultural practices which promote germination of diminished historical tree species, in addition to “business as usual” practices (Hupperts et al., 2020). Continued, long-term monitoring of species-specific responses is imperative to understanding how anthropogenetic disturbances continue shaping plant and animal communities within our forested ecosystems. Though no singular management-style fully promotes sustainability, experimental forests throughout the Great Lakes Region can provide invaluable long-term replicates of NDBM and successful regeneration methods applied elsewhere to observe and project how climate change, and other human-caused disturbances, may affect managed ecosystems by using a holistic approach.

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2 Effects of dissimilar forest management strategies on small mammal diversity in Michigan's Upper Peninsula

2.1 Introduction

Small mammals are sensitive to bottom-up processes, where variation in vegetative structure, climate, and microclimates affect the food resources upon which small mammals depend (Hunter & Price, 1992; Power, 1992; Meserve et al., 1999). Within communities of small mammals, species that feed on vegetation in the lower reaches of the food web appear particularly sensitive to bottom-up changes in food availability relative to their generalist counterparts (Meserve et al., 2001). These differences likely reflect the close trophic linkages between herbivorous and granivorous small mammals and the surrounding vegetation they use as food resources and cover. Subsequent variation in small mammal community structure and abundance can result in cascading effects on carnivores; interestingly, this bottom-up effect is often delayed when compared to the immediate influence of consumptive and top-down effects of predators on prey abundance (Jaksic et al., 1997; Meserve et al., 2003). For example, long-term research in Chilean grasslands found that increased precipitation results in heightened small mammal abundance, followed by a delay in the population growth of raptors, suggesting that a lag effect exists at higher trophic levels (Meserve et al., 1995, 1999; Jaksic et al., 1997; Lima et al., 1999). Recognition that changes in habitat and climate alter the trophic dynamics between small mammals and their predators has begun to influence management strategies for forest carnivores (Fuller & Harrison, 2005; Godbout & Ouellet, 2010).

In northern hardwood forests throughout North America, both American marten (*Martes americana*) and fisher (*Pekania pennanti*), two economically valuable and culturally significant forest carnivores, have experienced population declines in northern Wisconsin (Manlick et al., 2017; Williams et al., 2007). Potential drivers of marten and fisher population declines include diminished diversity and abundance of prey, (Kujawa et al., 2014; Kirby et al., 2018), habitat degradation, and climate change (Manlick et al., 2017). Similarly, in Scotland, researchers found that forest management can have cascading effects on the availability of small mammal food resources for pine martens (*Martes martes*; Caryl, 2008; Caryl et al., 2012; Zalewski, 2005). Specifically, martens in Scotland selected edge habitat where small mammal food resources were highest, when compared to landscapes dominated by intensively managed tree plantations with closed canopies and fewer small mammals (Caryl et al., 2012). Interestingly, high quality marten habitat contained only moderate amounts of edge, suggesting that when forest cover dropped below a threshold, martens were subjected to increased amounts of predation (Caryl et al., 2012). Dynamics between food availability and threat of predation, suggest that mammals foraging at different trophic levels are affected by varying pressures from top-down and bottom-up effects, which in turn, are influenced by patterns of forest structure.

Renowned for its scenery and working landscapes, Michigan's Upper Peninsula (UP) is 72% forested, dominated by northern hardwood forest, with a third of the land privately owned by individuals and families (Schubert & Mayer, 2012). Coupled with natural disturbances (e.g., fire, winter, windthrow), the patchwork of private ownership across the UP has created a heterogenous landscape where conflicting objectives of timber extraction and maintenance of wildlife habitat affect a diversity of mammalian species. Forests across the UP host 23 species of small mammals (not including bats) (Orders Soricomorpha and Rodentia), including shrews, moles, voles, mice, rats, lemmings, chipmunks, and squirrels (Supplemental Table1; Kurta, 2017; Naughton, 2011). The diversity of small mammals in the UP represents a collection of dissimilar life history strategies and ecological guilds, making small mammals potentially useful bioindicators of habitat quality for wildlife and forest managers (Lindenmayer et al., 2000; McLaren et al., 1998; Pearce & Venier, 2005). For example, the Ontario Ministry of Natural Resources (OMNR) Wildlife Assessment Program – using multiple criteria – chose mammal, bird, amphibian, and reptile species representatives as fine-filter indicators of sustainable forest management (McLaren et al., 1998). However, Lindenmayer et al. (2000) expressed doubt as to whether taxon-based indicators are a comprehensive measure of biodiversity, recommending structure-based measures of habitat quality, such as plant communities, connectivity, structural complexity, and heterogeneity. Furthermore, Pearce and Venier (2005) observed that, although more easily measured, habitat measurements only provide pre- and/or post-management habitat availability, whereas integrated measures of both habitat and wildlife indicator species considers how forest management decisions impact sustainability of both wildlife and their habitats.

Working landscapes in the UP have been shaped by logging practices for over a century (Brandis, 1897; Pinchot, 1899). Historically, silviculture has focused on the regeneration of timber for harvest and, more recently, integrated the maintenance of ecosystem processes and services into the discipline’s collection of techniques (Metzger & Schultz, 1984; Crow et al., 2002; Fahey et al., 2018). Dependent upon desired outcomes, silviculture techniques vary from the removal of a predetermined percentage of canopy cover (i.e., shelterwoods and selective harvest) to the total removal of all trees within a site (i.e., clearcut; Leak et al., 2014). Prescriptions may also include forest-floor treatments, such as scarification (large equipment is used to disturb the understory vegetation; Johansson, et al., 2013) or artificial tip-up (mechanically felling trees to create tip-up mounds; Kern et al., 2019). Such techniques can be used to mimic a region’s historical and natural disturbance regimes (e.g., fire, windthrow, disease, insect outbreaks, etc.) to improve management of ecosystem processes, ecosystem services, and the native biotic community adapted to historical disturbance regimes (Hupperts et al., 2019; Crow et al., 2002).

Application of differing silvicultural techniques can further our understanding of how wildlife habitat changes in response to anthropogenic disturbances, such as timber harvest. Because disturbances occur at varying levels of intensity, habitat responses also vary. For example, scarification is a commonly applied technique to aid in seed germination; however, it is an intensive disturbance, causing both short- and long-term effects on primary productivity and food web dynamics (Johansson et al., 2013). Such ground-floor disturbance alters bottom-up processing, which can affect small mammals and those predators reliant upon them as prey. For example, scarification also decreases coarse woody debris (CWD; Freedman et al., 1996) in the long-term by creating smaller pieces which decompose faster, altering important habitat features providing microclimates, food, and shelter at multiple trophic-levels (Maser & Trappe, 1984). Landscape heterogeneity, including CWD, has positive effects on American marten and fishers, providing heightened food availability (Fuller et al., 2004; Godbout & Ouellet, 2010; Manlick et al., 2017). Conversely, loss of canopy cover caused by clearcutting has been observed to have either neutral or positive short-term effects on multiple small mammal species (Kaminski et al., 2007; Kellner et al., 2013; Klenner & Sullivan, 2009), yet negative effects on marten and fisher populations (Fuller & Harrison, 2005; Godbout & Ouellet, 2010; Thompson, 1986). Understanding how dissimilar forest management strategies affect small mammal communities—species that provide food resources for a diversity of carnivorous animals—represents an important step towards biodiversity conservation and sustainable forest management.

To determine how different forest management strategies affect small mammals, I captured-marked-released (CMR) small mammals across multiple canopy regeneration methods (i.e., clearcut, shelterwoods, and single tree selection) and site preparations (i.e., control, artificial tip-up, and scarification) at the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) in the UP. Observing how small mammals in the UP respond to silvicultural techniques, not commonly applied in the area, can inform future timber and wildlife management when incorporation new regeneration methods. My goal was to determine how specific silviculture techniques affected estimates of small mammal richness. Additionally, I aimed to measure how silviculture techniques shifted patterns of small mammal community diversity. Because within-stand heterogeneity typically creates more ecological opportunities for a larger number of small mammals, I predicted that experimentally increased complexity within shelterwood low-residual regeneration managements (i.e., 30% canopy retention) and artificial tip-up site preparations, diversifying forest-floor habitat, will result in higher small mammal species richness (Ecke et al., 2002; Gray et al., 2019). However, I also predicted that increased canopy cover within single tree selection regeneration methods will produce more stable microclimates within the forest understory (Rambo & North, 2008, 2009; Xu et al., 1997; Zheng et al., 2000), resulting in less diverse but more stable small mammal communities when compared to experimental treatments with reduced canopy cover (i.e., clearcuts and shelterwoods). My study provides an improved understanding of how forest management affects changes in the lower reaches of the food web, which has implications for carnivore conservation in the UP and beyond.

2.2 Materials and methods

2.2.1 Study area

My study took place at the NHSEED experimental forest, located near the village of Alberta, MI in Michigan's Upper Peninsula. Managed by Michigan Technological University (MTU), the NHSEED was established within the Ford Center and Forest (FCF) in early 2017. As described by Bailey (1983), the surrounding ecoregion of my study area is defined as a Laurentian mixed forest province within a humid warmsummer continental division encompassed within the humid temperate domain, in which, the regional landscape ecosystem of our study area is Winegar Moraine (Figure 2.1). Rocky, acidic, sandy loam soils from iron-rich, Precambrian bedrock merged with ice-stagnation features, moraines, and outwash have created large areas of irregular topography with poor drainage, leading to formation of acidic, nutrient-depleted kettle lakes with low water movement save for ground-flow (Bailey, 1983). At an elevation of ~401 m (for Alberta, MI; USGS, 1981), average monthly temperatures ranges from 14°F in January to 66°F in July (1991-2020; NOWData, 2022) and annual average snowfall of 147 inches (1956-2016; Western Regional Climate Center, 2016), the area is susceptible to windthrow; wherein, early vegetation consisted of sugar maple (*Acer saccharum* Marshall), hemlock (*Tsuga canadensis* (L.) Carrière), yellow birch (*Betula alleghaniensis* Britton), red maple (*Acer rubrum* L.), and American basswood (*Tilia americana* L.) (Bailey, 1983).

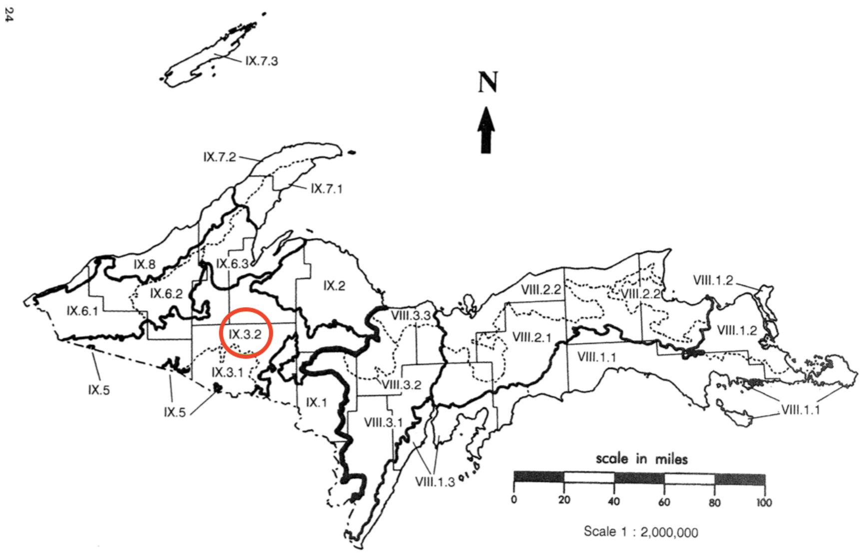

Figure 2.1. Regional landscape ecosystems of the Upper Peninsula of Michigan. Trapping conducted at the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites, Alberta, Michigan in 2019 is located within the Sub-Subsection IX.3.2. Winegar Moraine (circled in red; Albert, 1995), modified.

Previous to experimental harvests, the NHSEED study area was dominated by sugar maple, amidst less frequent species: red maple, yellow birch, American elm (*Ulmus americana* L.), eastern hemlock, ironwood (*Ostrya virginiana* (Mill.) K. Koch), green ash (*Fraxinus pennsylvanica* Marshall), white spruce (*Picea glauca* (Moench) Voss), balsam fir (*Abies balsamea* (L.) Mill.), eastern white pine (*Pinus strobus* L.), paper birch (*Betula papyrifera* Marshall), northern white cedar (*Thuja occidentalis* L.), trembling aspen (*Populus tremuloides* Michx.), northern red oak (*Quercus rubra* L.), black spruce (*Picea mariana* (Mill.) B.S.P.), black ash (*Fraxinus nigra* Marsh.), and black cherry (*Prunus serotina* Ehrh) (Hupperts, 2019; Neuendorff et al., 2007).

2.2.2 Experimental design

NHSEED was designed to compare alternative “even-aged” methods of natural regeneration with single tree selection, an approach to “uneven-aged” silviculture that is most commonly employed in the Upper Great Lakes Region. Thus, in addition to single tree selection (STS, n = 3 units), NHSEED includes the following even-aged regeneration treatments: clearcut (CCU, n = 3 units), shelterwood-high residual (SHR, n = 6 units), and shelterwood-low residual (SLR, n = 6 units) (Hupperts, 2019; Hupperts et al., 2020). Each of the aforementioned experimental treatments was divided into three levels of site preparations – control (CON, n = 6 sites), scarification (SCA, n = 6 sites), and artificial tip-up (TIP, n = 6 sites) – for a total of 54 sites (Hupperts, 2019. Figure 2.2). Within the center of each site are 400 ft^2 deer exclosures, totaling 54 exclosures throughout the study area. Due to shelterwood replicates being identical during data collection in 2019 (after the establishment cut but prior to the final overstory removal), observations were grouped as follows: SHR and IHR (irregular shelterwood-high residual; hereafter referenced as SHR) and SLR and ILR (irregular shelterwood-low residual; hereafter referenced as SLR). This novel silvicultural experimental was designed to test whether the use of a variety of canopy regeneration methods (i.e., STS, CCU, SHR, SLR) and site preparations (i.e., CON, TIP, SCA) within Great Lakes northern hardwoods can restore historical tree species by promoting recruitment, which have been reduced through application of conventional forestry practices – single tree selection (Hupperts et al., 2020).

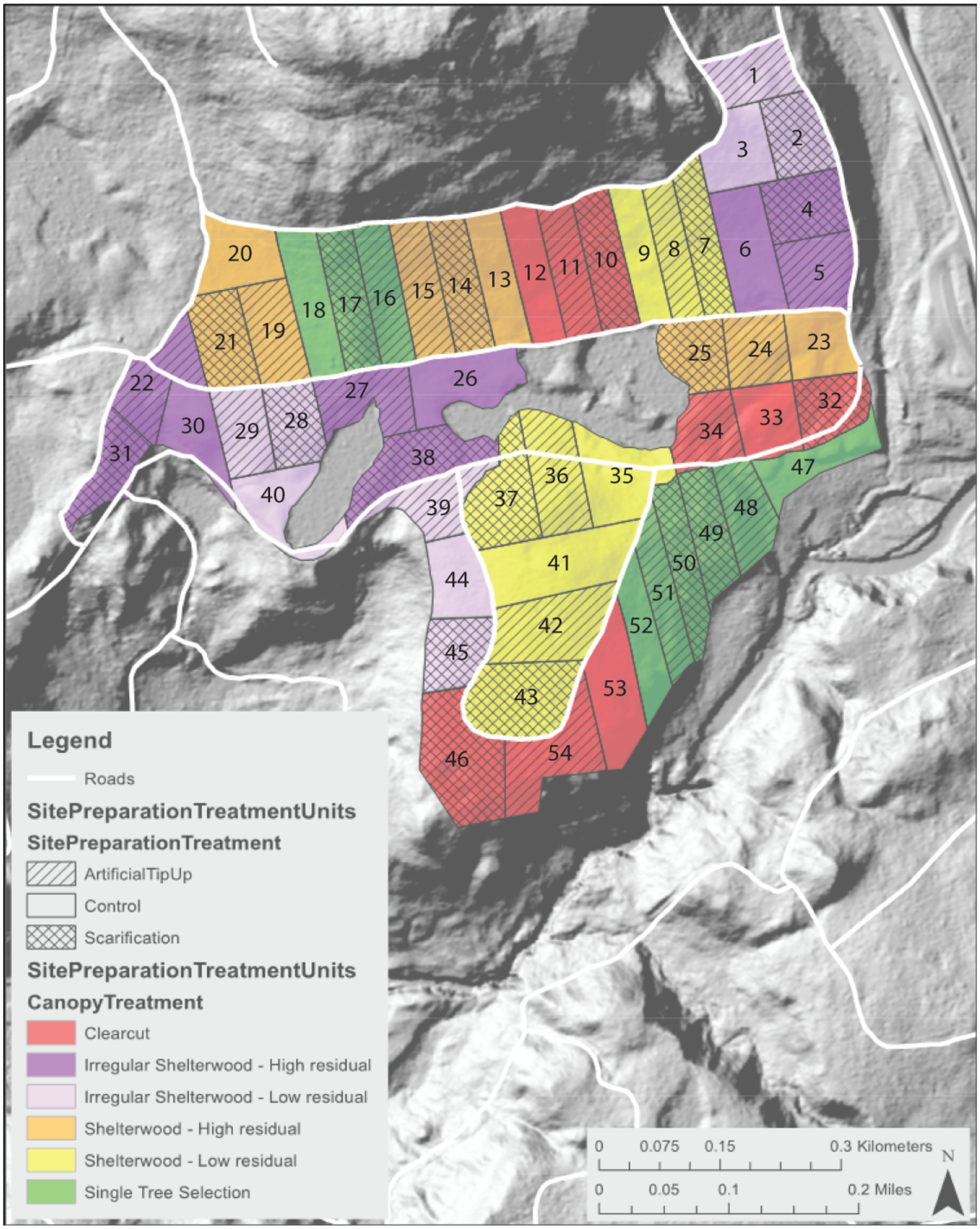

Figure 2.2. Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites at the Ford Center and Forest, Alberta, Michigan. Site numbers coincide with small mammal capture data in 2019 (From Wolfe & Brzeski, 2018, proposal).

Experimental treatments at the NHSEED were chosen to establish the four individual silviculture regeneration methods (commercial harvest February – March 2017) and site preparations (October 2017) in a randomized block design (Hupperts, 2019). A silvicultural cleaning was implemented to mechanically remove all hardwood seedlings and saplings < 5 cm diameter at breast height (DBH) in the clearcut and shelterwood treatment units in August 2017 (Hupperts et al., 2020). All conifer seedlings and saplings were retained. The CCU treatment was established by removing all trees in the commercial and cleaning events; whereas such trees were not removed from the STS treatment since regular, sustainable harvests will be conducted approximately every 10 – 20 years (Hupperts et al., 2019). In the SHR treatment, an initial harvest removed trees, resulting in 60% of the canopy remaining, while trees were removed from the SLR regenerations, resulting in 30% of the canopy remaining (Hupperts, 2019; Hupperts et al., 2020). A second harvest to remove remaining overstory in both the SHR and SLR sites, creating two-aged stands of IHR and ILR, will occur when the regeneration is fully stocked in approximately five years (Hupperts, 2019; Hupperts et al., 2020). The initial commercial harvest conducted in the shelterwood treatments during February and March 2017, resulted in the irregular shelterwood and shelterwood replicates (i.e., SHR and IHR, and SLR and ILR) being identical (Hupperts et al., 2020) at the time of my study in 2019.

During the initial commercial harvest (February and March 2017), the artificial tip-up site preparation treatments were created by mechanically felling trees to simulate windthrow events, averaging 9 to 15 tip-ups per site (Hupperts, 2019). Lastly, the scarification site preparation treatment was completed in October 2017, using a bulldozer and salmon blade to create soil disturbances and remove approximately 50% of the ground vegetation from the sites (Hupperts, 2019; Hupperts et al., 2020).

2.2.3 CMR methods

Small mammal live trapping was conducted using Sherman small traps (2.0 x 2.5 x 6.5 inches, model SFA) and Sherman non-folding traps (3.0 x 3.0 x 10.0 inches, model 3310A). All trap locations were georeferenced when deployed throughout the NHSEED sites. At each site, four traps were deployed, in which two Sherman traps were placed inside the deer exclosure and two additional traps placed 25 m due North from the location of the traps within the exclosure. If obstructed (e.g., roads, thick vegetation, steep landscapes, etc.), traps were placed 25 m due East or West dependent upon further impedance. There was no minimum or maximum sample size of trap nights for this study; however, based on pilot studies, a minimum of three trap nights was recommended for the greatest detection of small mammal species (Manley et al., 2002). When conducting a preliminary habitat inventory, Jones et al. (1996) recommended a minimum of 400 – 500 trap nights. Small mammal bait consisted of a mixture of seeds and peanut butter and was prepared prior to trap deployment and stored properly during each session. Unused portions were discarded after each session to avoid spoilage. When deployed, all traps were set and baited in the evening of every trap night (a trap night is every dusk to dawn trap effort) of each session (Hoffmann et al., 2010). Traps were deployed within protected areas from weather and predation where possible (e.g., under a shrub or downed wood) and bedding material was provided in preparedness for animals trapped overnight (Sikes & Gannon, 2011). To minimize capture mortalities, all traps were checked at sunrise the following morning and repeated the duration of each session in accordance with suggestions by Sikes and Gannon (2011). Retrieval of all traps occurred the morning after the final trap night of each session.

2.2.4 Animal processing

Target species were defined in our study as small mammal species which, if captured, would be "measured" and either "processed" or "fully processed", while non-target species (i.e., northern or southern flying squirrels) would be "recorded" and immediately released. The previous terms are defined as; 1) "recorded" is the site of capture, date, technician's initials, species identification code, ear tag number or shave pattern, fate of the animal, trap number, overstory and treatment preparations, and whether or not the animal was captured inside the deer exclosure; 2) "measured" is the sex, age, breeding status, total length, tail length, foot length, ear length, total weight of bag and all contents, and bag weight after removal of the animal; 3) "processed" is "measured" and feces and ticks collected from trapped animal; and 4) "fully processed" is both "recorded" and "processed". Due to difficulty or concern when handling squirrels or rats (*Ictidomys* spp., *Sciurus* spp., *Tamiasciurus* spp., *Glaucomys* spp., or *Rattus* spp.), individuals were to be recorded and released immediately if captured; however, no individuals of these species were captured during our study. Chipmunks (*Neotamias minimus* and *Tamias striatus*) were the largest, small mammals captured and were fully processed. Also fully processed, were sensitive species (i.e., *Sorex* spp. and *Condylura cristata*) and northern short-tailed shrews (*Blarina brevicauda*), which are venomous. Remaining species of mice (*Peromyscus* spp., *Mus* spp., *Napaeozapus* spp., and *Zapus* spp.), voles (*Myodes* spp. and *Microtus* spp.), and lemming (*Synaptomys cooperi*) were marked by either a metal ear tag or shaved patterns into fur.

2.2.5 Capturing and handling

Upon capture, animals were removed from traps by placing a plastic bag over the door-end of the trap. Once the bag was secured over the trap door without any gaps, the door was opened inside the bag and the animal gently guided into the collection bag. After identification as either a target or non-target species, the animal was processed accordingly, feces and ticks collected when present, and released. Any animal displaying signs of stress or distress, as described by the National Research Council (National Research Council [NRC], 1992, p. 43), was released after gathering minimal data to avoid further suffering or death. Collected feces were stored in labeled tubes of Longmire buffer; whereas ectoparasites were stored in labeled tubes of ethanol. Both sample-types were recorded, if collected, and stored properly before transportation to MTU for future environmental DNA (eDNA) and genetic analysis in Dr. Kristin Brzeski's lab. When healthy and having large enough ear pinnae to support tagging, captured mice were permanently marked with a metal ear tag (National Band and Tag company, STYLE 1005-1) in accordance to Thibault et al. (2015). Using an electric trimmer, captured voles and moles were temporarily marked by shaving a line into the fur on either the left front, left rear, right front, or right rear portion of the animal. After processing, animals were released near their capture site and observed until they returned to normal activities. If any animal did not recovery properly, they were placed in a cool, quiet location and monitored further. Any animal captured with a fatal injury was humanely euthanized in accordance to the American Veterinary Medical Association (AVMA) guidelines for euthanasia of wild caught rodents (Underwood et al., 2013). Animals found deceased in traps were collected, processed, and stored in a labeled plastic bag for transfer and freezer storage at MTU for future genomic analysis in Dr. Kristin Brzeski's lab.

When processing captured animals in the field, small mammals were identified to the species-level, when possible, but no less than genus. A field guide was created for this study with the 23 potential species to be encountered within the NHSEED study sites at the Ford Center and Forest in Baraga, MI. A "species code" was created for each of the 23 possible species, consisting of the first two letters of the genus and first two letters of the species (e.g., southern red-backed vole, *Myodes gapperi*, MYGA). If a species was unidentifiable, it was labeled with the first two letters of the genus, when able to identify, followed by "SP" for "species" (e.g., unidentified vole, *Microtus* spp., MISP). Status of each individual was recorded and defined as follows: 1) "fate" was new, shaved, or recaptured; 2) "sex" was male, female, or unknown; 3) "age" was juvenile, adult, or unknown; and 4) "breeding status" was yes, no, or unknown. Other processing measurements included; 1) "total length", 2) "tail length", 3) "foot length", 4) "ear length", 5) "total weight", and 6) "bag weight". The age status of an animal followed descriptions by Barnett and Dutton (1995), while sex and breeding status followed observations by Jacques et al. (2015). All length measurements were recorded in millimeters, following the guidelines of Hoffman et al. (2010) and Thibault et al. (2015), and weight was recorded in grams. All animal sampling was done in accordance to the AVMA (Underwood et al., 2013), American Society of Mammalogists ([ASM]; Sikes & Gannon, 2011), and IACUC 1307331-3.

2.2.6 Statistical analyses

Non-metric multidimensional scaling (NMDS) in program R (R Core Team, 2019) was used to visualize and examine whether NHSEED small mammal communities differed across canopy regeneration methods (i.e., clearcut, shelterwood, and single tree selection) and/or site preparations (control, artificial tip-up, and scarification), as I predicted that communities would become less diverse but more stable within stands of increased canopy cover and stable microclimates, such as single tree selections. (Kruskal, 1964; Everitt & Hothorn, 2011). I used the 'metaMDS' function in package 'vegan' (Oksanen et al., 2019), where I applied Bray-Curtis distance metric to assess differences in species composition relative to site preparations and canopy regeneration methods based on each species' weighted abundance (Fischer et al., 2011; Legendre et al., 2005; Van Nimwegen et al., 2008). To measure goodness-of-fit by means of ordination distances, I assessed stress plots (i.e., Shepard plot; Oksanen et al., 2019) as utilized by Gheler-Costa et al. (2013) and Van Nimwegen et al. (2008). Statistical significance was measured using functions 'adonis', a PERMANOVA testing dispersion within groups with 999 permutations and method = "bray" (Anderson & Walsh, 2013; Stephens et al., 2017), and 'betadisperser', an ANOVA testing dispersion similarity between differing groups and their composition using function 'vegdist' (Oksanen et al., 2019), as applied by Yamashina and Hara (2019).

To observe how NHSEED small mammals species richness was influenced by canopy regeneration method, site preparation, and treatment (i.e., regeneration method and site preparation treatment; clearcut-scarification treatment), and whether additional sampling effort could increase observed species, rarefaction and extrapolation were conducted, as I predicted that species richness would increase within more heterogenous sites, such as, shelterwood low-residual regenerations and tip-up site preparations. Rarefaction and extrapolation, in which estimated species richness is representative of only a sub-sample of the pooled assemblage by randomly resampling without replacement from the reference sample (Gotelli & Colwell, 2001; Colwell, 2013), was used to estimated species richness in program EstimateS 9.1 (Colwell, 2013; Kok et al., 2013; Torre et al., 2016) for sample-based abundance data. I then constructed rarefaction curves with their associated unconditional 95% confidence intervals (CI) in program R (R Core Team, 2019) with estimated species richness plotted as a function of the number of trap nights (samples).

As variance can greatly increase with extrapolation, total samples (trap nights) were not extrapolated beyond doubling the lowest number of trap nights within a single regeneration method or site as suggested by Colwell (2013). To reduce variance, “Total extrapolation samples” of canopy regeneration methods and treatments were calculated by doubling the lowest number of trap nights within a regeneration method or treatment, then randomized and rearranged in ascending numerical order, and clipped to a final total of the lowest sample size doubled, before extrapolation. No clipping was conducted within the site preparations data due to similar reference sample trap nights. I also compared 95% CIs of canopy regenerations, site preparation, and canopy regenerations with site preparations (i.e., treatments) with the lowest and highest estimates species richness to assess statistical significance, wherein, significance at the $P \leq 0.05$ level (mean $\pm$ 1.96 SD) is supported by the lack of overlap between 95% CIs, failing to include zero (Colwell et al., 2012; Colwell, 2013).

Additionally, to further observe NHSEED small mammal species richness between regeneration methods, site preparations, and treatments – including undetected species – Chao1 and abundance-based coverage estimators (ACE) were also conducted in program EstimateS 9.1 (Colwell, 2013. In contrast to rarefaction and extrapolation curves, non-parametric estimators (i.e., asymptotic species richness estimators) of species richness Chao 1, estimating ‘minimum richness’ (Shen et al., 2003), and ACE, estimating the spread of the reference sample abundance distribution (Chao et al., 2000; Chazdon et al., 1998), were also examined. Within dissimilar communities, extrapolation may underestimate species richness; however, Chao1 and ACE estimate the total species richness of a sample, including undetected species (Colwell, 2013). Therefore, both asymptotic estimators typically increase with sample size (Colwell, 2013) and have sizeable CIs and variances (Colwell & Gotelli, 2001). During computation of non-parametric estimators in EstimateS 9.1 (Colwell, 2013), Lee and Chao (1994) recommend re-computing Chao1 using the classic formula and reporting the larger of Chao1 and ACE as the better estimate when the coefficient of variation (CV) of the abundance-distribution > 0.5, while computing Chao1 using the bias-corrected (default) formula;

however, several ACE values did not make biological sense in our results. Therefore, we chose to conduct further comparisons using only Choa1 estimates.

2.3 Results

2.3.1 Results overview

A total of 525 small mammals (including 396 unique captures and 129 recaptures), representing 11 species, were captured during 1,387 trap nights between June through September of 2019, at the NHSEED forest (Table 2.1). The month of August had the greatest number of captures, 298 captures over 533 trap nights (Table 2.1). Conversely, September had the lowest number of trap nights (212), yet the second most total captures (91; Table 2.1). The four most commonly captured small mammal species were the southern red-backed vole (*Myodes gapperi*, n = 150), white-footed mouse (*Peromyscus leucopus*, n = 131), deer mouse (*Peromyscus maniculatus*, n = 128), and meadow jumping mouse (*Zapus hudsonius*, n = 38); all of which were marked or tagged (Table 2.1).

Table 2.1. The 11 observed species at the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites, Alberta, Michigan in 2019. Total individual captures and (recaptures) are recorded by Month, Canopy regeneration, and Site preparation by species. Overall totals for each row and column are designated as 'Totals'. Total trap nights for each Month, Canopy regeneration, and Site preparation are also shown. CCU = clearcut, SHR = shelterwood-high residual, SLR = shelterwood-low residual, STS = single tree selection, CON = control, SCA = scarification, and TIP = artificial tip-up.

	Month				**Canopy regeneration**				**Site preparation**			
Species	**Jun**	**Jul**	**Aug**	**Sep**	**CCU**	**SHR**	**SLR**	**STS**	**CON**	**SCA**	**TIP**	**Totals**
Sorex arcticus	0	0	1	1	2	0	0	0	1	1	0	2
Sorex cinereus	1	2	9	3	4	2	8	1	3	7	5	15
Blarina brevicauda	0	0	10	7	7	3	7	0	8	6	3	17
Microtus pennsylvanicus	0	0	1	0	0	0	0	1	0	1	0	1
Myodes gapperi	9(1)	32(2)	86(9)	23(1)	25(3)	35(6)	70(3)	20(1)	56(7)	51(4)	43(2)	150(13)
Peromyscus maniculatus	8(1)	23(5)	84(38)	14(6)	2(0)	55(22)	49(20)	22(8)	46(16)	32(14)	50(20)	128(50)
Peromyscus leucopus	23(11)	18(9)	55(31)	34(15)	2(1)	59(32)	43(18)	27(15)	41(19)	27(12)	63(35)	131(66)
Zapus hudsonius	3(0)	4(0)	29(0)	2(0)	21(0)	4(0)	10(0)	3(0)	12(0)	16(0)	10(0)	38(0)
Synaptomys cooperi	5	0	0	0	1	2	2	0	1	2	2	5
Tamias striatus	3	4	18	7	3	8	13	8	16	7	9	32
unknown vole spp.	1	0	5	0	1	4	1	0	2	3	1	6
Total captures	53(13)	83(16)	298(78)	91(22)	68(4)	172(60)	203(41)	82(24)	186(42)	153(30)	186(57)	525(129)
Total trap nights	351	291	533	212	230	453	481	223	469	449	469	1387

Of the marked mammals, *P. leucopus* had 66 recaptures, *P. maniculatus* had 50 recaptures, *M. gapperi* had 13 recaptures, and Z. *hudsonius* had zero recaptures (Table 2.1). Shelterwood-low canopy regeneration methods had the most captures of any other canopy regeneration, while both control and tip-up site preparations had similar captures (186 captures, Table 2.1). Conversely, clearcut canopy regenerations had the lowest number of captures and recaptures (68 and 4, respectively); yet ten of the 11 captured species were detected within clearcuts (Table 2.1). Southern red-backed voles had the most individuals captured during a single month with 86 captures in August (deer mice had 84 captures in August) and greatest number of individuals of a single species captured within a single canopy regeneration method, with 70 captures across shelterwood-low treatments (Table 2.1). Across site preparations, white-footed mice were the most captured with 63 individuals captures within tip-up treatments (Table 2.1).

2.3.2 Community structure

Small mammal community composition was assessed across canopy regeneration method and site preparations using NMDS ordinations with applied Bray-Curtis distance metrics. As a goodness-of-ft measure, I measured stress between samples within two-dimensions by means of a Shepard plot, which yielded a stress value of 0.10 (non-metric $R^2 = 0.99$, linear fit $R^2 = 0.95$), suggesting a good representation of our data in two-dimensions. Based on a bootstrapping analysis, I found no statistically significant difference between small mammal community assemblage across site preparations ($p = 0.702$, Figure 2.3); however, I did find that canopy regeneration method had a significant effect on community assemblage ($p = 0.001$, Figure 2.4), with clearcut and single tree selection treatments responsible for the greatest differences in species assemblage between communities.

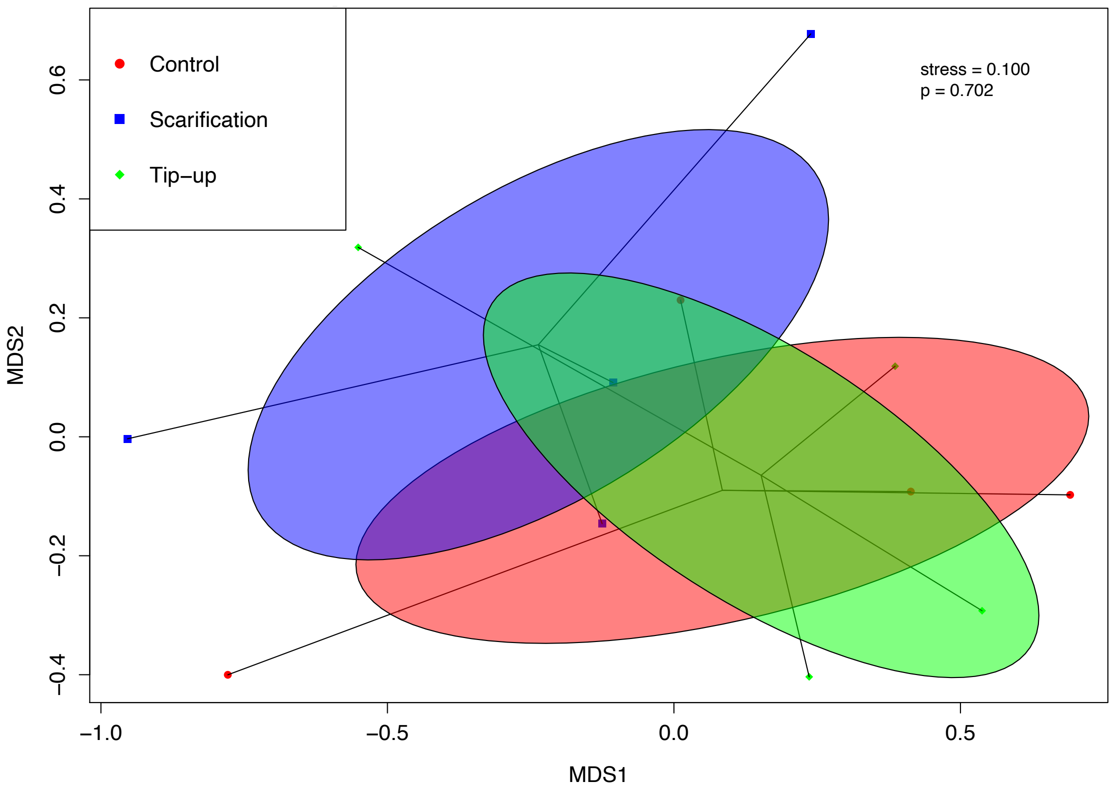

Figure 2.3. NMDS (non-metric multidimensional scaling) ordination representing small mammal communities across site preparations at the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites, Alberta, Michigan in 2019. Ellipsoids represent 95% confidence intervals. Bray-Curtis distances metric was applied and statistical significance based on bootstrapping analysis.

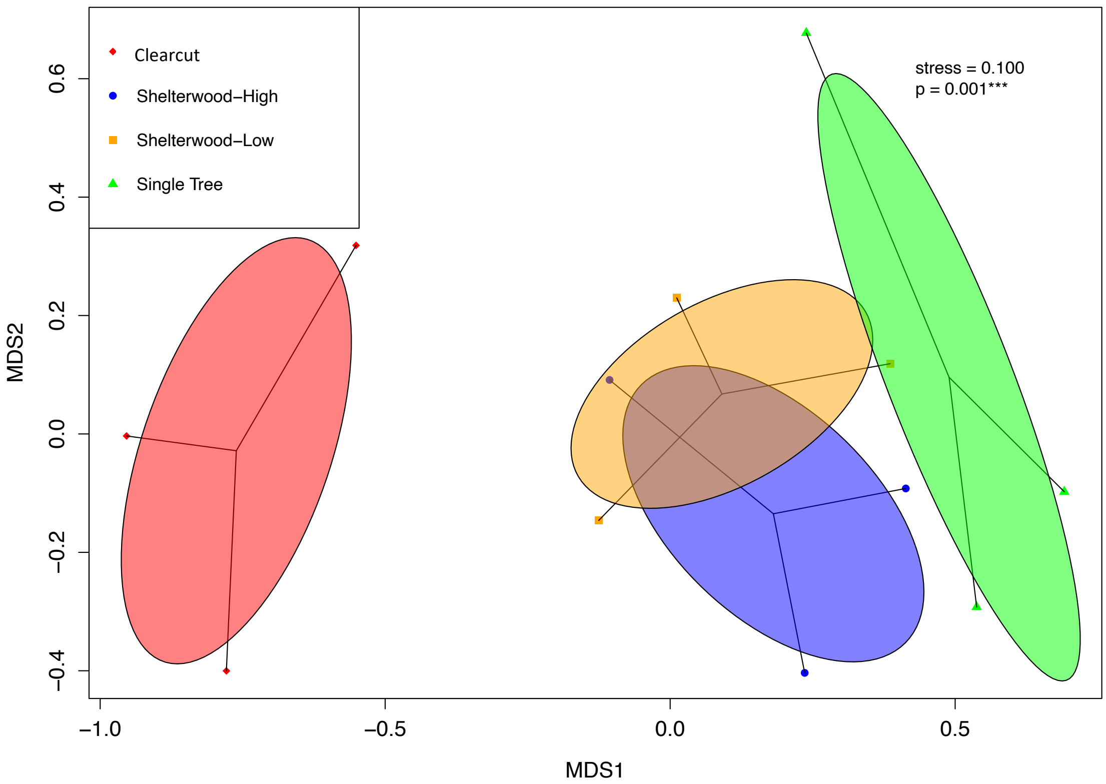

Figure 2.4. NMDS (non-metric multidimensional scaling) ordination representing small mammal communities across canopy regeneration methods at the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites, Alberta, Michigan in 2019. Ellipsoids represent 95% confidence intervals. Bray-Curtis distances metric was applied and statistical significance based on bootstrapping analysis.

2.3.3 Species richness

Species richness was estimated by rarefaction and extrapolation by trap nights (samples). Across site preparations, species richness was lowest within tip-up preparations (9.06 species; 95% CI = 7.7, 10.42) and greatest within scarification preparations (11.21 species; 95% CI = 8.6, 13.83) (Figure 2.5). Among canopy regenerations, species richness was lowest in single tree selection preparations (7.86 species; 95% CI = 5.07, 10.65) and greatest in clearcut preparations (10.84; 95% CI = 7.98, 13.71) (Figure 2.6, Table 2.2). Throughout the NHSEED sites, species richness was lowest within single tree selection-control sites (4 species; 95% CI = 4, 4) and greatest within single tree selection-scarification sites (10.13 species; 95% CI = 3.74, 16.51) (Figure 2.7, Table 2.3).

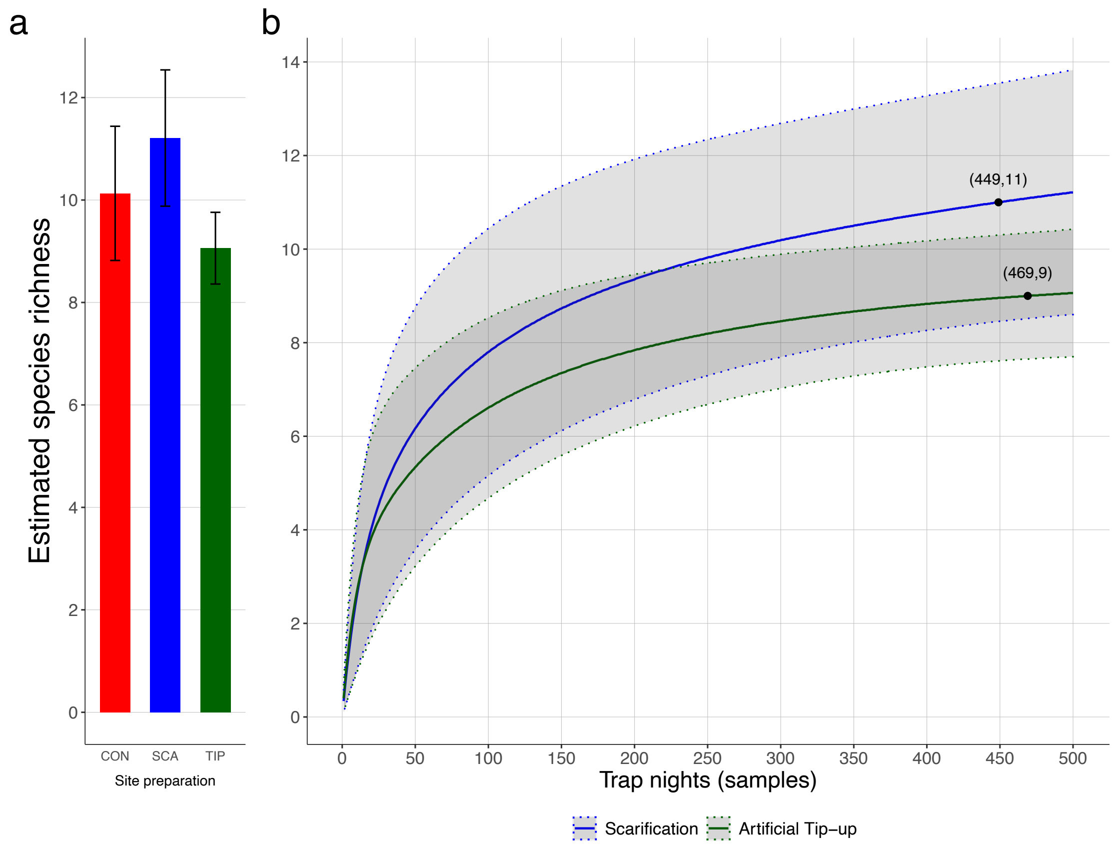

Figure 2.5. Estimated species richness (a) for each site preparation (n = 3) for small mammal data collected at the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites, Alberta, Michigan in 2019. Black bars represent standard deviation (SD). Rarefaction curves (b) compare lowest and highest estimated species richness between site preparations, including 95% confidence intervals (CI, shaded areas). Lowest estimated species richness (tip-up, n = 9.06 species, 95% CI = 7.7, 10.42) and greatest estimated species richness (scarification, n = 11.21 species, 95% CI = 8.6, 13.83). Reference sample species and trap nights also displayed [•; (trap nights, species)]. CON = control, SCA = scarification, and TIP = artificial tip-up.

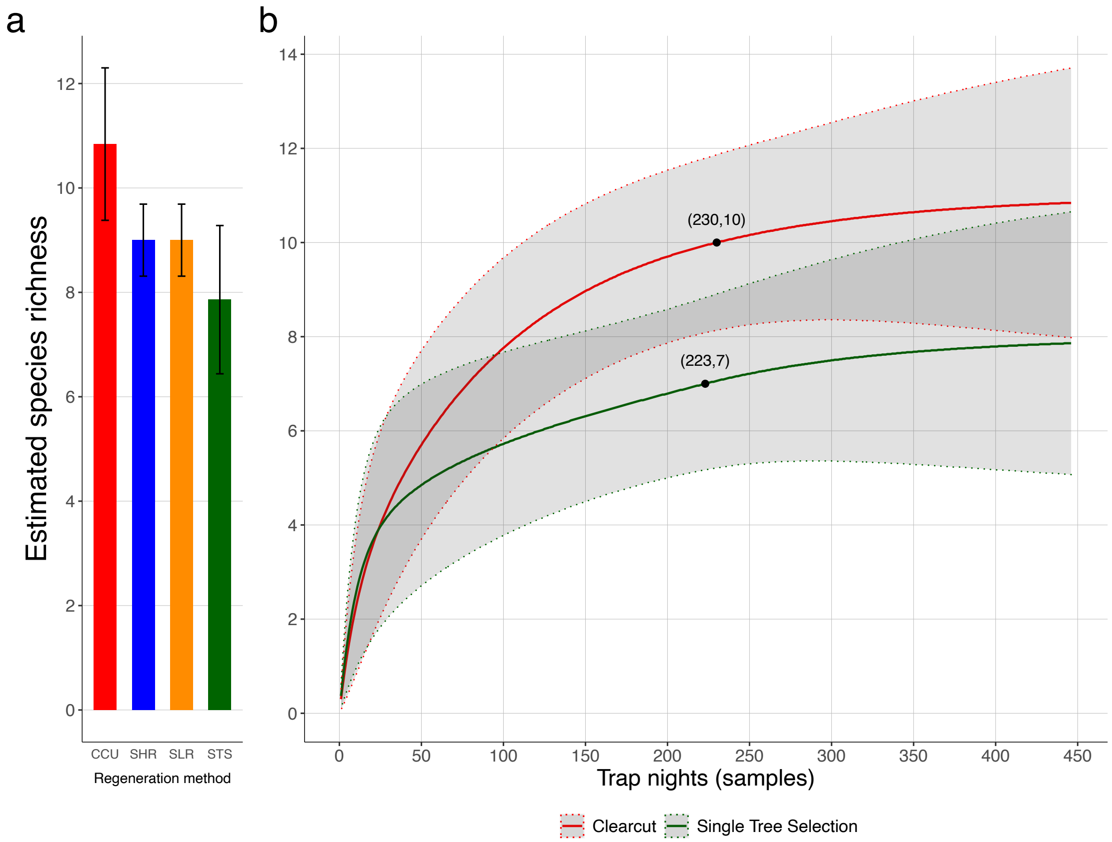

Figure 2.6. Estimated species-richness (a) for each canopy regeneration method (n = 4) for small mammal data collected at the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites, Alberta, Michigan in 2019. Black bars represent standard deviation (SD). Rarefaction curves (b) compare lowest and highest estimated species richness between canopy regenerations, including 95% confidence intervals (CI, shaded areas). Lowest estimated species richness (single tree selection, n = 7.86 species, 95% CI = 5.07, 10.65) and greatest estimated species richness (clearcut, n = 10.84, 95% CI = 7.98, 13.71). Reference sample species and trap nights also displayed [•; (trap nights, species)]. CCU = clearcut, SHR = shelterwood-high residual, SLR = shelterwood-low residual, and STS = single tree selection.

Table 2.2. EstimateS 9.1 (Colwell, 2013) output summary for regeneration methods and site preparations data collected at the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites, Alberta, Michigan in 2019. CCU = clearcut, SHR = shelterwood-high residual, SLR = shelterwood-low residual, STS = single tree selection, CON = control, SCA = scarification, and TIP = artificial tip-up.

Regeneration method	**Reference sample species**	**Reference sample trap nights**	**Total extrapolation samples**	**Individuals (computed)**	**S(est)**	**S(est) 95% confidence intervals (CI)**	**S(est) SD**
CCU	10	230	446	131.86	10.84	(7.98, 13.71)	1.46
SHR	9	446	446	169	9.00	(7.65, 10.35)	0.69
SLR	9	446	446	184	9.00	(7.65, 10.35)	0.69
STS	7	223	446	164	7.86	(5.07, 10.65)	1.42
CON	10	469	500	198.29	10.13	(7.56, 12.69)	1.31
SCA	11	449	500	170.38	11.21	(8.6, 13.83)	1.33
TIP	9	469	500	198.29	9.06	(7.7, 10.42)	0.70

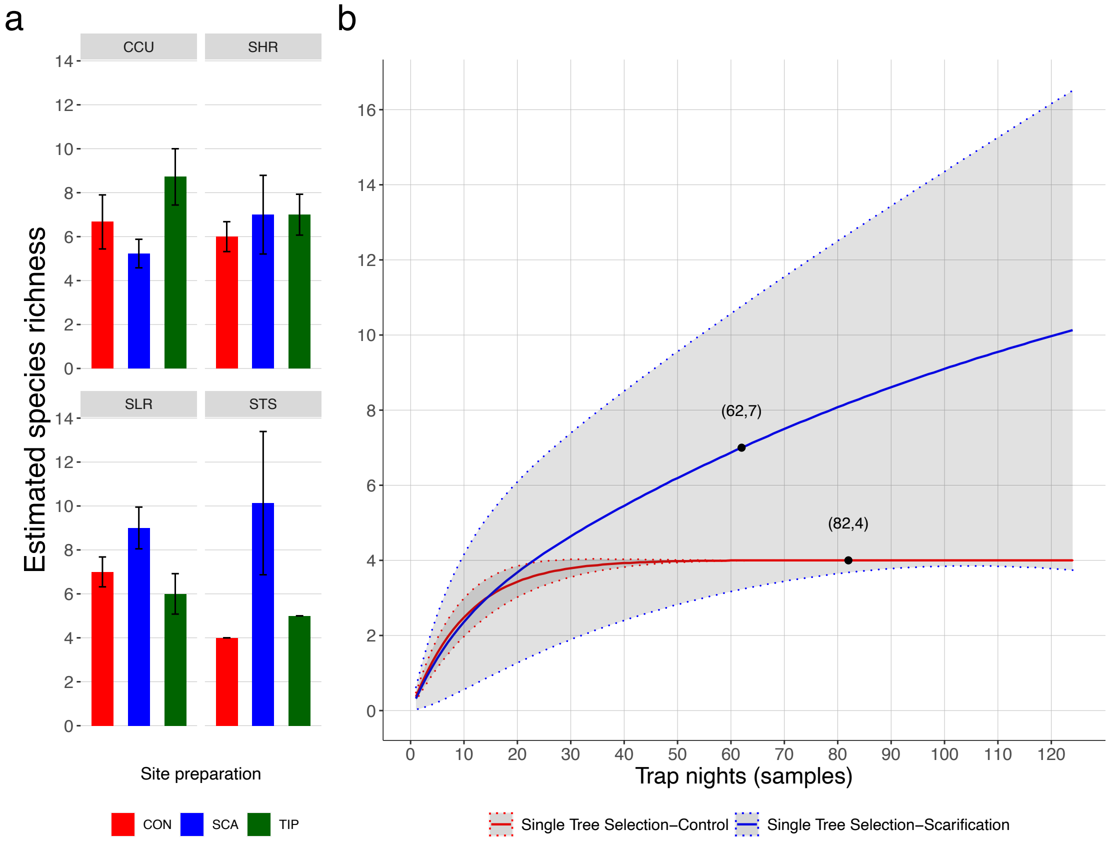

Figure 2.7. Estimated species richness (a) for each site preparation (n = 3) by canopy regeneration method (n = 4) (i.e., treatment) for small mammal data collected at the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites, Alberta, Michigan in 2019. Black bars represent standard deviation (SD). Rarefaction curves (b) compare lowest and highest estimated species richness between treatments, including 95% confidence intervals (CI, shaded areas). Lowest estimated species richness (single tree selection-control, n = 4.00 species, 95% CI = 4, 4) and greatest estimated species richness (single tree selection-scarification, n = 10.13 species, 95% CI = 3.74, 16.51). Reference sample species and trap nights also displayed [•; (trap nights, species)]. CCU = clearcut, SHR = shelterwood-high residual, SLR = shelterwood-low residual, STS = single tree selection, CON = control, SCA = scarification, and TIP = artificial tip-up.

Table 2.3. EstimateS 9.1 (Colwell, 2013) output summary for each regeneration method and site preparation treatment data collected at the Northern Harwood Silviculture Experiment to Enhance Diversity (NHSEED) sites, Alberta, Michigan in 2019. CCU = clearcut, SHR = shelterwood-high residual, SLR = shelterwood-low residual, STS = single tree selection, CON = control, SCA = scarification, and TIP = artificial tip-up.

Regeneration method	Site preparation	Reference sample species	Reference sample trap nights	Total extrapolation samples	Individuals (computed)	S(est)	S(est) 95% confidence intervals (CI)	S(est) SD
CCU	CON	6	79	124	42.38	6.67	(4.26, 9.08)	1.23
CCU	SCA	5	76	124	32.63	5.23	(3.95,6.5)	0.65
CCU	TIP	8	75	124	34.72	8.72	(6.2, 11.23)	1.28
SHR	CON	6	124	124	51	6.00	(4.67, 733)	0.68
SHR	SCA	7	124	124	36	7.00	(3.48, 10.52)	1.79
SHR	TIP	7	124	124	55	7.00	(5.17, 8.83)	0.93
SLR	CON	7	124	124	57	7.00	(5.67, 8.33)	0.68
SLR	SCA	9	124	124	51	9.00	(7.15, 10.85)	0.95
SLR	TIP	6	124	124	50	6.00	(4.19, 7.81)	0.92
STS	CON	4	82	124	45.37	4.00	(4, 4)	0.00
STS	SCA	7	62	124	40	10.13	(3.74, 16.51)	3.26
STS	TIP	5	79	124	50.23	5.00	(5, 5)	0.00

When analyzing asymptotic species richness estimators, several ACE values did not make biological sense; therefore, we chose to conduct further comparisons using the Chao1 estimates. Chao1 estimates yielded similar results to the rarefaction and extrapolation species richness estimates, only differing marginally between site preparations. Across site preparations, estimated species richness was lowest within tip-up preparations (9 species, 95% CI = 9.08, 10.12) and greatest within control preparations (11.99 species, 95% CI = 10.18, 32.02) (Figure 2.8). Among canopy regenerations, species richness was lowest in single tree selection preparations (7.99 species, 95% CI = 7.07, 20.64) and greatest in clearcut preparations (10.33 species, 95% CI = 10.02, 15.9) (Figure 2.8). Throughout the NHSEED sites, species richness was lowest within single tree selection-control sites (4.00 species, 95% CI = 4, 4.29) and greatest within single tree selection-scarification sites (14.6 species, 95% CI = 7.94, 68.7) (Figure 2.8, Table 2.4).

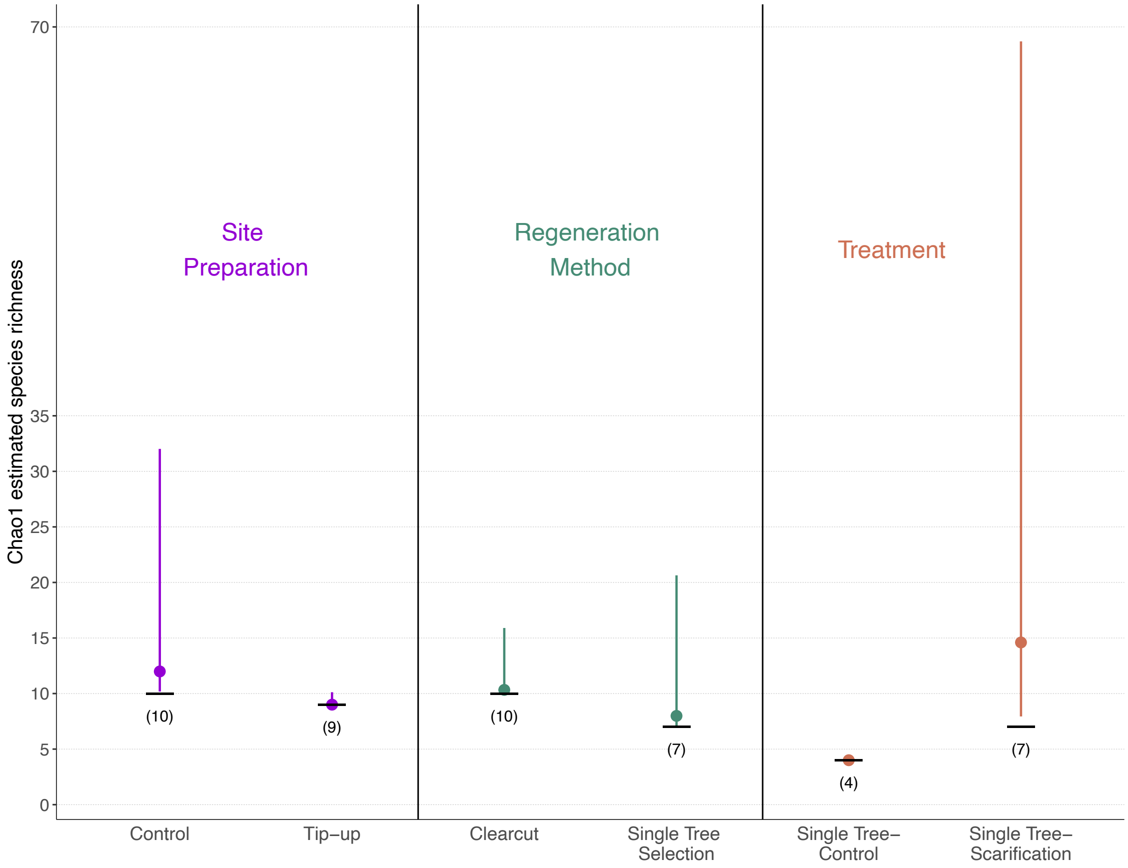

Figure 2.8. Chao 1 comparing lowest and highest estimated species richness between site preparations, regeneration methods, and treatments, including 95% confidence intervals (CI, colored vertical lines). Site preparation with lowest (tip-up, n = 9, 95% CI = 9.08, 10.12) and greatest (control, n = 11.99, 95% CI = 10.18, 32.02) estimated species richness, regeneration method with lowest (single tree selection, n = 7.99, 95% CI = 7.07, 20.64) and greatest (clearcut, n = 10.33, 95% CI = 10.02, 15.9) estimated species richness, and treatment with lowest (single tree selection-control, n = 4, 95% CI = 4, 4.29) and greatest (single tree selection-scarification, n = 14.6, 95% CI = 7.94, 68.7) estimated species richness for small mammal data collected at the NHSEED sites, Alberta, Michigan in 2019. Number of (observed species) is represented by the black line [—].

Table 2.4. Chao1 and (**ACE**) estimated species richness's, calculated using EstimateS 9.1 (Colwell, 2013), across the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites, Alberta, Michigan in 2019. Full canopy estimates represent the estimated species richness for each regeneration methods (n = 4) regardless of site preparation. Full site estimates represent the estimated species richness for each site preparation (n = 3) regardless of regeneration. Reported (**ACE**) estimates represent re-computation using the classic formula of Chao1 as recommended. CCU = clearcut, SHR = shelterwood-high residual, SLR = shelterwood-low residual, STS = single tree selection, CON = control, SCA = scarification, and TIP = artificial tip-up.

		Site			
		CON	**SCA**	**TIP**	**Full canopy estimates**
Canopy	**CCU**	6.96 (**9.54**)	5.00	8.32	10.33
	SHR	6.49 (**6.91**)	12.83 (**22.59**)	7.98 (**9.99**)	9.00
	SLR	7.00	9.33	6.98 (**9.9**)	9.00
	STS	4.00	14.60	5.00	7.99 (**9.8**)
	Full site estimates	11.99 (**12.52**)	11.50	9.00	

2.4 Discussion

Integrating wildlife conservation into the planning of working landscapes represents an important step towards sustainable forestry management. Forests provide multiple services to people and ecosystems, including provisioning habitat to small mammals and their predators, as well as timber products for human wellbeing. To further our understanding of the response of mammal communities to dissimilar silviculture prescriptions in working landscapes, I trapped small mammals across multiple experimental site preparations and canopy regeneration methods. My study yielded several important findings, which can help improve current forest management practices in the UP and beyond.

First, site preparations– scarification, artificial tip-ups, and control sites – had little effect on small mammal community assemblage or richness (Figures 2.3 and 2.5, respectively). Specifically, I estimated 10.13, 11.21, and 9.06 species in the control, scarification, and artificial tip-up site preparations, respectively (Table 2.2). The marginal differences were surprising given my initial prediction that disruptions to the forest-floor would likely alter the microhabitats and food resources upon which small mammal communities depend (Carey et al., 1999; Laigle et al., 2021; Zheng et al., 2000). My prediction was supported by a similar study from Sweden, where residual CWD after harvest appeared to support more diverse mammal communities (Ecke et al., 2002). Similarly, in Kansas, soil disturbances caused by black-tailed prairie dog (*Cynomys ludovicianus*) burrowing activity was found to have a cascading effect on the local composition of rodent communities (VanNimwegen et al., 2018). Our contrasting results begs the question: why did I detect the fewest number of species in artificial tip-ups at NHSEED? Given that tip-up preparations at the NHSEED forest were less than two years old at the time of sampling, it is possible that both tip-ups and CWD have not decayed to the point of provisioning the resources upon which specialist species depend, such as fungus and insects, and other habitat characteristics associated with older CWD (Maser & Trappe, 1984). Alternatively, other variables such as microhabitat characteristics (soil moisture, temperature, and nutrients) may be more influential in driving small mammal richness and assemblage in the UP. Although site preparations were similar in their small mammal composition (Figure 2.3), I detected substantial variation in species richness within control and scarification replicates, both with standard deviations greater than one (Table 2.2); importantly, "control" sites were not truly experimental controls given that they were subjected to disturbance through harvest activity. As such, my results may suggest that artificial tip-ups serve as a stabilizing force, reducing the amount of variation in small mammal richness across replicates.

Second, canopy regeneration methods exhibited a strong and pronounced effect on both small mammal diversity and assemblage, where more extensive canopy cover resulted in decreased species richness (Figures 2.4 and 2.6, respectively) and heightened variability in community structure between replicates (Table 2.2), which does not fully support my prediction of more stable small mammals communities within higher canopy retention regenerations. This trend was exemplified by single tree selection—the highest amount of canopy cover among experimental treatments—which exhibited the lowest species richness amongst canopy regenerations (Figure 2.6, Table 2.2), yet maintained relatively high variance in both richness and assemblage between replicates (Table 2.2 and Figure 2.4, respectively). Conversely, clearcuts exhibited the highest number of species with high amounts of variance in richness and structure between replicates (Table 2.2 and Figure 2.4, respectively), partially supporting my prediction of greater small mammal species richness between regeneration methods with lower canopy retention.

These results suggest a strong bottom-up effect of canopy cover on small mammal communities across my study sites. Although reductions in canopy cover may serve as the ultimate factor in driving observed differences in small mammal richness and community structure, the proximate mechanisms remain unknown, but likely include changes in temperature, humidity, cover, and food resources. Variability in community assemblage found between multiple clearcut and single tree selection replicates, across a small spatial scale, suggests a concordant variability in available resources and microhabitat conditions with both elevated amounts of cover as well as when it is completely removed; the removal of forest will sometimes result in heightened small mammal diversity, and other times low diversity (Kaminski et al., 2007; Kirkland, 1990; LeBlanc et al., 2010; Sullivan & Sullivan, 2001). Given that my study was based on a single-year of data two years after initial harvest, I am uncertain how temporal dynamics will affect changes in both small mammal richness and assemblage within clearcuts. Potentially, measures of diversity will stabilize in clearcuts as the shrub layer begins to shade and stabilize microclimate conditions in the understory. Effects of temporal dynamics within dissimilar silvicultural treatments may explain dissimilar results found in other studies.

For example, Sullivan and Sullivan (2001) observed species richness and community assemblage between harvested (i.e., clearcut, single tree, group harvest, and patch cut) and unharvested sites in British Columbia, and found that within the first year, species richness was lowest in clearcuts. However, after eight years, species richness within these British Columbian clearcuts rebounded (Sullivan et al., 2008). Differences in the timing of harvest and timing of mammal sampling likely produced the dissimilar results between my study and Sullivan and Sullivan (2001). Such differences suggest that within one-year following a clearcut, there are few mammal species; after several years, species richness can dynamically increase resulting in a community unlike the one found in single tree selection (Sullivan et al., 2008). The highly diverse assemblages within clearcuts at the NHSEED forest may be due to the presence of generalist and early-seral species (Sullivan & Sullivan, 2001; Sullivan et al., 2008) utilizing abundant yet variable food resources following disturbance (Yahner, 1986, 1992; Perry & Thill, 2005), while low intensity single tree selection preparations provided more stable food resources, resulting in more stable late-seral species communities (Kaminski et al., 2007; Martell, 1983). During future sampling in clearcuts, I would expect a gradual shift in small mammal communities from early-successional to mid-to-late seral species, while species richness and assemblage would begin to stabilize between replicates.

Third, I found little difference in species richness and assemblage across both the high and low-residual shelterwood treatments (Figures 2.6a and 2.4, respectively). Given that the high regeneration method removed 40% of the canopy, and the low residual removed 70% of the canopy, it was surprising to find striking similarities in small mammal diversity between the two treatments. For instance, LeBlanc et al. (2010) reported no relationship between tree retention and forest-dwelling small mammal species richness; however, community composition was marginally influenced by vertical cover in boreal forests. Furthermore, Vanderwel et al. (2009) evaluated the effects of stand-level partial harvesting techniques on late-successional, forest-associated vertebrates, in which they reported a 40% reduction in abundance of all taxa within 50% canopy retention and unstable habitat for nearly 25% of late-successional species and many others within 30% retention sites. Given documented differences in both richness and assemblage between clearcuts and shelterwood low-residual, there likely exists a canopy cover threshold effect whereby species associated with open environments drop out and begin to be replaced by forest obligates. This threshold, although unknown, appears to occur at less than 30% canopy cover at NHSEED, demonstrating the sensitivity of non-forest obligates to a moderate increase in canopy cover (Figure 2.4, Table 2.2).

In conclusion, small mammal communities in the UP were strongly influenced by reductions in canopy cover, while being only marginally affected by site preparation. Our results did not fully support our predictions, in which, more heterogeneous stands would support more diverse and species-rich small mammal communities. I recommend treating my effort as a historical benchmark from which future studies can be compared to determine temporal patterns of species gains, losses, and stabilization as the canopy in clearcut treatments continues to develop and provisions more structural complexity.

2.5 Management implications

Clearcuts and single tree selections were most influential in changing small mammal community assemblages at NHSEED, two years post-harvest, wherein, clearcuts supported the greatest number of species and single tree selections the least. Site preparations appeared to have only a marginal effect on mammal diversity. Although small mammal species richness has been observed to decline with increasing canopy cover (Sullivan et al., 2000; Sullivan & Sullivan, 2001), sensitive, late-successional species respond positively to greater canopy retention (LeBlanc et al., 2010; Vanderwel et al., 2009). Thus, unique species found in more structurally complex forests contribute to broader patterns of both beta and gamma diversity in the UP. Although we found little effect of site preparation on small mammal diversity, maintenance of CWD has been demonstrated to maintain moisture and microclimates for soil organisms; decay for fungal and insect species; and food and microhabitat features for small mammals (Carey & Johnson, 1995; Laigle et al., 2021; Maser & Trappe, 1984). Stand homogeneity created by loss of CWD also results in altered predator-prey relationships. For example, habitat homogenization led to niche compression and strong interspecific competition between American marten (*Martes americana*) and fishers (*Pekania pennanti*) in the Great Lakes Region (Manlick et al., 2017). Small mammals are important prey for marten and fishers (Hales et al., 2008; Kirby et al., 2018; Thompson & Colgan, 1990); hence, more diverse habitat features should provide a more diverse prey-base, supporting resilient mesopredator populations. Therefore, I recommend maintaining a diversity of silviculture practices across the landscape to maintain a "diversity of diversities" to maximize patterns of biodiversity at the regional scale. I also suggest incorporating shelterwood harvested sites, which retain approximately 30 – 60% canopy cover, with tip-ups as CWD to provide suitable habitat heterogeneity and food resources, as the core prescription to maintain stable small mammal communities upon which mesopredator populations depend.

My study offered a snapshot of small mammal presence during the summer, two years post-harvest at the NHSEED forest, representing differing silviculture canopy regeneration methods and understory preparation techniques. Lacking pre-harvest capture data, I was unable to account for preexisting patterns of mammalian diversity; as such, I recommend sampling the small mammal community before and after future harvests at NHSEED to account for implicit dissimilarities across the study area.

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3 Literature review: Responses of forest-dwelling small mammals of the Great Lakes Region to differing silvicultural practices

3.1 Introduction

3.1.1 Ecosystem services

Globally ecosystem services were estimated at $125 trillion per year, with forest biome services estimated at $16 trillion per year in 2011 (in 2007 US$, assuming unit and biome area changes; Costanza et al., 2014). However, loss of biodiversity by way of human disturbance and forest degradation may lead to the collapse of such goods and services (Food and Agriculture Organization of the United Nations [FAO], 2020, p. 95). Globally, as informed by 165 countries, the Global Forest Resources Assessment (FRA) reported 424 million ha (approximately 11% of the reporting countries' total forested area) designated for "conservation of biodiversity" in 2020 (FAO, 2020, pp. 65, 57). This category includes but is not limited to areas designated for biodiversity conservation in protected areas. Contrarily, forest product production is an economically important and lucrative industry, in which, the FRA reported nearly 1.15 billion ha of forest, equivalent to approximately 31% of the total forested area across 160 reporting countries, to be managed for "production" in 2020 (FAO, 2020, pp. 58 – 59).

Worldwide, 1.15 billion ha of forested area was reported as production-designated in 2020, with nearly 2.26 million ha reported across North America (FAO, 2020, p. 59). Exports for North America were greatest in "other paper and paperboard" products, resulting in ~7.1 billion US$ – second only to Germany with ~7.9 billion US$ in revenue – and lowest in "wood fuel, non-coniferous" products with ~278,000 US$ (FAO, 2021). Economically, full-time employment within the forestry and logging sector has shown a decrease between 1990 – 2015 globally, with nearly 12.5 million full-time individuals reported in 2015 (FAO, 2020, pp. 103 – 104). Conversely, forestry-related education displayed an upward trend from 2000 to 2015 globally, including an increase in the number of female students across education levels, aside from a slight decrease during 2010 to 2015 at the doctoral-level (FAO, 2020, pp. 105 – 106).

Due to its social and economic importance, demand for timber may lead to production-focused management, minimizing forest sustainability and conservation of biodiversity, damaging ecosystem services. As broadly classified by the FRA, naturally regenerating forests are thought to provide important ecosystem services and further conserve biodiversity, whereas, planted forests may provide additional – and equally important – ecosystem services, while reducing harvesting pressures on natural forests (FAO, 2020, p. 27). Yet, continued debate over the values of services provided by differing forests (as defined by the FRA) may lead to disregard of sustainably managed forests (FAO, 2020, p. 27). Uninformed timber harvest applications have potential to result in cascading effects on local ecosystems and their inhabitants, which may impact human health and well-being (Collins & Larry, 2008; Costanza et al., 1997; Millennium Ecosystem Assessment [MEA], 2005; Smith et al., 2011, p. 1), including spiritual, cultural, and aesthetic values (Smith et al., 2011, p.1). To nurture productive systems, Tilman et al. (2014) urges the conservation of biodiversity by promoting highly diverse communities, preserving invaluable ecosystem services.

3.1.2 Productivity

Landscapes forever changed by timber harvest alter trophic dynamics and, in turn, productivity within terrestrial ecosystems. Forests are considered productive ecosystems, in which, net primary productivity is dependent on the successional stage of the area being sampled (Oksanen & Oksanen, 2000). For example, respiration in mature forests lowers net productivity, while potential productivity is high in early-successional woodlands (Oksanen & Oksanen, 2000). Further, Franklin et al. (2002) stated that forest structure is a direct measurement of stand productivity and function, wherein, canopy closure is more rapid within productive sites, yet slower or never achieved within less productive sites of similar tree densities.

Regardless of stand age, abiotic and biotic factors influence forest productivity by modifying species diversity (Hunter & Price, 1992; Oksanen & Oksanen, 2000) and reducing soil productivity (Fleming et al., 2006; Marshall, 2000). For example, forest harvest activities, such as compaction and organic matter removal, deplete soil nutrition and reduce soil organisms necessary to carry out biological processes, leading to decreased forest productivity (Marshall, 2000). Furthermore, fungal community responses vary to differing organic matter removal depths and intensities (Mushinski et al., 2018). In addition, Marshall (2000) reported microflora and soil biota responses to be as complex as their community compositions and relationships in response to forest harvest intensity. Such studies demonstrate how forest-floors modified by anthropogenic disturbances indirectly influence productivity by altering biotic interactions, resulting in cascading effects throughout established biological communities (Laigle et al., 2021; Marshall, 2000; Mushinski et al., 2018).

3.1.3 Cascading effects

Although accepted amongst ecologists, the directionality (i.e., top-down or bottom-up) and weight of cascading effects on biological communities has been debated (e.g., Hairston et al., 1960; Hunter & Price, 1992; Oksanen et al., 1981; Oksanen & Oksanen, 2000; Polis & Strong, 1996; Power, 1992). As presented by Hairston et al. (1960), the green world hypothesis (HSS), suggests that producer, carnivorous, and decomposer populations are density-dependent controlled within their respective guilds, while interspecific competition for resources exists between trophic-levels; however, top-down forces (i.e., predation) regulate herbivore populations, rather than resource limitations and competition. Similarly, the hypothesis of exploitation ecosystems (EEH) of Oksanen et al. (1981) and Oksanen and Oksanen (2000), though in agreeance with HSS across productive systems, suggests that predation of folivores fails in unproductive systems subjected to natural folivory, unable to support upper trophic-level predators. Contrary to both HSS and EEH, the defense diversity hypothesis (DDH; as referred to by Oksanen & Oksanen, 2000) discussed by Hunter and Price (1992) and Polis and Strong (1996) suggests that heterogeneity, dependent upon primary producer species diversity through bottom-up controls, determines the diversity, composition, and distribution of higher trophic-level populations, cascading upward.

While the directionality and weight of abiotic and biotic forces may not be fully understood, continued efforts must be made to study particular influences on species-of-interest to improve conservation of biodiversity. For example, Laigle et al. (2021) observed soil disruption caused by forest management to shift species diversity at multi-trophic-levels by creating heterogeneity within highly disturbed areas and mature forest features across undisturbed and low-disturbance sites. Furthermore, the same soil disturbances resulted in selective pressures towards opportunistic, early-successional, mobile insect species able to exploit new niches in disturbed areas, while highly sensitive species were observed in mature sites (Laigle et al., 2021). Additionally, bottom-up food web effects caused by harvest disturbance altered species communities across multi-trophic soil layers from detritovores to predatory insects (Laigle et al., 2021). Consequently, stand-level disturbances result in altered stand biodiversity and productivity, ultimately, resulting in modified food resources to species of higher trophic-levels – such as small mammals (Barlow et al., 2007; Dunham, 2008; Pearce & Venier, 2005; Tylianakis et al., 2008).

3.1.4 Forest-dwelling mammals

Forest-dwelling small mammals comprise important guilds within forest ecosystems: prey to predators (Carey & Harrington, 2001; Clotfelter et al., 2007; Gray et al., 2019), invertebrate control (Carey & Johnson, 1995; Carey & Harrington, 2001), soil mixing and aeration (Carey & Harrington, 2001), and fungal spore (Maser et al., 1978; Trappe & Maser, 1976) and seed dispersion (Carey & Harrington, 2001; Yamashina & Hara, 2019). As such, the Ontario Ministry of Natural Resources (OMNR) Wildlife Assessment Program in Ontario, Canada, monitors seven small mammal species (i.e., mice, voles, lemmings, and shrews) as bioindicators to assess sustainable forest management practices (McLaren et al., 1998; Pearce & Venier, 2005). For example, southern red-backed voles (*Myodes gapperi*) are a commonly studied indicator species of old-growth forests due to their observed associations with heterogeneous shrub layers and course woody debris (CWD) within mature forests of complex vertical structure (Klenner & Sullivan, 2009; Le Blanc et al., 2010; Merritt, 1981; Pearce & Venier, 2005; Ransome et al., 2009). In contrast, the northwestern chipmunk (*Tamias amoenus*) and meadow vole (*Microtus pennsylvanicus*), for example, are early-successional forest species, observed in clearcut sites with reduced tree retention comprised of herbs and grasses (Getz, 1961; Klenner & Sullivan, 2009). Though the natural histories of many small mammals are well studied and understood, anthropogenic disturbance and climate change have begun to alter historic species-specific responses to disturbances (Guiden & Orrock, 2021; Myers et al., 2009; Roy-Dufresne et al., 2013; Tylianakis et al., 2008); consequently, long-term studies considering both animal and habitat conditions have never been more important for biodiversity conservation and ecosystem health (Cardinale et al., 2012; Daily et al., 2009; Moore et al., 2014; Tilman et al., 2014).

As the presence, absence, fecundity, or survival of a species can provide qualitative and quantitative measurements of overall ecosystem health, so can forest age and health be indicative of its ability to support healthy animal population, allowing informative decisions and predictions of how long-term, cascading effects of anthropogenic environmental disturbances affect fauna. For example, land cleared for farming and European settlement across Australia has created patches of poor quality forests, resulting in extreme declines of small mammal species (Moore et al., 2014). Within these patches, remaining tree canopy experiences dieback, which alters forest-floor vegetation, leading to further small mammal displacement and extinction (Moore et al., 2014) and reduction of important food resources for local forest predatory species, such as the sooty owl (*Tyto tenebricosa*; Bilney et al., 2010). Similarly, in the Pacific Northwest (PNW), symbiotic relationships between ectomycorrhizal fungi and the roots of various tree species is facilitated by mycophagous small mammals dispersing fungal spores (Jacobs & Luoma, 2008; Maser et al., 1978). Without facilitated dispersal from small mammals, obligate tree species' health would decline, resulting in loss of biodiversity, food sources, and habitat for a multitude of species, including humans reliant upon provided ecosystem services (Jacobs & Luoma, 2008; Maser et al., 1978). As forested ecosystems become less diverse due to habitat loss, they analogously become less resilient to human-induced climate change.

3.1.5 Climate change

Productive ecosystems provide services beneficial to human well-being, requiring an understanding of how human disturbances impact species across trophic-levels. Regulating services are provided by natural processes influencing water purification, pollination, climate, and flood and disease control (MEA, 2005, p. V; Smith et al., 2011, p. 1), all of which, are declining at unsustainable rates (MEA, 2005, p. 6). Pollination, for example, is a regulating service provided to humans by means of habitats supporting pollinating insect, bird, bat, and bee species (Smith et al., 2011, p. 16). For example, loss of biodiversity due to climate change has caused chain-reactions, resulting in declining global coffee crops over the last 30 years (Chain-Guadarrama et al., 2019; Jha et al., 2014). Because coffee systems rely on biodiversity-regulated ecosystem services provided by birds and bees (pest control and pollination, respectively), researchers suggest a shift back to shade-coffee systems, which support diversification, resilience to climate change, and sustainable livelihoods of such an economically important crop (Chain-Guadarrama et al., 2019; Jha et al., 2014). Additionally, a mutualism exists between the endangered Mexican long-nosed bat (*Leptonycteris nivalis*) and multiple *Agave* spp., which are of socio-economic importance (e.g., food, fibres, and beverages; Gómez-Ruiz & Lacher Jr., 2019). When modeling potential climate change effects on species distributions of *L. nivalis* and agaves in 30 and 50 years, Gómez-Ruiz and Lacher Jr. (2019) observed a reduction of suitable habitat for all nine *Agave* spp. modelled and a 75% decrease in Mexican long-nosed bat and agave species overlap, resulting in greater vulnerability of both agave and bat species to future climate change.

The cascading effects of climate change on ecosystems and human well-being are of concern. For instance, the 2005 MEA (2005, pp. 1, 18) had four main findings regarding the world's ecosystems: 1) to meet rapidly growing demand for necessities over the past 50 years, humans have caused irreversible loss of diversity by altering ecosystems; 2) although net gains in human well-being and economic value have been achieved, the degradation caused to ecosystems will result in greatly diminished and/or loss of ecosystem services for future generation; 3) ecosystem degradation is predicted to be much worse during the first half of this century, resulting in failure to achieve the eight Millennium Development Goals agreed on by the United Nations in 2000; and 4) without significant changes to policies, institutions, and practices, reversal of ecosystem damages, while still meeting increased demands for services, is unlikely. Ecosystem degradation by humans has led to amphibian extinction rates over 1,000-times the historic rate, with projected future extinction rates to be ten-times more than the current rate across all species (MEA, 2005, pp. 4 – 5). Further, Costanza et al. (2014) reported a conservative estimate of $4.3 – 20.2 trillion per year (in 2007 US$) of ecosystem services lost between 1997 and 2011 due to global land-use changes. Expression of ecosystem services in monetary units allows one to visualize the significance of these systems to human well-being and the magnitude at which anthropogenic disturbance has altered them (Costanza et al., 2014). Although astonishing at the time, it should be noted that these estimates are more than ten years old and may have changed significantly. Loss of biodiversity at such staggering rates is unsustainable; therefore, decision-makers must apply ecosystem-based management to promote sustainability with growing demand for economically important ecosystem services necessary to human well-being.

The effects of climate change are mitigated by diversification, wherein, ecosystem health and function are strengthened by increased biodiversity (MEA, 2005). The value of critical processes provided by ecosystem services is recognized within the mission of governmental agencies, such as, the USDA Forest Service (Smith et al., 2011, p. 3), suggesting that forested systems are worth understanding. For example, Smith et al. (2011, p. II) present a collaboration between The Forest Service Pacific Northwest Research Station and the Deschutes National Forest in Oregon, in which, the goal was to "explore how an ecosystem service approach can enhance forest stewardship in central Oregon". By conducting management projects within national forests, governmental agencies like the US Forest Service, can gain better understanding of these complex relationships to inform decision-makers and clearly communicate the importance of stewardship with the public (Smith et al., 2011, p. 22). In addition to public awareness of protected forested landscapes, there must exist clear communication and collaboration between public and private landowners across areas economically reliant upon timber harvest products, fostering stewardship by means of sustainable forest management for future generations. The Great Lakes Region is one such area, wherein, anthropogenic disturbance and conflicting management practices has led to immense biodiversity loss (Schulte et al., 2007; Seymour et al., 2002). To continue sustainable harvests throughout the Great Lakes, public and private land managers must cultivate resilience to climate change by understanding local natural histories, cascading effects of trophic relationships, and promoting diversity within forested ecosystems (Franklin, 1993).

3.2 The Great Lakes Region

3.2.1 A brief overview

The Great Lakes Region encompasses Minnesota, Wisconsin, Illinois, Michigan, Indiana, Ohio, Pennsylvania, and New York, USA (from west to east), and Ontario, Canada, all of which, border the five Great Lakes: Superior, Michigan, Huron, Erie, and Ontario. When measured at low water, the combined volume of water within these five lakes is approximately 5,439 cubic miles, which is 84% of North America's and 21% of the world's surface fresh water (U.S.EPA, 2021). Such large bodies of water strongly influence the climate of the area. For instance, the 2021 average temperature recorded for the region was lowest at 6.5°F during February in Minnesota, while the highest was 75.4 and 75.1°F during August in Illinois and Indiana, respectively (NOAA, 2022; Weather Spark, 2022). Precipitation across the Great Lakes Region in 2021, had the highest recording of 8.1 inches during July in New York and the lowest with 0.3 inches during February in Minnesota (Environmental and Climate Change Canada, 2022; NOAA, 2022). Though the region's climate is quite variable, ease of transportation across the area, by way of the great lakes, led to extensive settlement in the early 1800s (Beeton, 2022).

Abundant natural resources of timber, minerals, wildlife, and natural beauty form the economic base of the Great Lakes Region (Beeton, 2022); however, extensive habitat degradation and pollution by anthropogenic disturbance has forever changed the forested landscape of the region. For example, a review by Whitney (1987) observed that pre-settlement hemlock-white pine-northern hardwood forests of the Great Lakes were converted to sugar maple-types by extensive selective logging and further altered by slash and burn fires, which destroyed pine seed trees and seedlings, converting industry to pulp-oriented management. A recent review estimated the population of the entire Great Lakes Region, including Ontario, Canada, to be over 99.5 million (World Population Review, 2022). Timber harvesting remains an economically important industry across the Great Lakes; therefore, managers must adopt forestry practices which encourage biodiversity and sustainability for growing populations reliant upon timber industry within northern hardwood forests.

3.2.2 Northern hardwoods and mammals

The highly modified northern hardwood forests of Great Lakes have been shaped by natural and anthropogenic disturbances, both of which, have altered its historic composition. Rapid industrialization and settlement in the late nineteenth century, fostered by several decades of intensive logging (i.e., the "cutover"; Gough, 1997) and followed by widespread slash fires, forever changed the landscape and heavily depleted local biological legacies (Whitney, 1987). Historically, natural fire regimes in northern hardwoods occurred at 130 to 260 year-intervals (Whitney, 1987). Such extensive disturbance resulted in the promotion of sprouting species: maple (*Acer* spp.), oak (*Quercus* spp.), paper birch (*Betula papyrifera* Marshall), and aspen (*Populus tremuloides* Michx. and *P. grandidentata* Michx.) (Hupperts, 2019). Furthermore, increasing white-tailed deer (*Odocoileus virginianus*) populations pressuring a conifer to hardwood dominance transition (Rooney & Waller, 2003). By 1912, after almost three decades of intensive pine (*Pinus* spp.) and hemlock (*Tsuga* spp.) harvesting, conifers were nearly depleted, shifting lumber from pine to sugar maple (*Acer saccharum* Marsh.) species (Whitney, 1987). Long-lived and resilient sugar maple and oak trees are important silviculture species within northern hardwood forests (Crow et al., 2002; Leak et al., 2014, p. 19), which also provide cover and food resources for wildlife (DeGraaf & Shigo, 1985, p. 19).

Hard mast provided by trees such as oaks and conifers, directly affect forest-dwelling small mammals, which are indicative of forest productivity (Carey & Harrington, 2001; Carey et al., 1999; Carey & Johnson, 1995; Gray et al., 2019). For example, Carey et al. (1999) and Carey and Harrington (2001) found northern flying squirrels (*Glaucomys sabrinus*) and Townsend's chipmunks (*Tamias townsendii*) to be important prey species and indicators of seed, fruit, and truffle producing forests. Similarly, seed availability can be indicative of small mammal species' presence, such as big-leaf maple seeds (*Acer macrophyllum* Pursh.) being a strong predictor of deer mice (*Peromyscus maniculatus*) presence across the Olympic National Forest in Washington – as observed by Carey and Harrington (2001).

Contrarily, forest-dwelling small mammals can function as seed predators, hindering regeneration (Côté et al., 2003; Guiden & Orrock, 2021; Hsia & Francl, 2009; Ostfeld et al., 1997). For example, Ostfeld et al. (1997) observed meadow voles (*Microtus pennsylvanicus*) and white footed mice (*Peromyscus leucopus*) densities to play a direct role in young forest seed and sapling survival in old fields in southeastern New York. In plots of higher vole populations, seed predation by mice was reduced; however, saplings were negatively affected by vole presence (Ostfeld et al., 1997). Côté et al. (2003) reported similar findings, wherein, black spruce (*Picea mariana* (Mill.) BSP) seeds and juvenile seedlings in Canadian boreal forest were more heavily consumed during winter across recent burn sites, suggesting such vegetation may be an important food resource leading to elevated small mammal abundance.

In-hand with potential regeneration failure, increased small mammal abundance can also be mutualistic with seed dispersal and survival of certain tree species. Oaks, for example, produce excessive mast crops of large and energy-rich seeds during irregular interannual intervals, attracting granivorous, scatter-hoarding small mammals and birds to disperse and cache their seeds (Vander Wall, 2001, 2010). Trees utilizing caching strategies have exhibited seed establishment probabilities of nearly 75% (Zwolak & Crone, 2012), wherein, abandoned seeds are more reproductively successful (García & Houle, 2005). Furthermore, seed fate is often dependent upon seed-type, selection, and availability. Lichti et al. (2014) tagged seeds of northern red oak (*Quercus rubra* L.), white oak (*Quercus alba* L.), and American chestnut (*Castanea dentata* (Marshall) Borkh.) to track their fates over two years at sites in Wisconsin and Pennsylvania. Scatter-hoarder cache behaviors in these deciduous forests were observed to support Lichti et al.'s (2014) trait-availability hypothesis (combining trait-mediated interactions of Vander Wall [2010] and availability-mediated conditional mutualism of Theimer [2005]), in which, seed perishability and long-term storage were prioritized over tannin avoidance at the time of dispersal.

3.2.3 Habitat heterogeneity

Seed availability, diversity, and masting events support forest-dwelling animals across taxa by serving as food resources, as well as initiating successional changes that maintain the vegetative structure upon which small mammal communities rely. Diversification of seed-, fruit-, and nut-bearing understory and canopy species leads to habitat heterogeneity and the ability to support coexistence among potentially competing species, while mitigating mast predation (Carey & Harrington, 2001). For example, Carey and Harrington (2001) recommended that managers plant favorable seed-bearing deciduous trees, such as maples (*Acer* spp.), to negate predation by species such as *P. maniculatus*, while fostering forest complexity.

In conjunction with reducing mast predation (either hard or soft mast), increasing forest composition heterogeneity also leads to diversification and greater densities of animals by providing habitat variety. For instance, vertical heterogeneity within mixed northern hardwoods of Michigan provides foraging niches and denning or nesting sites for forest-dwelling birds and mammals, such as blue jays and barred owls (*Cyanocitta cristata* and *Strix varia*, respectively; Tekiela, 2019), bats (multiple members of Vespertilionidae), red squirrels (*Tamiasciurus hudsonicus*), and American marten (*Martes americana*; Kurta, 2017, pp. 65 – 91, 131, 225). Remaining upright and following natural decomposition, snags support cavity-dwelling flickers, sapsuckers, and woodpeckers (family Picidae; Tekiela, 2019); and both northern and southern flying squirrels (*Glaucomys* spp.; Kurta, 2017, pp. 134, 137) throughout mixed forests in Michigan. Similarly, horizontal heterogeneity created by leaf litter, CWD, herbaceous plants, and rocks are important ground-floor characteristics in determining small mammal community composition (Degrassi, 2018). For example, in Oregon, the western red-backed vole (*Myodes californicus*) was associated with late-decayed logs, which provided protection from predation and mycorrhizae as a food source, whereas, *Microtus oregoni* (creeping vole) was observed in early-successional sites containing vast amounts of shrub and herbaceous cover, providing both protection and lichen food sources (Doyle, 1987; Maser et al., 1978). Diversification of habitat at micro- and macro-scales is necessary to support biodiversity.

Habitat complexity and biodiversity are often synonymous; thus, the cascading effects of anthropogenic disturbances are long-term throughout managed environments (Crow et al., 2002; Franklin et al., 2002; Smith et al., 2011). Landscapes – such as the Midwest – transformed by timber harvest are highly disturbed, resulting in permanent changes to both habitat and animals, wherein, long-term management plans can be implemented to support biodiversity (Crow et al., 2002; Fischer et al., 2011; Smith et al., 2011). For example, Fischer et al. (2011) found small mammal abundance, species richness, and diversity to increase across more complex landscapes within a 500 m radius of conventionally (intensified agriculture) managed fields, while species-specific responses varied to habitat complexity across a gradient of spatial scales (i.e., 100 m, 250 m, and

500 m radii of managed fields), suggesting that scale and ecological requirements of species-of-interest need consideration during conservation management plans within agricultural areas.

In northern hardwood forests of Michigan's Upper Peninsula (UP), Crow et al. (2002) observed similar results of plant species structure and composition when comparing managed and unmanaged forest, in which, structural heterogeneity within old-growth sites led to highly variable species richness, while managed stands supported greater species richness, including disturbance-adapted species. While objectives of current hardwood management are to promote efficiency by improving tree quality to produce valuable commercial products, in-turn, leading to simplified and uniform forests, Crow et al. (2002) suggest that supporting plant and animal diversity by retaining old-growth features and forest complexity are also important. Prior to current management regimes, extensive logging and slash and burn fires throughout the Great Lakes during the early nineteenth century created homogenous landscapes (Whitney, 1987). Following the plundering of old-growth forests, unregulated hunting and trapping led to the extinction and near-loss of animal species reliant upon mature habitat characteristics, such as woodland caribou (*Rangifer tarandus caribou*; Langston, 2021), elk (*Cervus canadensis*; Kurta, 2017, p. 267), Canada lynx (*Lynx canadensis*; Kurta, 2017, pp. 255 – 256), and wolverine (*Gulo gulo*; Kurta, 2017, p. 247). Another example is the near-loss and reintroduction efforts of American marten and fishers (*Pekania pennanti*) in Michigan and Wisconsin, United States, due to extensive habitat loss and homogenization of their habitats (Williams et al., 2007; Manlick et al., 2017).

Across the Great Lakes Region and beyond, *M. americana* and *P. pennanti* occupied similar mature forest habitats, comprised of closed canopies and substantial CWD (Kurta, 2017, pp. 225, 228; Williams et al., 2007, p. 8; Zielinski et al., 2013); however, habitat degradation, coupled with unregulated trapping caused both species to become extirpated from much of their historical, southern territories during the 19th and early 20th centuries (Williams et al., 2007, pp. 1, 8). In Michigan and Wisconsin, reintroduction efforts of both species began in the 1950s (Williams et al., 2007). Spurred by concerns of extensive timber damage and loss due to an increasing North American porcupine (*Erethizon dorsatum*) population, Michigan began reintroducing fisher, a porcupine predator, to reestablish top-down control (Williams et al., 2007, pp. 3, 10). As the larger of the two extant, large, mustelid forest-dwelling carnivores, fishers have thrived, whereas, the less adaptable marten has been marginally successful due to strong niche overlaps of habitat and food resources, and increased intraguild competition with fisher across homogenized landscapes (Kurta, 2017, pp. 223, 228 – 230; Manlick et al., 2017; Williams et al., 2007).

Though neither fisher nor marten are federally listed as threatened or endangered in Michigan, and their recovery represents only a singular example of carnivore restoration, it is a story of caution. One, in which, Manlick et al. (2017) suggest that marten reintroductions could have been more successful with application of a better understanding of the requirements of and interactions between the two carnivores. Carey and Harrington (2001) expressed that increasing environmental complexity throughout forested systems increases multidimensional habitat space, allowing for coexistence and success of competing species by providing habitat and food resource diversity and reducing interspecific interactions. For example, fishers, though larger and more successful during reintroductions in Michigan, are still sensitive to anthropogenic disturbances such as the removal of dense overstories and homogenization of forest-floors (Zielinski et al., 2013). Understanding competition and trophic interactions between carnivores and their food resources can help managers make informed, long-term plans for biodiversity conservation (Fuller et al., 2004; Fuller & Harrison, 2005).

3.2.4 Michigan's Upper Peninsula

Balancing ecological function, maintenance of biodiversity, and economic sustainability are hallmarks of sustainable forest management practices. The MEA (2005, pp. 1 – 5) reported that the greatest anthropogenic change to ecosystems occurred during the latter-half of the twentieth century to meet demand for food, water, fiber, fuel, and timber. For example, the world population doubled to nearly 6 billion people between 1960 and 2000, leading to a tripling of wood harvested for paper-products, and timber production to increase by more than 50% (MEA, 2005, p. 5). Emblematic of these trends is Michigan's Upper Peninsula (UP), USA, wherein, over 70% of the landscape is forested and one-third is privately owned (Schubert & Mayer, 2012).

Early records estimated that approximately 95% of Michigan was forested during the early- to mid-1800s (Matson et al., 2013). Prior to European settlement, the UP was influenced by natural fire and windthrow disturbances, with the eastern UP dominated by beech-sugar maple, lowland conifer swamp, and fir-spruce-cedar swamp forest-types (~67%; Matson et al., 2013) and the western UP dominated by fir-spruce-cedar swamp, beech-sugar maple, and hemlock-yellow birch forest-types (~66%; Hamel et al., 2013). Throughout the Upper Peninsula, fur trade conflict between early settlers and Native Americans shaped the landscape, resulting in diminished furbearing species (Hamel et al., 2013; Matson et al., 2013). The discovery of iron ore and copper in the 1840s, ignited a boom of intensive mining across the Keweenaw Peninsula resulting in increased settlement (Hamel et al., 2013; Matson et al., 2013). By the late-1800s, increased demand for timber as wood fuel and for home construction, in-hand with forest clearing for crops and railroad construction, depleted forests and forever changed the landscape (Matson et al., 2013). Extensive human disturbance and significant droughts led to severe fires, of which, the impacts can still be seen today (Matson et al., 2013). Degradation of land and water quality led to the loss of many terrestrial and aquatic species, wherein, governmental intervention was necessary (Matson et al., 2013). In 1902, Michigan hired their first Forestry Warden and later established the Michigan Department of Conservation in 1921, to reduce exploitation of Michigan's natural resources (Matson et al., 2013). Though human development has forever changed the landscape and wildlife assemblages in the UP, timber management has shifted towards more sustainable practices (Hamel et al., 2013).

As of 2017, forested-land in Michigan has increased from 18 to over 20 million acres since the 1980 inventory, with nearly 19.3 million acres (95%) designated as 'timberland' for timber production (Pugh, 2018). In addition, of the forested landscape, approximately

43.7% is privately owned by families and individuals, which is greater than State of Michigan, USDA Forest Service, and other public group ownership combined (~38.1%; Pugh, 2018). According to a Michigan contributions' report by Leefers (2017), wood furniture and secondary paperboard and other paper products provided a combined 18,755 direct jobs and a direct output of over $6 billon in 2015. Furthermore, 5.9% of the 2015 manufacturing jobs in Michigan were in forest product industries, wherein, approximately one-third of these jobs were in the UP (Leefers, 2017). Recent inventories estimate that 45% of Michigan's forests exist across only 29% of its area in the Upper Peninsula (Pugh, 2018). To achieve sustainable forestry management in the UP, managers must consider the impacts their forest harvest will have on local floral and faunal communities by integrating biodiversity conservation into silvicultural prescriptions (Carey & Curtis, 1996; Smith et al., 2011). By fostering sustainability and resiliency through implementation of differing harvest techniques, we can ensure continued ecosystem function and subsequent services.

3.3 Silvicultural practices

3.3.1 Silviculture overview

Forest management by means of silviculture has become common practice throughout the United States (Baker, 1994; Franklin et al., 2002; Sharitz et al., 2002; Smith et al., 2011). As defined by the USDA Forest Service Manual (FSM, 2014), silviculture is "the art and science of controlling the establishment, growth, composition, health, and quality of forests and woodlands to meet the diverse needs and values of landowners and society on a sustainable basis" (p. 17). Prior to silvicultural treatment application, the landowner's objective(s) and goals are clarified (Leak et al., 2014, p. 2), then tailored to the appropriate scale (Franklin et al., 2002; Kern et al., 2014). For instance, regional-scale objectives may be to minimize loss of biodiversity within forested ecosystems and reduce the loss of invaluable ecosystem services, while maintaining productive forests and meeting regional timber needs (Crow et al., 2002; Seymour & Hunter, 1999). Though similar goals may be desired, stand-scale management may also focus on local economic value and wildlife management by industrial landowners, whereas private landowner objectives may be esthetics, recreation, or future income (Leak et al., 2014, p. 2). Furthermore, management applied at the patch- or gap-scale may include forest ground-layer vegetation health and diversity (Crow et al., 2002; Kern et al., 2006, 2014). Once objectives and spatial scale are established, managers must address, and incorporate, disturbances (e.g., human and natural) and species-specific natural histories into their planning (Leak et al., 2014, pp. 2 – 3).

Since forested ecosystems and their biodiversity are dependent upon the rotation period and severity of local natural disturbances (Hupperts, 2019; Seymour et al., 2002), historic disturbance regimes can serve as a reference to guide silvicultural prescriptions (Franklin et al., 2002; Hupperts et al., 2019; Zhang et al., 1999). For instance, wind and fire have played important roles in shaping the landscapes of the Great Lakes Region (Frelich & Lorimer; 1991; Hupperts et al., 2019; Zhang et al., 1999). Windthrow, for example, has shaped eastern hemlock (*Tsuga canadensis* (L.) Carrière) and white pine (*Pinus strobus*

L.) dominated northern hardwood forests throughout the UP (Hupperts, 2019; Whitney, 1987). Frelich and Lorimer (1991) estimated rotation periods of low windthrow to severer blowdown events (i.e., treefall to stand-leveling) ranging from 51 – 236 years across the Great Lakes Region, wherein, gap size determines species-composition and diversity by either promoting shade-tolerant species (within small, treefall gaps) or intolerant species (within large, blowdown gaps) (Hupperts, 2019; Kern et al., 2014). For example, hemlock-forests in the UP have persisted due to low severity, frequent windthrow occurrences (Frelich & Lorimer, 1991). In addition, fires throughout the area have also influenced the landscape by exposing mineral soil and decreasing sugar maple competition, recruiting species such as white pine, red oak, and paper birch (Frelich, 2002, pp. 33 – 34, 99). Forest composition and diversity throughout the Great Lakes Region have been driven by species-specific responses to historic fire and wind disturbance regimes (Frelich, 2002, p. 2; Frelich & Lorimer, 1991; Zhang et al., 1999); therefore, ecosystem-based management shaped by historic disturbance should serve as the philosophical basis of forest management in the UP.

Trophic cascades within forested ecosystems are infinitely complex and sensitive to both natural and anthropogenic disturbances, altering environment interactions and changing ecosystem function (Carey et al., 1999; Zhang et al., 1999, Zheng et al., 2000). For example, researchers have found that modified forest structure due to timber harvest, directly affects sensitive microclimates, which influence ecosystem function and structure by altering soil processes and vegetation diversity (Chen et al., 1999; Kern et al., 2014; Zheng et al., 2000). Furthermore, landscapes modified by extensive timber harvest no longer follow historic disturbance regimes (e.g., wind and fire), evermore changing local dynamics of a forest's ecology (Zhang et al., 1999). To minimize human-disturbance and foster complexity, forest managers may implement ecosystem-based management to emulate ecological processes and support long-term productivity and sustainability (Franklin et al., 2002; Raymond et al., 2009; Smith et al., 2011).

3.3.2 Silviculture in the UP

Throughout North America, forest management has shifted to more ecological-focused systems of timber harvest; the goals, of which, are sustainable forestry by emulating natural disturbance regimes that promote biodiversity (Kern et al., 2019; Seymour & Hunter, 1999; Seymour et al., 2002). For instance, as sustainability is at the core of silviculture's definition, silvicultural applications should strive to conserve local ecosystem services by either maintaining natural processing or restoring those which have been lost to anthropogenic stress (Kern et al., 2019; Seymour & Hunter, 1999). Though many silvicultural practices do not account for natural disturbances, creating homogenous stands which lack diversity (Franklin et al., 2002; Schulte et al., 2007), natural disturbance-based management (NDBM) attempts to mimic historic natural disturbance regimes (Kern et al., 2014, 2019; Raymond et al., 2009; Seymour et al., 2002). Application of NDBM was a focus during silvicultural management across Michigan Technological University's (MTU) experimental forest: the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED; Hupperts et al., 2020). Located in the Michigan's Upper Peninsula (Alberta, Michigan), both canopy regeneration methods and ground preparations emulating short-term historic wind and fire regimes and timber production practices used elsewhere were applied within the NHSEED to monitor the long-term effects and diversity of differing silviculture practices using NDBM and successful methods differing from common UP practices in northern hardwood forests (Hupperts et al., 2020).

3.3.3 Even-aged stands

Across the NHSEED forest, two even-age systems were employed – clearcuts and shelterwoods. Within stands containing 50 – 60% mature timber, clearcutting is an overstory removal of all merchantable and sub-merchantable trees > 2 in diameter at breast height (DBH; Leak et al., 2014, p. 15). When applying clearcut prescriptions, removal of stems < 2 in DBH is also recommended to provide high intensity ground disturbance (Leak et al., 2014, p. 15). True clearcutting favors early successional, shade intolerant species, such as pin cherry (*Prunus pensylvanica* L.f.) and paper birch (*Betula papyrifera* Marshall), 10 – 12 years post-harvest (Leak et al., 2014, p. 15). Clearcut stands across the NHSEED forest are approximately two acres each (Hupperts, 2019), classifying them as small patch clearcuts, according to Leak et al. (2014, pp. 4, 12); wherein, there was complete overstory removal and silviculture cleanup removing all hardwood saplings and seedlings < 5 cm DBH (Hupperts et al., 2020).

Considered a mid-intensity harvest, the additional even-age management applied at the NHSEED sites consisted of shelterwood regeneration methods. Shelterwoods retain differing basal areas (BA) or canopy density, providing seed trees and promoting seedling establishment and tolerant to mid-tolerant vegetation and tree species (Hupperts, 2019; Leak et al., 2014, p. 17). Approximately 5 – 15 years following the initial harvest, a second harvest removing residual canopy may occur within shelterwood regenerations to promote growth of established seedlings from the initial cut (Hupperts, 2019; Leak et al., 2014, p. 17). Using shelterwood regeneration methods, mature trees are retained as seed sources for the regeneration of preferred species after harvest disturbance (Leak et al., 2014, p. 17). Retained trees may also serve as shade and wind buffers (Hupperts, 2019; Hupperts et al., 2020; Raymond et al., 2009). Shelterwood regenerations also promote vertical and horizontal stand heterogeneity (Raymond et al., 2009). Throughout the NHSEED forest, two shelterwood regenerations were established, in which, ~ 30% of the canopy (i.e., shelterwood-low residual) and ~ 60% of the canopy (i.e., shelterwood-high residual) were retained (Hupperts, 2019; Hupperts et al., 2020). A second harvest is planned after regeneration of these stands is fully stocked in 2022 – approximately five years post-harvest (Hupperts et al., 2020).

3.3.4 Uneven-aged stands

Single tree selection was applied at the NHSEED forest as the uneven-age stand regeneration method and control. Single tree selection harvest is considered a low intensity ground disturbance method, wherein, trees ranging in diameter size are harvested over a 10 – 20-year rotation to maintain a predetermined stand BA (Hupperts, 2019; Hupperts et al., 2020; Leak et al., 2014, pp. 4, 14). Application of uneven-age management strategies support multiage stands (Raymond et al., 2009) of three or more age classes by retaining high crown canopy (Leak et al., 2014, p. 4), supporting tolerant species (Leak et al., 2014, pp. 4, 10, 27), while decreasing mid-tolerant species over time (Raymond et al., 2009). Single tree selection has become a common practice, resulting in homogenized landscapes across the Upper Great Lakes Region (Hupperts et al., 2019, 2020). Silviculture studies at the NHSEED sites established single tree selection regenerations as the "experimental control" due to its widespread application as the standard management operation in Michigan's Upper Peninsula (Hupperts, 2019; Hupperts et al., 2020). More recently, the long-term effects of single tree selection have prompted managers to apply alternative regeneration methods to minimize homogenization (Hupperts et al., 2020; Schulte et al., 2007), while encouraging disturbance-tolerant species with greater canopy and soil disruption during harvest (Raymond et al., 2009).

3.3.5 Ground preparations

In addition to differing canopy regeneration methods simulating commonly practiced timber harvest techniques, the NHSEED forest also applied ground-floor preparations to observe how both historic natural and anthropogenic disturbances (i.e., human disturbance by timber harvesting) effects forest health. Natural disturbances regimes throughout the Great Lakes Region include fire, windthrow, and blowdown (Hupperts et al., 2019; Schulte et al., 2007; Zhang et al., 1999). Such disturbances shape landscapes, alter ecosystems, and drive species diversity (Hupperts et al., 2019; Zhang et al., 1999). To better understand the long-term effects of windthrow and variable-intensity timber harvest on northern hardwood stand resilience and species diversity, tip-up mounds were created, and scarification used throughout the NHSEED sites to mimic both natural and human disturbances (Hupperts et al., 2020).

Natural disturbance, such as windthrow, creates gaps within forests, which are important for mid-tolerant to intolerant species' survival and diversity (Hupperts et al., 2020; Kern et al., 2014). In-hand with windthrow severity, tree size is a determinant of gap size, wherein, larger mature trees toppled by windthrow create larger gaps than smaller toppled trees, favoring shade-intolerant species (Frelich & Lorimer, 1991). However, common forest management styles (i.e., single tree selection) tend to select for large trees, resulting in smaller gaps during windthrow events (Neuendorff et al., 2007). Long-term application of systems, such as single tree selection, has led to homogenization of forested landscapes across northern hardwoods in the UP (Crow et al., 2002; Kern et al., 2014; Neuendorff et al., 2007; Schulte et al., 2007). To diminish these effects, tip-ups (i.e., mounds) have been experimentally applied to forested areas to emulate blowdown, creating gaps, soil disruption, leaf litter alteration, CWD, and browse protection (Hupperts et al., 2020; Kern et al., 2019). Within the NHSEED forest, tip-up sites were mechanically created throughout the differing canopy regeneration to mimic windthrow and inform managers how this natural disturbance historically shaped northern hardwood forests across the UP and restore diversity (Hupperts, 2019; Kern et al., 2019).

Additionally, mechanical scarification was also implemented across the NHSEED canopy regeneration methods to mimic intensive ground disturbance effects during harvesting

(Gauthier et al., 2016; Hupperts et al., 2020). For example, scarification removes the organic layer(s), displaces the leaf litter layer, and exposes mineral soil, which promotes the germination of species unable to penetrate deep leaf litter, such as yellow birch (*Betula alleghaniensis* Britt.; Gauthier et al., 2016; Hupperts et al., 2020). Furthermore, successful germination of the small-seeded (Hupperts et al., 2020), intermediate-tolerant yellow birch (Leak et al., 2014, pp. 2, 18) was observed within sugar maple dominated (*Acer saccharum* Marshall) microsites retaining high residual canopy cover, sufficient seed source, and treated by scarification across the NHSEED (Hupperts, 2019; Hupperts et al., 2020). Scarification during harvest is also used to remove undesired understory, promote softwood regeneration, prepare seed beds, and diversify species composition (Leak et al., 2014, pp. 13 – 14, 18, 25). Dependent upon the desired outcome, timing of scarification application – including masting events and snow-off or -on harvest – must be considered (Leak et al., 2014, pp. 13 – 14, 25). For instance, to promote softwood, Leak et al. (2014, p. 25) suggest removal of the understory and intense scarification in long strips during a seed crop to mimic softwood success along previous skid trails and cut roads. Though further studies are needed, scarification ground preparation during canopy regenerations can potentially create the heterogeneity necessary to promote species diversity (Gauthier et al., 2016), restoring species lost across northern hardwoods in the UP (Crow et al., 2002; Hupperts, 2019; Hupperts et al., 2020).

3.4 Effects of silvicultural practices on organismal diversity

3.4.1 Responses to forest disturbance

Severity of timber harvest practices vary greatly, with different wildlife species responding in equally variable ways to dissimilar silviculture practices. For example, meta-analyses conducted by Riffell et al. (2011), across the southeast and Pacific northwest, USA, and Verschuyl et al. (2011), across Norther America, observed limited responses (effects sizes) of forest amphibians, invertebrates, and reptiles to the removal of harvest residual biomass (i.e., woody debris). Reptile abundance and diversity, though limited in effect size, were observed to decrease with snag addition, while bird abundance and diversity increased, demonstrating possible prey-avoidance behavior by reptiles (Riffell et al., 2011). Further, in thinned and fuels-treatment thinned versus un-thinned forests, Verschuyl et al. (2011) observed a slightly positive to neutral response of all taxa's diversity metrics to managed forests; however, analyses of reptile and amphibian responses were conducted with effect sizes of less than 20 each.

Forest-dwelling plant and animal responses to anthropogenic disturbance are influenced by the magnitude of and time since the disturbance. Across multi-taxa in Europe, substrate-dependent species (i.e., saproxylic beetles, bryophytes, lichens, and fungi) increased in species richness within unmanaged forests due to stable conditions and heterogenous microhabitat availability; vascular plants, on the other hand, had greater species richness across managed forests (Paillet et al., 2010). For example, scarce, natural soil disturbances resulting in dead wood-presence (e.g., CWD, snags, mounds), greatly increasing bryophyte and lichen diversity, whereas, total species richness of understory vascular plants increased with frequent, more intense soil disturbances, including canopy regeneration methods and leaflitter removal (Paillet et al., 2010). Furthermore, Paillet et al. (2010) reported that effects size was significantly influenced by time since abandonment (TSA), in which, overall species richness was greater in managed than unmanaged forests in the first 20 years after harvest; however, 20 years post-harvest, unmanaged forests (> 20 years post-harvest) supported greater overall species richness than managed forests. In addition to TSA, intensity of the harvest also influenced species richness, wherein, clearcut sites with changes in tree species composition demonstrated the greatest difference from unmanaged forests (Paillet et al., 2010). Conversely, clearcut sites without changes to tree community composition displayed similar species richness to unmanaged forests (Paillet et al., 2010).

During timber management, soil biota communities are also variably impacted by disturbance intensity to the forest-floor. Following intensive canopy regeneration methods, such as clearcutting, soil organisms necessary for biological processes are reduced; however, such organisms are thought to recover gradually to their pre-harvest levels when left undisturbed by extended crop rotation lengths (Marshall, 2000). Therefore, Marshall (2000) suggests that extended crop rotations and/or shelterwood harvest with extend rotations may impact soil biota less drastically. Though forest-floor disruption is a byproduct of timber production, managers may also directly apply site preparations (i.e., ground-treatments) during harvest strategies. For example, at the surface soil-level, Mushinski et al. (2018) observed significantly different soil fungi communities and abundance of functional guilds – including guilds regulating soil temperature and nitrogen – within highly intensive-organic matter removal (OMR) ground-treatments, but no overall differences below 30 cm.

To further investigate short-term effects of habitat manipulation on forest-soil communities, Laigle et al. (2021) compared a 51-year-old mature stand (control) and two harvest treatments differing by high and low severity ground-floor treatments in Ontario, Canada. In this novel multi-trophic investigation, community composition was found to be influenced by bottom-up effects related to harvest intensity (Laigle et al., 2021). For six of the eight measured groups, total abundance was reduced throughout high intensity treatments (full-tree removal and complete removal of all organic matter and top 5 cm of mineral soil), while ground beetle and spider abundance increased within lower intensity treatments (full-tree removal followed by trenching and replanting) and rove beetles increased across high intensity sites (Laigle et al., 2021). Species at lower tropic levels were found to influence leaflitter decomposition and food web interactions, including prey availability (Laigle et al., 2021). Complex above- and below-ground interactions, disrupted by forest harvest, impact short- and long-term food and habitat availability to ground-dwelling organisms, comprising important functional guilds for forested ecosystem function and productivity (Dunham, 2008; Mushinski et al., 2018).

3.4.2 Timber harvest disturbance and small mammals

Global demand for timber products creates varying degrees of disturbance intensities across multi-biomes and ecosystems, altering habitat for forest-dwelling animals. Within forested ecosystems, ground-dwelling small mammals provide ecological services (Fischer et al., 2018; Greenler et al., 2019; Nocera & Dawe, 2008; Poe et al., 2019; Yamashina & Hara, 2019) and can serve as bioindicators of their habitats (Brown et al., 2020; Leis et al., 2008; McLaren et al., 1998; Pearce & Venier, 2005; Sullivan et al., 2011). Contributing to both top-down and bottom-up processes, many forest-dwelling small mammals have fast life history strategies and belong to ecologically important functional guilds, such as seed dispersers (Vander Wall, 2002; Vander Wall et al., 2005). Understanding how forest-dwelling small mammals respond to differing anthropogenic disturbances, by means of timber harvest, can provide valuable information for the maintenance of biodiversity in working landscapes (Brown et al., 2020).

Studies focused on intense forest management techniques and their effects on small mammals, such as clearcutting and/or wildfire, are well documented (see Bogdziewicz & Zwolak, 2014; Converse et al., 2006a, b; Fontaine & Kennedy, 2012; Kirkland, 1990; Sasmal et al., 2017; Sullivan & Sullivan, 2014; Sullivan et al., 1999; Zwolak & Foresman, 2007; Zwolak, 2009), while less intense treatments, such as shelterwood and selective harvest, are gaining interest (see Kalies & Covington, 2012; Kellner et al., 2013, 2016; Sullivan et al., 2001, 2005; Zwolak, 2009). Additionally, site preparations and small mammal responses are even less understood (see Balcˇiauskas et al., 2019; Martell, 1983; Paragi & Haggstrom, 2005; West et al., 1980; Zwolak et al., 2016). For example, Bogdziewicz and Zwolak (2014) concluded that clearcuts 0 – 20 years post-harvest had an overall positive influence on nine small mammal species abundance within temperate and boreal forests across Europe when compared to unharvested stands. When stands were grouped and analyzed in 10-year age classes, Zwolak (2009) observed a negative effect on three of eight North American small mammal species in clearcuts < 10 years old, whereas three of six species responded negatively to 10 – 20 year-old clearcuts. Across multiple forest ecological zones in British Columbia, Canada, mean total small mammal abundance, richness, and diversity increased within clearcuts that retained structural complexity on the forest floor, suggesting that canopy regeneration method effects on forest-dwelling small mammals may be mitigated by differing retention-levels of woody debris structures (Sullivan & Sullivan, 2014). In an earlier study by Sullivan et al. (1999), small mammal mean species richness was significantly greater in clearcut sites and lowest within clearcut-burned sites, and abundance of all species was either higher or remined the same in clearcuts, while diversity remained similar across all treatments in northern spruce-fir forests (hybrid Engelmann *P. engelmannii* Parry x white spruce, subalpine fir *Abies lasiocarpa* (Hook.) Nutt and lodgepole pine *Pinus contorta* Doug.). Furthermore, clearcuts which retain some structural complexity can support more abundant and diverse small mammal communities by providing habitat and food resources otherwise removed by fire regimes (Sullivan & Sullivan, 2014). The results of Sullivan et al. (1999) and Sullivan and Sullivan (2014) demonstrate the importance of studying small mammals throughout replicates across differing forest-types, ecological zones, harvest treatments, and study lengths.

Natural wildfire and prescription burning are additional disturbances which vary in intensity and influence on small mammal communities, alter habitat heterogeneity, and shape ecosystems (Zwolak & Foresman, 2007). For instance, after stand-replacing fire in

Montana, USA, rodent diversity was greater in unburned than burned sites during the first-year post-fire, while such differences were no longer observed two years after fire (Zwolak & Foresman, 2007). Across a range of fire-severity regimes, including low/mod- to high-severity, Fontaine and Kennedy (2012) observed marginally positive responses by small mammals 0 – 4 years after low/moderate-severity fire. Significant responses to low/moderate-severity fire were positive for four species and negative for one; additionally, only a single species response was obtained for high-severity fire – *Peromyscus maniculatus* –, which was significantly positive (Fontaine et al., 2012). In British Columbia, Canada, small mammal mean species richness was lowest within clearcut-burn treatments (3 – 8 years after harvest and 3 – 9 years post-burn), yet, species diversity was similar across uncut, clearcut, and clearcut-burn sites (Sullivan et al., 1999). Furthermore, when comparing three fuel-reduction harvest techniques (i.e., mechanical thinning, prescribed fire, or thinning and fire), short-term total small mammal biomass increased regardless of prescription (Converse et al., 2006a). Irrelevant of disturbance-intensity, rapid regeneration of ground-floor vegetation following fire, may expedite ground-dwelling mammal recolonization 0 – 10 years post-management (Fisher & Wilkinson, 2005), maintaining divergent small mammal communities for longer (Zwolak & Foresman, 2007).

Less intense regeneration management such as green tree retention (GTR), thinning, selective harvest, shelterwood harvest, and partial harvest are thought to maintain small mammal communities by mitigating harvest-disturbance effects (Bogdziewicz & Zwolak, 2014; Sullivan & Sullivan, 2014; Zwolak, 2009). For example, each-year following thinning treatments (six years total) in ponderosa pine forest (*Pinus ponderosa* P & C Lawson.), small mammal community composition differed, while total biomass and density remained the same; however, total species biomass and density were observed to increase after thinning (Kalies & Covington, 2012). Throughout coniferous and mixed forests in North America, Zwolak (2009) reported positive responses to partial harvest by all eight small mammal species reviewed. Additionally, a long-term study within large-scale, commercially thinned lodgepole pine (*Pinus contorta*) stands revealed mean total small mammal abundance to be similar across stands at both 2 – 10 years and 12 – 14 years post-harvest; however, treatment-type (thinning to densities of 500, 1000, and 2000 stems/ha; low, medium, and high, respectively), though significant for species richness and diversity two, three, and ten years post-harvest, had not significant effects on small mammal communities 12 – 14 years post-harvest (Sullivan et al., 2001, 2005). It seems that less intensive harvest practices support greater small mammal abundances though species richness and diversity differ in the short-term following harvest (i.e., 1 – 10 years post-harvest).

During timber management, heavy equipment causes extensive forest-floor disruption to ground- and soil-dwelling flora and fauna, which can be mitigated by winter-harvest to reduce ground and understory disturbance (Leak et al., 2014, p.27). In addition to burning or herbicide treatment, other silvicultural site preparations, such as mounding or scarification, are commonly applied to aid in seedling germination (Johansson et al., 2013). Scarification, however, is an intensive ground-floor disturbance by inverting soil-layers, removing horizontal habitat structures, such as CWD and/or leaflitter to reduce competition (Gauthier et al., 2016; Johansson et al., 2013). Although loss of structural heterogeneity tends to reduce small mammal diversity (Bunnell & Houde, 2010; Fauteux et al., 2012, 2013), very few studies have measured the direct responses of forest-dwelling small mammals to scarification-type treatments.

Small mammals, for example, were trapped across Lithuanian commercial fruit farms of varying agricultural and mowing practice intensities, resulting in reduced small mammal abundance and diversity within increased agricultural intensity (including scarification), in which, small mammal presence was undetected in the most intensely treated farms (Balcˇiauskas et al., 2019). Across replicates of closed-canopy and shelterwood European beach (*Fagus sylvatica*) stands, small mammal trapping was conducted four years post-scarification site treatments within half of the shelterwood sites in Poland (Zwolak et al., 2016). Abundance of yellow-necked mice (*Apodemus flavicollis*) responded positively to denser vegetation cover of shelterwoods, while bank vole (*Myodes glareolus*) abundance showed a strong negative response to scarification but not a clear effect of harvest-type, suggesting greater sensitivity of bank voles than yellow-necked mice to soil disruption (Zwolak et al., 2016).

Scarification may also be applied as a means of controlling small mammal pests acting as seed-predators (Hooven & Black, 1978). Scarification influences small mammal populations by strongly affecting food resource abundance (North & Greenberg, 1998) by promoting germination and colonization of disturbance-adapted ground-floor vegetation and fruiting- and flowering-plants (Greenberg et al., 2011). Prolific regeneration of such species results in high quality food patches important to a multitude of taxa within young, recently disturbed forests (Greenberg et al., 2011).

Forest-dwelling small mammals respond dissimilarly to harvest disturbance, wherein, the effect-magnitude is determined by the intensity of the management applied: as suggested by Zwolak's (2009) meta-analysis of small mammal responses to wildfire and timber harvest across North America. Stand productivity is drastically altered soon after disturbance, especially with increasing harvest intensity (Paragi & Haggstrom, 2005); however, early-successional and disturbance-tolerant species may be able to take advantage of newly available and abundant resources, such as hard and soft mast and pulse-driven prey-species, mitigating disturbance effects (Greenberg et al., 2007, 2011).

3.4.3 Small mammals provide ecological services

Invaluable ecosystem services, such as climate control, air-quality control, pollination, water filtration, even esthetic and spiritual value, all directly impact human well-being; yet human-caused disturbances continue to threaten ecosystem health by reducing biodiversity (Smith et al., 2011). Ecosystem functions are complex, involving below-ground organisms to apex-predators through trophic interactions. Across ecosystems, ground-dwelling small mammals play important ecological roles through differing functional guilds, directly impacting ecological services humans rely on (Lacher Jr. et al., 2019). For example, within temperate grassland ecosystems, herbivorous small mammals strongly influenced productivity and shaped producer communities by increasing plant species richness and diversity through mitigation of invertebrate herbivore and soil nitrogen effects (Poe et al., 2019). Furthermore, linked closely to prey-abundance, insectivorous masked shrews (*Sorex cinereus*) were observed in greater abundances within old-field habitat than adjacent hayfields in Novia Scotia, Canada; hence, Nocera and Dawe (2008) suggest that agriculturalists support shrew populations by providing old-field habitat within agroecosystems, benefiting from agricultural pest-control.

Like grassland and agroecosystems, forested ecosystems are significantly impacted by anthropogenic disturbance through overt-harvesting, influencing ecological services provided by forest-dwelling small mammals. Oak (*Quercus* spp.) establishment favors intermediate light availability and is predicted to respond positively to fire; however, granivorous, scatter-hoarding rodents are negativity impacted by habitat loss from fire and discontinuous understory vegetation within closed-canopy forests (Greenler et al., 2019). As such, Greenler et al. (2019) suggest a union of the oak-fire and oak-granivore conditional mutualism hypotheses by incorporating group shelterwood harvests and prescribed fire, which increases predator-risk of rodents by removing forest-floor cover within canopy-gaps, while supporting rodent populations in adjacent habitats to encourage mutualistic seed caching: both of which favor oak regeneration. Forests supporting insectivorous small mammals can also benefit from predator-control. For example, in Minnesota northern hardwoods, increasing earthworm biomass decreased understory herbaceous plant diversity and abundance (in 50% of plots), and seedling abundance and density in (in 75% of plots; Hale et al., 2006). To mitigate earthworm damage, forest managers could maintain mesic forest characteristics (e.g., moist environments, leaflitter, CWD), supporting insectivorous moles and shrews (i.e., *Blarina*, *Condylura*, *Cryptotis*, *Parascalops*, *Sorex*, and *Scalopus* spp.), which consume earthworms (Kurta, 2017). Small mammals that support forest health by providing ecological services, also serve as sentinels of ecosystem health as bioindicators (Brown et al., 2020; Pearce & Venier, 2005). Bioindicator species play important roles by identifying ecosystem stressors and guiding management decisions towards more sustainable harvest practices.

3.4.4 Forest-dwelling small mammals of the Great Lakes Region

3.4.4.1 Beneficial relationships

A once intact landscape of vast forests, human-caused disturbance has shaped the Great Lakes Region into an economy reliant upon agriculture, mining, timber and non-timber wood production, and tourism (Council of the Great Lakes Region [CGLR], n.d.). Ease of travel and an abundance of natural resources for trade, led to extensive early settlement across the area (Hamel et al., 2013; Matson et al., 2013). But unsustainable harvest of furbearers, timber, and minerals resulted in depleted ecosystems and homogenized landscapes (Hamel et al., 2013; Matson et al., 2013); centuries later, the long-term effects are still observed across taxa today. The Great Lakes Region is home to two Orders, encompassing seven Families of terrestrial and arboreal small mammals (≤ 1,100 g for our review; Kurta, 2017), wherein, relationships – both beneficial and detrimental – between forested ecosystems and forest-dwelling small mammals are well documented.

Beneficial relationships and functions provided by small mammals include; seed dispersion (Kellner et al., 2016; Steele et al., 2001, 2014; Vander Wall et al., 2005), fungal dispersion (Izzo et al., 2005; Maser et al.,1978; Pyare & Longland, 2001, 2002), soil aeration (Bakker et al., 2004; Hole, 1981; Laundré & Reynolds, 1993), pest-control (Hale et al., 2006; Larsen et al., 2018; Liebhold et al., 2000, 2005; Muzika et al., 2004), prey-sources (Carey et al., 1992; Fryxell et al., 1999; Weigl, 2007), and bioindicators of ecosystem health (Bowman et al., 2005; McLaren et al., 1998; Pearce & Venier, 2005). Consisting of nine species throughout the Great Lakes Region (Kurta, 2017), squirrels and chipmunks (Family Sciuridae) fulfill multiple roles within forested habitats: seed dispersion and caching of oak (*Quercus* spp.) acorns, supporting germination (Steele & Smallwood, 2002; Vander Wall et al., 2005); symbiotic relationships between fungi species and canopy trees, supporting stand health (Maser & Maser, 1988); and as prey to aerial and terrestrial predators (Carey et al., 1992; Fryxell et al., 1999; Weigl, 2007). For example, mutualistic relationships between scatter-hoarding granivores within oak, hardwood forests have been observed to increase germination when cached (e.g., stored) acorns are not recovered and remain buried (Steele & Smallwood, 2002; Vander Wall, 2001); however, this relationship seems to be oak species- and habitat-specific (Kellner et al., 2016; Steele et al., 2001, 2014).

Additionally, dispersal-obligate fungal species (i.e., underground fruiting bodies of hypogeous fungi and truffles) symbiotic to forest dynamics, rely on dispersal and germination through digestion of mycophagous small mammals (Johnson, 1996; Trappe & Maser, 1976; Maser et al., 1978) – particularly *Glaucomys* species (Izzo et al., 2005; Pyare & Longland, 2002). Northern flying squirrels (*Glaucomys sabrinus*), for instance, are extremely sensitive to habitat disturbance, relying on old-growth forest characteristics (e.g., legacy retention and snags; Carey, 2000; Carey et al., 1999; Weigl, 2007), wherein, they have been observed to associate with fine-scale habitats containing high abundances of truffles (Pyare & Longland, 2002). Furthermore, squirrels serve as an important prey-base for forest-dwelling avian predators, such as the endangered spotted owl (*Strix occidentalis caurina*; Carey et al., 1992) and other raptors (Jaksic et al., 1996, 1997), and terrestrial fishers (*Pekania pennanti*; Weigl, 2007) and American martens (*Martes americana*; Fryxell et al., 1999).

Burrowing and tunneling small mammals provide soil-services within ecosystems (Bakker et al., 2004; Hole, 1981), which includes 12 species of moles and shrews (Order Soricomorpha) and eight species of voles and lemmings (Rodentia: Cricetidae) – specific to the Great Lakes Region (Kurta, 2017). Due to their below-ground ecology and larger sizes, the hairy-tailed mole (*Parascalops breweri*), eastern mole (*Scalopus aquaticus*), and the star-nosed mole (*Condylura cristata*) all predate on and control invasive species, such as earthworms (Catania, 2008; Kurta, 2017, pp. 51 – 59). Similarly, the northern short-tailed shrew (*Blarina brevicauda*) is the largest North American shrew (Kurta, 2017, p. 48) and venomous, paralyzing prey for caching (Kita et al., 2004). Furthermore, above-ground pest control has been observed by *Peromyscus* species, which predate on gypsy moth pupae (*Lymantria dispar*), shaping moth dynamics within low-density populations (Larsen et al., 2018; Liebhold et al., 2000, 2005). Intense forest management – often used in oak regeneration (Larsen et al., 2018) – seems to favor disturbance-tolerant *Peromyscus* species in the short-term (Greenberg et al., 2006). Pest-control provided by these species is invaluable within economically important hardwood forests managed for sustainable timber and non-timber wood products, in which, invasive earthworms affect forest productivity by reducing herbaceous species richness and diversity and sapling survival (Hale et al., 2006), and gypsy moths causing high mortality rates of oak trees through defoliation (Larsen et al., 2018).

Throughout the Great Lakes Region and beyond, southern red-backed voles (*Myodes gapperi*) and *Peromyscus* species are abundant and well-studied species (e.g., Boonstra & Krebs, 2012; Bowman et al., 2008; Cramer, 2014; Sasmal et al., 2017; Tisell et al., 2019; Wolf 1985); they also serve as prey-base to both common (coyotes, foxes, and weasels; Kurta, 2017) and economically important carnivores, such as fisher (Jensen et al., 2012; Kirby et al., 2018) and martens (Andruskiw et al., 2008; Hales et al., 2008; Jensen et al., 2012; Kurta, 2017, p. 225). Red-backed voles and flying squirrels also serve as bioindicators of habitat quality. For example, both species are often defined as indicators of mature forest across differing habitat-types in Ontario, Canada (McLaren et al., 1998). To further test feasibility of voles as bioindicators, Pearce and Venier (2005) conducted three years of forest, stand habitat features, and small mammal surveys, resulting in strong habitat association observations for voles and deer mice (*Peromyscus maniculatus*). However, strong temporal population fluctuations, along with the lack of knowledge of compounding forest harvest effects (e.g., canopy regeneration methods and ground-floor preparation intensity, herbicide application, fire, rotation time; Raybuck et al., 2012), suggest the need for a more holistic examination of disturbance impacts.

Flying squirrels are another bioindicator species, sensitive to climate change and human-disturbance (Bowman et al., 2005; Smith, 2012; Weigl, 2007). Loss of mature canopy and legacy retention habitats, by harvest-disturbance, have significantly reduced protection from predators, den sites, and food resources, while creating fragmentation and reducing gliding ability (Smith, 2007, 2012). Furthermore, Bowman et al. (2005) observed a north-south latitude threshold, of which, low temperatures and failed mast events resulted in an energetic bottleneck, causing southern flying squirrels (*Glaucomys volans*) to increase their northern expansion by more than 200 km. Competition from range overlap between the two species has not been observed, however, parasitism (*Strongyloides robustus*), presents as benign in most squirrels, in including southern flying, yet causes high mortally of northern flying squirrels (Espenshade & Stewart, 2013).

3.4.4.2 Detrimental relationships

Though regional small mammals provide many beneficial ecological services, they can also be detrimental as seed predators (Kellner et al., 2016; McShea, 2000; Steele et al., 2001; Ostfeld et al., 1996), nest predators (Schmidt et al., 2008; Schmidt & Ostfeld, 2008; Yahner, 2003), and zoonotic hosts (Ostfeld & Keesing, 2000; Perz & LeBlancq 2001; Scheidler et al., 2006). For instance, eastern gray squirrels (*Sciurus carolinensis*) were observed to be influential in dispersing and caching red oak (*Q. rubra*) acorns, with embryo excision < 4%; yet, greater than 70% of white oak (*Q. alba*) acorns recovered were excised and less than 3% of those cached germinated (Steele et al., 2001). Similarly, the eastern chipmunk (*Tamias striatus*) and white-footed mouse (*Peromyscus leucopus*) rely on acorns as a primary food source (Kellner et al., 2016; McShea, 2000). Oak regeneration practices tend to include scarification or burning to be successful (Greenler et al., 2019; Raybuck et al., 2012); however, gypsy moth invasions continue to defoliate oaks. Short-term responses to successful oak regeneration result in greater mast abundance, giving rise to increased small mammal abundances, leading to greater moth pupae predation-events (Elkinton et al., 1996). Yet, despite mice seeming to reduce gypsy moth pupae, oak forests will continue to be parasitized without long-term intervention (Muzika et al., 2004). Additionally, increased small mammal abundance in response to successful mast production, leads to incidental predation on non-pest species, such as ground- and low-nesting birds (Schmidt et al., 2001, 2008; Schmidt & Ostfeld, 2008; Yahner, 2003). Furthermore, increased small mammal populations heightens opportunities for human-small mammal-interactions, resulting in greater risks of zoonotic disease transmission (Moscarella et al., 2019; Myers et al., 2009; Roy-Dufresne et al., 2013).

Common small mammals across the Great Lakes Region serve as reservoirs and/or hosts to several concerning zoonotic diseases, including West Nile virus and Encephalitis, which are both transmitted by the mosquito species *Aedes triseriatus* ((Say); Scheidler et al., 2006). West Nile was first reported in North America in 1999 and in Ohio in 2001, while Encephalitis was first observed in Wisconsin in 1964 (Scheidler et al., 2006). In addition, Cryptosporidium is spread via fecal-oral route through ingestion of contaminated water (Perz & LeBlancq, 2001; Ziegler et al., 2007). Furthermore, Cryptosporidia are a waterborne parasitic protozoan, associated with watershed ecosystems, and an obligate parasite, requiring a host to complete its life-cycle (Ziegler et al., 2007). Two species of Cryptosporidia (*C. parvum* and *C. hominis*) have been reported within New York and New York City water-sources (Ziegler et al., 2007). Though host-specific strains were observed by Ziegler et al. (2007), most are generalists, utilizing small mammal reservoirs, regardless of species (Perz & LeBlancq 2001; Scheidler et al., 2006).

A widespread, tick-borne disease of great concern within the Great Lakes Region and United States is Lyme disease (Ostfeld & Keesing, 2000). Transmitted through the bite of an infected tick (*Ixodes scapularis* or *I. pacificus*), this bacterium's (*Borrelia burgdorferi*) principal reservoir is mice – predominantly *P. leucopus* (Guerra et al., 2002; Larson et al., 2018; Ostfeld & Keesing, 2000; Roy-Dufresne et al., 2013). *Ixodes* tick densities have been observed with similar habits associations across endemic areas: deciduous, dry mesic forests in Wisconsin and Illinois (Guerra et al., 2002); low forest cover near high urbanization in New York (Khatchikian et al., 2012); and dense understory in Ontario, Canada (Clow et al., 2017). Similarly, densities of white-footed mice were considerably greater within woodlots than continuous forests across eastern and central North America, suggesting that lack of predators and competition, and abundant food resources, supports this species within forest-patches (Nupp & Swihart, 1996, 1998).

Abiotic factors, such as temperature, precipitation (Burtis et al., 2016; Clow et al., 2017; Khatchikian et al., 2012), and elevation influence *Ixodes* species densities (Clow et al., 2017). For example, temperatures between 0 and 25 ℃ increased movement of *Ixodes* species (Burtis et al., 2016; Clow et al., 2017), whereas temperatures above 25 ℃ reduced nymph questing (i.e., movement; Burtis et al., 2016). Further, during hot (> 25 ℃), dry, summer weather in New York, questing of established populations was reduced, while questing-behaviors within new populations were not (Burtis et al., 2016). However, during extreme summer weather, nymph-burden on small mammal hosts (*P. leucopus* and *Tamias striatus*) were not reduced, regardless of population status (i.e., established or new; Burtis et al., 2016). As climate change produces shorter and milder winters across the range of *Ixodes* ticks, range-expansion (Khatchikian et al., 2012; Roy-Dufresne et al., 2013) and species evolution (Johnson et al., 2017; Hersh et al., 2014) coincide.

Range-expansion of both disease-transmitting ticks (Khatchikian et al., 2012) and their predominant hosts, white-footed mice (Roy-Dufresne et al., 2013), have led to reports of co-infection agents (Hersh et al., 2014) and new bacterium members (Johnson et al., 2017). In New York, Hersh et al. (2014) observed common co-infections of human granulocytic anaplasmosis (*Anaplasma phagocytophilium*) and human babesiosis (*Babesia microti*) in small mammals, not including squirrels. Both are transmitted by *Ixodes* species and can increase health-risk severity in humans when co-infected with Lyme or one another (Hersh et al., 2014). In 2016, Johnson et al. (2017) isolated the first record of *Borrelia mayonii* in Wisconsin and Minnesota: another bacteria spread by Ixodes ticks, causing Lyme disease. Rapid poleward expansion of white-footed mice, due to more favorable conditions, was projected by Roy-Dufresne et al. (2013) to expand northward 3° latitude by 2050, subsequently, spreading Lyme disease throughout unimpacted northern regions and impacting public health.

3.5 Management concerns for northern hardwood small mammals

3.5.1 Information gaps and conclusions

Peer-reviewed literature of small mammals and their habitats across the Great Lakes Region has been well documented; however, as new silvicultural techniques and anthropogenic disturbance continues shaping landscapes, persistent monitoring is necessary. Small mammals provide important ecological services (Lacher Jr., et al., 2019) and respond variably to differing degrees of habitat-disturbance (Zwolak, 2009). For example, Zwolak (2009) suggests that the magnitude of responses by small mammals is strongly influenced by disturbance-type, which was ranked as mild, moderate, and severe: partial harvest, clearcutting, and stand-replacing fire, respectively. To mitigate the effects of intensive canopy regenerations (e.g., clearcutting) or prescribed fire on forest-dwelling small mammals, many studies recommend the retention of woody debris or other structural complexes within these sites (Converse et al., 2006b; Sullivan & Sullivan, 2014); though Fritts et al. (2017) cautions that inconsistent relationships between small mammal abundances and woody debris volume retention may be driven by species-specific responses, and should not be applied generally. Furthermore, as small mammals can serve as bioindicators of forest health (Klenner & Sullivan, 2009; Pearce & Venier, 2005), quality of small mammal habitats are often measured by habitat indices (Corry & Nassauer, 2005; Jorgensen, 2002). Though such indices may be useful for landscape pattern comparisons, they should be used cautiously when making ecological inferences (Corry & Nassauer, 2005) and can be improved by applying appropriate spatio-temporal scales and species-specific ecologies (Jorgensen, 2002, 2004; Wang et al., 2012).

Much of modern forestry strives to maintain biodiversity by implementing natural disturbance regimes to develop resiliency and restore natural process, in-turn, supporting sustainable ecosystem services and goods, while ensuring continued economic services (Bengtsson et al., 2000; Kern et al., 2019; Zhang et al., 1999). Though forest harvest by means of natural disturbance-based management (NDBM) may be an improvement towards sustainable management, Drever et al. (2006) suggests that managers must understand how harvest techniques, which select for only "desired" states, impact slow ecosystems process and the stand's ability to recover after disturbance. For example, to evaluate efficacy in maintaining biodiversity, Wilson and Carey (2000) sampled small mammals across two differing management strategies, commonly applied to promote late-seral attributes in second-growth forests; however, neither application was found to support typical communities within late-serial forests. As NDBM attempts to mimic historic disturbance-regimes by implementing anthropogenic disturbance, further research is necessary to understand small mammal responses to applied-mimicking. For instance, both Sullivan et al. (1999) and Zwolak (2009) reported that small mammals did not respond equivalently to timber harvest strategies used to mimic natural disturbance, such as clearcutting to mimic burning, or clearcutting followed by burning to mimic stand-replacing wildfire.

Small mammals respond variably to differing disturbance-types and intensities. Species-specific responses suggest there is no one-size-fits-all management style to maintaining biodiversity. The need for long-term studies across various landscapes and harvest practices is necessary for understanding the short-, long-term, and compounding effects that forest management has on small mammal communities. Throughout the Great Lakes Region, experimental forests can provide important, long-term replicates to observe and project how climate change, and other human-caused disturbances, may affect these ecosystems using a holistic approach. Though the literature is vast with studies observing small mammal responses to differing silviculture techniques, the following research is lacking for small mammals across the Great Lakes Region:

- Pre-harvest small mammal data to observe changes in metrics before and after disturbance
- Long-term studies to observe changes in small mammal metrics across time
- Long-term studies to observe compounding effects of multi-harvest treatments within a single-study on small mammals (i.e., differing canopy regenerations and forest-floor preparations and canopy/forest-floor treatment combinations)
- Silvicultural canopy regeneration and site preparation replications within the same study to observe disturbance effects on small mammals within a single ecosystem

- Research on small mammal responses to commonly applied forest-floor treatments within NDBM stands (i.e., mounds, tip-ups, scarification)
- Studies using multi-scale approaches to understand how small mammals utilize habitats at differing scales
- Research focused on understanding cryptic small mammal species
- Peer-reviewed studies utilizing experimental forests to document short-and long-term small mammal responses to human-caused disturbance within a semi-controlled forest
- Climate change modelling of responses, including distributions, by small mammals across time and space
- Holistic approach to understanding small mammal responses of varying magnitude
- Peer-reviewed studies reporting multiple small mammal metrics (i.e., richness, diversity, evenness, abundance)
- More peer-reviewed studies on less prominent or emergent zoonotic diseases affecting Great Lakes public health
- Updated small mammal inventories

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4 Supplemental material

Supplemental Table 1. Habitat selection features of the 23 possible species to encounter at the Northern Hardwood Silviculture Experiment to Enhance Diversity (NHSEED) sites and their final Total captures, Alberta, Michigan in 2019.

Scientific name	Common name	Species code	Total captures	Habitat features	References
Sorex arcticus	Arctic shrew	SOAR	2	moist areas adjacent to water; occasionally found in dryer woodland-edges and fields	Kurta, 2017, p. 26; Naughton, 2012, p. 259
Sorex cinereus	masked shrew	SOCI	4	moist areas with abundant cover and leaf litter; recorded in restored prairie and wetlands	Kurta, 2017, p. 30; Harder et al., 2014
Sorex hoyi	pygmy shrew	SOHO	0	heavily ground-covered, moist boreal habitats of varying vegetation cover; observed generalist behaviors	Kurta, 2017, p.36; Stephens and Anderson, 2014
Sorex palustris	American water shrew	SOPA	0	areas of extensive cover near standing and moving water; observed in moist habitats with no open water	Kurta, 2017, p. 41; Naughton, 2012, p. 279
Blarina brevicauda	northern short-tailed shrew	BLBR	17	cool, moist microhabitats with thick leaf litter and CWD; locally found in mixed and deciduous woodlands	Kurta, 2017, p. 48; Naughton, 2012, p. 253
Condylura cristata	star-nosed mole	COCR	0	water-saturated soils along fields, woods, swamps, and waterways; recorded in dry uplands and seasonally wet areas	Kurta, 2017, p. 58; Naughton, 2012, pp.292-293
Microtus pennsylvanicus	meadow vole	MIPE	1	moist, grassy meadows, marshes, and bogs; prosperous in open forest edges and pasture lands	Kurta, 2017, p. 172; Naughton, 2012, pp. 150-151
Myodes gapperi	southern red-backed vole	MYGA	150	mixed forests with moist habitats, deep leaf litter, and LWD; habitat generalist with water availability	Fauteaux et. al, 2013; Kurta, 2017, p. 160; Naughton, 2012, p. 165
Mus musculus	house mouse	MUMU	0	abundant near agricultural land and buildings; highly associated with human-food resources	Kurta, 2017, p. 185; Naughton, 2012, p. 202
Peromyscus leucopus	white-footed mouse	PELE	131	diverse habitats associated with understory vegetation, distributing further north annually due to climate change	Kurta, 2017, p. 151; Stephens and Anderson, 2014; Myers et al., 2009
Peromyscus maniculatus	deer mouse	PEMA	128	extensive ranges across diverse habitats; positive correlations to mixed forest live tree basil area and CWD	Naughton, 2012, pp. 195-196; Stephens and Anderson, 2014
Napaeozapus insignis	woodland jumping mouse	NAIN	0	cool, moist areas within mixed or purely deciduous forests; associated with abundant cover, rocks, and CWD	Kurta, 2017, p. 193; Naughton, 2012, p. 109
Zapus hudsonius	meadow jumping mouse	ZAHU	38	moist, grassy meadows with dense vegetation for travel to water; habitat quality more important than habitat-type	Naughton, 2012, p. 112; Urban and Swihart, 2009
Rattus norvegicus	Norway rat	RANO	0	strongly associated with humans, especially areas of poor sanitary conditions	Kurta, 2017, p. 189; Naughton, 2012, p. 205
Synaptomys cooperi	southern bog lemming	SYCO	5	moist, grassy areas near bogs, swamps, and streams; observed in pastures, grasslands, and clearcuts due to competition	Kurta, 2017, pp. 181-183; Naughton, 2012, pp.179-180

Tamias minimus	least chipmunk	TAMI	0	woodland edge habitats in disturbed areas of boreal and open forests; interspecific competition in forested areas	Kurta, 2017, p. 110; Naughton, 2012, pp.69-70
Tamias striatus	eastern chipmunk	TAST	32	deciduous forests with dry areas and cover-features; opportunistic of clearcuts and small wooded and brushy areas	Kurta, 2017, p. 114; Naughton, 2012, pp.73-74
Glaucomys sabrinus	northern flying squirrel	GLSA	0	old-growth forests for denning, travel, and food resources; keystone species due to seed and symbiotic spore dispersal	Naughton, 2012, p. 21; Smith, 2012
Glaucomys volans	southern flying squirrel	GLVO	0	various habitats of open, mixed forests with thick shrubs for groundcover; overlap with northern species due to climate change	Kurta, 2017, p. 137; Naughton, 2012, pp. 24-25
Ictidomys tridecemlineatus	thirteen-lined ground squirrel	ICTR	0	dry, short-grass, open and grazed areas; vegetation easily seen over without standing uprights	Kurta, 2017, p. 121; Naughton, 2012, p. 64
Sciurus carolinensis	eastern gray squirrel	SCCA	0	mature hardwood stands and dense woodlots with seed- and nut-bearing trees; reliant on large trees for winter denning	Kurta, 2017, p. 125; Naughton, 2012, p. 41
Sciurus niger	eastern fox squirrel	SCNI	0	ground-dwelling in open forests, woodlots, and field edges with sparse understory; observed in urban areas	Kurta, 2017, p. 128; Naughton, 2012, p. 45
Tamiasciurus hudsonicus	red squirrel	TAHU	0	dense, boreal coniferous forests for travel, safety, and conifer seeds and fungi; reported in mixed forests and urban areas	Kurta, 2017, p. 131; Naughton, 2012, p. 82