LIMITATIONS OF FOREST OVERSTORY COMPOSITION AND AGE AS PROXIES FOR HABITAT IN A HARVESTED BOREAL FOREST

By

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"To keep every cog and wheel is the first precaution in intelligent tinkering."

Aldo Leopold, *A Sand County Almanac (1949)*

ABSTRACT

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Despite the importance of wildlife habitat protection in meeting land use management objectives, criteria for habitat identification are surprisingly amorphous. For example, while much current habitat modeling has tended to avoid the term "niche modeling," niche assumptions are implicit – the presence of predators and competitors is essential to whether or not a species uses, or will use, an area. Nonetheless, there are species for which important elements of niche are not generally associated with legal interpretations of their "habitat". Woodland caribou (*Rangifer tarandus caribou*) are one such example. The range of the forest-dwelling ecotypes of woodland caribou has been declining in Canada since at least the late 1940s, and woodland caribou were assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada and were listed under the Federal Species at Risk Act in 2003. They are also protected under Ontario's Endangered Species Act (2007) and other provincial and territorial legislation. The consequences of management decisions, and the lens through which these decisions are assessed, have been intensified due to these legal implications.

Most current research supports the hypothesis that higher predation is the key factor in decline and that larger wolf (*Canis lupus*) populations are due to increased abundance of early seral stage, forage-rich hardwood and mixedwood forests, created largely by logging, which support additional prey for wolves, including moose (*Alces alces* L.). While predators and apparent competitors appear to play a primary role in habitat selection by caribou, habitat modeling generally relies on forest overstory and age as a surrogate for predator avoidance. Yet, how well these models correspond to caribou, wolf, and moose use is largely unknown. Legal interpretations of protection rest primarily on interpretations of forest overstory and age, making explicit only the importance of forest disturbance.

Here, I tested the ability of forest resource inventories (FRI), a key tool in identifying and quantifying wildlife habitat in forest management, to assess 3 key elements associated with caribou winter habitat: lichen, regenerating understory and predator use. I assessed the presence of *Cladonia* lichen, an important winter forage species for woodland caribou, using stand characteristics provided in FRIs. Further, I used ground data collected from regenerating areas (2009-2010) of previously conifer-dominated forests in northwestern Ontario, Canada, 10 and 30 years after logging, and 10 and 30 years after fire, to test if understory development and moose forage abundance differed between the two disturbance types and artificial or natural regeneration approaches. In addition, I used winter aerial surveys (2010-2013) and logistic regression to compare the characteristics of a conventional habitat model (forest overstory composition and age) to other habitat characteristics (and/or their surrogates). I also applied a novel approach

for Structural Equation Modeling (SEM) to explore causal and indirect caribou habitat relationships at broad and fine scales.

I found FRI was not capable of accurately predicting understory vegetation, specifically *Cladonia* lichen, in spite of the ability of field-based data using the same characteristics providing strong prediction. Further, I found understory composition varied significantly depending on post-harvest regeneration approach. Abundance of shrubs, as well as herbaceous plants (forage for apparent competitors for woodland caribou), was greater in naturally-regenerated post-harvest stands than similarly aged fire origin or post-harvest stands that used more intensive regeneration approaches. And lastly, I found that older, conifer forests alone, as depicted in FRI, did not provide good predictive capabilities of caribou use at broad scales.

While conventional models based on forest overstory composition and age may be useful as a coarse filter in interpreting caribou habitat, more attention should be given to their limitations in landscapes changed by industrial development, particularly where road networks are likely to facilitate predator access and the identification of such habitat has legal implications.

Keywords: boreal forest; woodland caribou; habitat models; overstory composition; Forest Resource Inventory; apparent competition; timber harvesting

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FIG. 3.3
As Fig. 3.2 except that ordination is for percent groundcover composition on (A) 10-year-old stands ($n = 60$), and (B) 30-year-old stands ($n = 60$) in northwestern Ontario, Canada. Groundcover classes were: vascular plants, moss, lichen, rock, exposed soil/litter, and coarse woody debris (CWD). Axes 1–3 (NMS 3-dimensional solution) had an R^2 of 0.931 cumulatively (0.504, 0.220 and 0.207, respectively) for 10-year-old stands and Axes 1 and 2 (NMS 2-dimensional solution) had an R^2 of 0.857 cumulatively (0.265 and 0.591, respectively) for 30-year-old stands.

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FOREWORD

       Throughout the thesis I use the first person singular, however, I acknowledge the contributions of members of the supervisory committee and the assistance of field technicians and volunteers. Of special note, the contributions of Dr. Brian McLaren and Dr. Jay Malcolm are recognized through co-authorships of related publications. Their review and advice was critical in achieving publication. However, as lead author, I developed the study design, organized and conducted the field studies, chose appropriate statistical techniques, analyzed and interpreted all data, wrote first drafts of the manuscripts, and produced subsequent drafts during the course of the review process.

Chapter 1: IDENTIFICATION OF HABITAT

The identification of habitat is a cornerstone of wildlife management. The field has been evolving for almost a century: Grinnell (1917), Leopold (1933), Hutchinson (1957), Daubenmire (1968), and Odum (1971) defined habitat in various ways. Originally, habitat was defined as a combined consideration of the resources required by an individual or population and the ability to compete with neighboring individuals or other species in the area. Yet, despite the frequent use of this definition by both scientists and land managers, and ongoing attempts to provide clarity (e.g., Whittaker et al., 1973; Hall et al. 1996), the meaning of the term "habitat" remains fairly amorphous, spanning a gradient from Hutchinson's (1957) classic niche-based definition to a definition restricted to the food resource consumed; from a broad, landscape-scale description of vegetation to detailed representations of a population's immediate physical environments and their observed use; from habitat as a "place" to habitat as a "state", reflecting resources and conditions present, which are dynamic over time and space (Gaillard et al., 2010; Block & Brennan, 1993).

While much current habitat modeling has tended to avoid the term "niche modeling", niche assumptions are implicit—meaning that the actions of predators and competitors are essential to whether an individual uses an area. If observed species distributions are already constrained by biotic interactions and limiting resources, these models are *de facto* quantifying Hutchinson's realized niche of species, albeit their distributions are temporally and spatially variable (Guisan, 2005).

The manner in which habitat is defined has important implications for habitat management, particularly for species at risk. For example, the loss or degradation of habitat is the central cause of declining numbers for many endangered species (Kerr et al., 2004; Venter et al., 2006). Protection of habitat has been a key objective of resources management strategies, in some cases, for several decades. The purpose of protecting habitat is to ensure species persistence, which implies that habitat is defined from the perspective of successful survival and reproduction. Clearly, where protection of habitat is intended to support species persistence, habitat and fitness (i.e., higher survival and reproduction rates) are necessarily linked. Habitat has been defined as an area with the combination of resources (e.g., food, cover, water) and environmental conditions (e.g., temperature, precipitation, presence or absence of predators and competitors) that promotes occupancy by individuals of a given species and allows those individuals to survive and reproduce (Caughley & Gunn, 1996; Morrison et al., 2002). Habitat selection can be viewed as a hierarchical process that involves both innate and learned behavioral decisions made by an animal regarding which environmental space to use (Hutto, 1985). Selection is inferred when an animal (or species) uses a habitat disproportionally to its availability (Krausman, 1999). Biologists assume an individual preferentially uses a habitat that maximizes fitness, as selection is ultimately based on survival and subsequent reproductive success (Hilden, 1965). Therefore, habitat selection can be linked to population-limiting factors (Rettie & Messier, 2000). However, since habitat selection is a result of complicated, unobservable processes driven by

physiological, behavioral and energetic constraints and demands, it can only be

measured by proxy (Aarts, 2007). And as a proxy, there are implications that

should be considered when assuming the provision of habitat defined in this

manner will support species' long-term survival.

The importance of successfully understanding "habitat" and all that it

entails is essential for populations that are considered "at risk" (i.e., species that

may become extirpated or extinct if factors leading to their decline are not

reduced). Inaccurate ecological definitions of habitat for species at risk have

contributed to court battles (e.g., regarding protection of forests in the US Pacific

Northwest), and "do-not-buy" campaigns (i.e., politically-driven movements that

discourage the purchase of products from corporations deemed to damage a

species' habitat; e.g., Jang, 2013). Designations of habitat for species at risk, such

as for woodland caribou (*Rangifer tarandus caribou*), have received much

attention in both scientific and policy realms.

The range of the forest-dwelling ecotypes of woodland caribou has been

declining in Canada since at least the late 1940s (deVos & Peterson, 1951;

Schaefer, 2003), and woodland caribou were assessed as "Threatened" by the

Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2002).

They were re-listed under the Federal Species at Risk Act (SARA) in 2003. While

the causes for range recession are thought to be multifaceted, a close correlation

exists between the recession of woodland caribou and the northward progression

of timber harvesting and associated road development in Ontario, Canada

(Schaefer, 2003; Vors et al., 2007). Many features have been shown to effect

habitat selection, including food availability (Schaefer, 1988), snow conditions (Brown & Theberge, 1990), harvesting by humans (Edmonds, 1988), and insect harassment (Downes et al., 1986); however, predation is considered in much of Canada to be the primary limiting factor for woodland caribou (Bergerud & Elliot, 1986; Seip, 1992; Stuart-Smith et al., 1997; Rettie & Messier, 1998; Wittmer et al., 2005).

Forest overstory composition as a proxy for woodland caribou habitat has been a focal point for natural resource management in Canada's boreal forest in recent decades, particularly in the realm of forests managed for timber harvest. The decision in favor of this approach was a pragmatic one, because the nature of the forest, both with respect to tree species composition and other stand characteristics, such as their age, stocking, and site class, are fundamental features considered in forest management decisions and forecasting. These same features are, of course, important in determining the conditions to which species respond, and can reasonably be thought of as proxies for habitat (Rettie et al., 1997). For example, caribou tend to use older forests with conifer-dominated overstory more frequently than other vegetation types (Hins et al., 2009).

However, such approximate definitions of habitat may fail under certain conditions. For example, while vegetation-based models may be a good proxy in landscapes with little anthropogenic change, they may have important limitations in areas modified by industrial extraction. First, woodland caribou are sensitive to changes in understory vegetation that may not follow changes in forest overstory (Johnson et al., 2003). Forage availability for other prey species (e.g., moose,

Alces alces) that share common predators (Rettie, 1998), are features specific to the forest understory. While communities with similar understory characteristics may be correlated with different overstory types (e.g., influence of overstory tree composition on the chemical and physical properties of the litter and the soil, and related understory development and growth), all of the information related to woodland caribou cannot be obtained directly from forest cover data (Rettie, 1998). Second, forest cover inventory systems were created with the objective of measuring merchantable timber (Leckie & Gillis, 1995). Weak to moderate correspondence between these maps and other ecosystem properties have resulted in recommendations of caution when using these maps for wildlife research and forest management planning (Maxie et al., 2010). Third, the extent to which future forests will return to pre-harvest forest composition, and the implications for the provision of wildlife habitat, is unclear (Malcolm et al., 2004; Jönsson et al., 2009). Due to the relatively short period over which mechanized harvesting has been undertaken in Ontario (< 60 years), combined with the fact that there is no requirement to monitor silvicultural effectiveness beyond the "Free to Grow" stage, it is unclear whether Ontario's monitoring programs are sufficient to evaluate the effectiveness of silvicultural practices over the long term (Bell et al., 2008). In the context of woodland caribou, these uncertainties have resulted in concern regarding the degree to which silvicultural practices are providing for adequate future caribou habitat (Suffling et al., 2008). While most hardwood stands can regenerate as stump sprouts and root suckers to their pre-harvest tree composition without post-harvest silvicultural treatments, the regeneration of

conifer-dominant stands, particularly on sites that were not pure conifer to begin with, may require more intensive approaches, such as planting and herbicide spraying. And lastly, predator-prey dynamics are associated with caribou decline, and a suggested outcome in fire-disturbed boreal forests is that woodland caribou and moose select different habitat over space and time (Cumming et al., 1996). Recently disturbed habitats, both anthropogenic and of natural origin, support increases in moose density through increased moose forage associated with early seral-stage forests. Higher wolf (*Canis lupus*) densities are argued to be the response to increased moose densities (Seip, 1992; James et al., 2004); yet to date, evaluation of predators and apparent competitors are not explicitly included in habitat identified through forest management models.

STUDY OBJECTIVES

I began thesis design and research in January 2009, followed by 3 summer (ground surveys) and 3 winter (aerial surveys) field seasons between 2009 and 2013. Geographically, my field assessments focused primarily on the Brightsand caribou range, located northwest of Thunder Bay, Ontario, Canada. My primary objective was to provide forest-resource planners and managers with a greater understanding of potential limitations of using tree overstory composition and age in predicting future woodland caribou habitat. I initiated my research focused on sampling post-harvest and post-fire understory vegetation in the context of forage for moose (and white-tailed deer, *Odocoileus virginianus*; however, this species was virtually absent in winter in the Brightsand range, at the time of my research). While the link between timber harvesting and caribou declines is well established

in the literature (e.g., Smith et al., 2000; Schaefer & Mahoney, 2007; Wittmer et al., 2007), I found no research that linked post-harvest regeneration and caribou habitat, from either the perspective of winter forage or spatial separation from moose.

This thesis is designed to explore assumptions associated with the identification of woodland caribou habitat in Ontario, which has almost exclusively focused on the maintenance and regeneration of older, conifer forests. Specific objectives were:

1) To test whether overstory vegetation type, as depicted in Ontario's Forest Resource Inventories (FRI), represents understory characteristics important to woodland caribou, specifically winter forage.

2) To explore effects of different approaches to post-harvest regeneration on forage for apparent competitors to woodland caribou.

3) To evaluate the performance of forest age and dominant tree composition, as depicted in Ontario's FRIs, as predictors of caribou use compared to indicators more directly linked to expected limiting factors (e.g., occurrence of predators and apparent competitors).

To direct research design, I tested the following hypotheses:

1) Forest overstory composition and age, as depicted in FRIs can be used to predict lichen, a critical component of winter forage for caribou,

2) Understory in conifer-dominated stands harvested and left to regenerate without management intervention supports higher forage availability for moose compared to similarly-aged, fire-origin stands, and moose use these stands more often,

3) Habitat models based on forest overstorey composition and age, alone, will not provide strong prediction of caribou presence, rather the presence of both wolves and moose will better explain caribou use,

4) The effects of the amount of area harvested and left to regenerate without management intervention and density of logging roads will indirectly impact caribou use, and,

5) These relationships will be scale-dependent.

THESIS ORGANIZATION

The body of the thesis represents a series of manuscripts that has been published in peer-reviewed scholarly journals. In Chapter 2, I compared the ability of field-based and forest inventories based on aerial photography to predict *Cladonia* lichen cover, a primary winter food source for woodland caribou. In Chapter 3, I examined regenerating areas of previously conifer-dominated forests in northwestern Ontario, Canada, 10 and 30 years after logging and 10 and 30 years after fire to test if understory development and moose forage abundance differed between the two disturbance types and for artificial or natural regeneration approaches. In addition, I surveyed moose pellet groups as a measure of moose use in relation to post fire, and post-harvest treatments. In Chapter 4, I examined vegetation composition and the presence of moose and wolves as predictors of winter caribou use. I presented results of logistic regressions and structural equation modeling to compare habitat identification based on overstorey vegetation and forest age as predictors of caribou use and models including predators and apparent competitors.

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Chapter 2: PREDICTING NON-INVENTORIED FOREST ELEMENTS USING FOREST INVENTORY DATA: THE CASE OF WINTER FORAGE FOR WOODLAND CARIBOU[1]

ABSTRACT:

Growing development pressures and expectations that forest managers provide future wildlife habitat require better understanding of species' habitat needs, particularly food, cover, and space requirements, and an ability to spatially depict these needs. In forest management in Canada, the primary data used to identify and quantify wildlife habitat reside in remotely sensed forest resource inventories (FRI) that were originally developed to assess timber values for merchantable tree species. Although FRI- and field-based sampling does not always show strong agreement, research has shown that FRI can be informative for wildlife habitat assessments. However, much uncertainty remains when investigating forest characteristics that are not visible to the interpreters, such as sub-canopy features. Here, I used 152 plots in northwestern Ontario to compare the ability of field-based and remotely sensed forest inventories to predict *Cladonia* lichen cover, a primary winter food source for woodland caribou. The best model for field-based data, which included percentage of jack pine and black spruce in the tree canopy, tree height, stand age, soil moisture, and stem density, correctly predicted 92% of cases where *Cladonia* spp. were absent ($n = 107$ plots) and 62% of cases where they were present (i.e., cover > 1%; $n = 45$ plots). FRI performed poorly by contrast, with corresponding percentages of 96 and 19%. FRI provide weak data support for differentiating winter forage availability for woodland caribou, an important habitat factor at the stand level. These findings have important implications for predictions of herd productivity, and suggest that improved remote-sensing capabilities are required in order to assess woodland caribou winter habitat.

2.1 INTRODUCTION

The concept of habitat, the place where a species lives (Odum, 1971), is a cornerstone of wildlife management. Contemporary literature further defines habitat as not just a place, but rather a "state"—based on the resources and conditions present, which are dynamic over time and space (e.g., Martin et al., 2010). Habitat quality varies, ranging from low (i.e., supports survival), to medium (i.e., supports reproduction), to high (i.e., supports population persistence; Hall, Krausman & Morrison, 1997). In forest management planning, habitat is usually defined as the set of environmental attributes that is expected to provide for the needs of a species throughout its life history. Typically, forest stands are assigned a habitat class (e.g., preferred, usable, or not used), often based on tree composition and age. Using tools compatible with timber harvest planning, the sum of these areas is presented as the "habitat supply". In many jurisdictions, planning for industrial timber operations is based on remotely sensed forest resource inventories (FRI). Although FRIs were originally developed to assess timber values for merchantable species, in recent decades they have also been used in wildlife habitat modeling (e.g., Rempel & Kaufman, 2003; Malcolm et al., 2004; Thompson et al., 2007). In addition to the quantification of habitat supply, associated mapped polygons provide an estimation of the spatial distribution of habitat. For example, in Ontario, winter preferred habitat for woodland caribou is identified based on forest cover and age for jack pine stands and forest cover and ecosite estimates for black spruce stands in the FRI (Elkie et al., 2012). In such a system, statistical modeling of present

and future states of habitat can occur over large areas owing to the continuous coverage of the FRI.

As a result of potential legal consequences, designations of habitat for species at risk, such as woodland caribou, (*Rangifer tarandus caribou*), have received much attention in both scientific and policy realms. The range of the forest-dwelling ecotypes of woodland caribou has been declining in Canada since at least the late 1940s (Schaefer, 2003), and woodland caribou were assessed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC, 2002) and were listed under the Federal Species at Risk Act (SARA) in 2003. They are also protected under Ontario's Endangered Species Act (2007) and other provincial and territorial legislation. Recent estimates suggest that 58% of Canada's woodland caribou herds are not self-sustaining (Environment Canada, 2011).

At the landscape level, woodland caribou select areas that reduce overlap with other ungulate species, likely to avoid areas of high predation risk associated with wolves (Rettie & Messier, 2000). Predation is considered to be the most important cause of population decline; however, population levels and productivity may also be influenced by forage availability and snow conditions (Darby et al., 1989). Habitat conditions at the scale of local population ranges affect caribou survival and reproduction, which ultimately determines whether or not a population will persist (Environment Canada, 2008). Nutrition influences many important aspects of caribou ecology, including juvenile growth rates and adult mass gain, body condition, probability of pregnancy, over-winter survival,

timing of parturition, neonatal birth mass, and calf growth rate and survival

(Parker, Barboza & Gillingham, 2009). While autumn body mass determines the

probability of caribou conceiving and carrying a fetus to term (Cameron et al.,

1993), winter and spring nutrition are closely linked to timing of parturition, birth

mass, and early survival of offspring (Skoogland, 1989). In other ungulates, low

birth weights and restricted early growth often result in smaller adults with fewer

offspring (Gaillard et al., 2003). Briand et al. (2009) proposed that female caribou

select habitats based on food availability in the winter; caribou may use areas of

higher predation risk in order to minimize energetic costs associated with travel

and foraging for lichen (Johnson et al., 2002). Assessments of trade-offs between

energy required for reproduction and mortality risks associated with predation

require accurate habitat information at multiple scales.

In winter, woodland caribou mostly use mature conifer forests, peatlands,

and other open areas with abundant terrestrial and arboreal lichens, especially

Cladonia spp., including *C. rangiferina*, *C. mitis*, and *C. stellaris* (Schaefer &

Pruitt, 1991; Courtois et al., 2004; Ferguson & Elkie, 2004; Wittmer et al., 2007).

Caribou's spatial distribution has been directly related to the occurrence of

Cladonia spp., which tends to be associated with nutrient-poor environments of

pine and black spruce forests. In particular, work in Newfoundland, Canada,

showed that selected foraging patches were richer and less variable in supply of

Cladonia spp. than surrounding areas of the same stand (Mayor et al., 2009). In

addition, research in north-central Canada has shown that from February to April,

Cladonia spp. comprised the majority of the caribou diet (Miller, 1976). Not

surprisingly, monitoring of *Cladonia* spp. availability is considered important in management strategies for woodland caribou habitat (Courtois et al., 2003). In northern Canada, ground cover of *C. mitis*, *C. stellaris*, and *C. rangiferina* is largely associated with black spruce/lichen forests (Damman & Johnston, 1980) or jack pine/lichen forests (Majcen, Gagnon & Benzie, 1980) and can include rock outcrops, muskegs, and peatlands (Ahti & Hepburn, 1967). *Cladonia* lichens are generally considered shade intolerant, and their abundance typically decreases with increasing canopy cover (Bloom & Mallik, 2004). Lichens, in general, are not as dependent on soil nutrients and moisture as vascular plants, as they absorb water and minerals from the air through the outer surface of the thallus (Ahti & Hepburn, 1967). As a result, they can occupy dry, nutrient-poor or well-drained sites (Corns, 1983). They are also associated with mid- and late-seral communities; mainly unlogged and mature forest stands (Brumelis & Carleton, 1989). In the absence of fire, as tree density increases, moss is expected to eventually replace lichen in black spruce/lichen forests (Kershaw, 1977; Damman & Johnston, 1980). However, if other site conditions inhibit tree growth and canopy closure, then *Cladonia* lichens can persist (Payette, 1980).

Habitat supply mapping using FRI is a regular component of forest management plan development to identify and manage wildlife values, including woodland caribou habitat (e.g., Malcolm et al., 2004; Holmes et al., 2007; Jokimaki & Solonen, 2011). Two important elements determine the usefulness of forest inventories in identifying wildlife habitat: 1) the accuracy of the data in the inventory and 2) the ability of mapped variables to serve as surrogates for habitat

attributes required by a wildlife species. Errors relating to map accuracy can be substantial; for example, 40% of mapped stands in a forest inventory for Ontario, Canada, were misclassified even when differentiated by broad stand composition classes of "conifer", "mixed", and "deciduous" stands and with a 20% buffer for proportions in the 3 composition classes (Thompson et al., 2007). In that study, proportions of jack pine (*Pinus banksiana*), black spruce (*Picea mariana*), and trembling aspen (*Populus tremuloides*), all common boreal trees, were found to be incorrectly estimated for nearly half of the inventory maps. The aerial photograph interpretation errors were not compensatory and were instead additive when averaged among adjacent stands of increasing spatial extents. The high rate of error in interpreting mixedwood forest types from aerial photos of the boreal forest has been shown to lead to poor predictions of habitat for species that use or avoid such forests (Potvin, Belanger & Lowell, 1999). Reliance on tree-layer interpretation from aerial photographs may cause wildlife habitat features that occur in shrub and herb layers to be overlooked (Bissonnette et al., 1997). Caution has also been suggested where these kinds of surrogates are used (Altmoos & Henle, 2007).

Woodland caribou habitat under forest management in Canada is usually estimated on the basis of FRI models, which ultimately require forest managers to use overstorey tree composition to assess caribou habitat. Although FRI errors with respect to canopy features have been evaluated (Pinto et al., 2007; Thompson et al., 2007; Maxie et al., 2010), errors with respect to sub-canopy features have not been examined, and models of terrestrial lichen that have used forest resource

inventories to date have not explicitly evaluated the impacts of inventory error on model predictions (Lesmerises, Ouellet & St-Laurent, 2011).

In this Chapter, I examine the ability of FRI to predict winter forage for woodland caribou, specifically, the presence of lichen ground cover. My objectives were to 1) evaluate the correspondence between FRI data and field-based data, 2) examine the relationship between the presence of *Cladonia* lichens in these plots and variables collected in field-based surveys and those interpreted from the FRI, and 3) examine implications of any errors of omission and commission in the forest inventory approach to assessing winter habitat for woodland caribou.

2.2   METHODS

2.2.1 *STUDY AREA*

I focused on a ca 11.5-million-ha area within the managed boreal forest zone in northwestern Ontario (FIG 2.1), overlapping primarily with the Brightsand and a portion of the Churchill woodland caribou management ranges (Environment Canada, 2011). The Brightsand range has 42% total non-overlapping disturbances (18% fire and 28% anthropogenic, of which 4% is overlapping), and Environment Canada's critical habitat report (updated July 2011) concluded that there was an approximately 50% chance that the current habitat conditions would fail to maintain self-sustaining local populations.
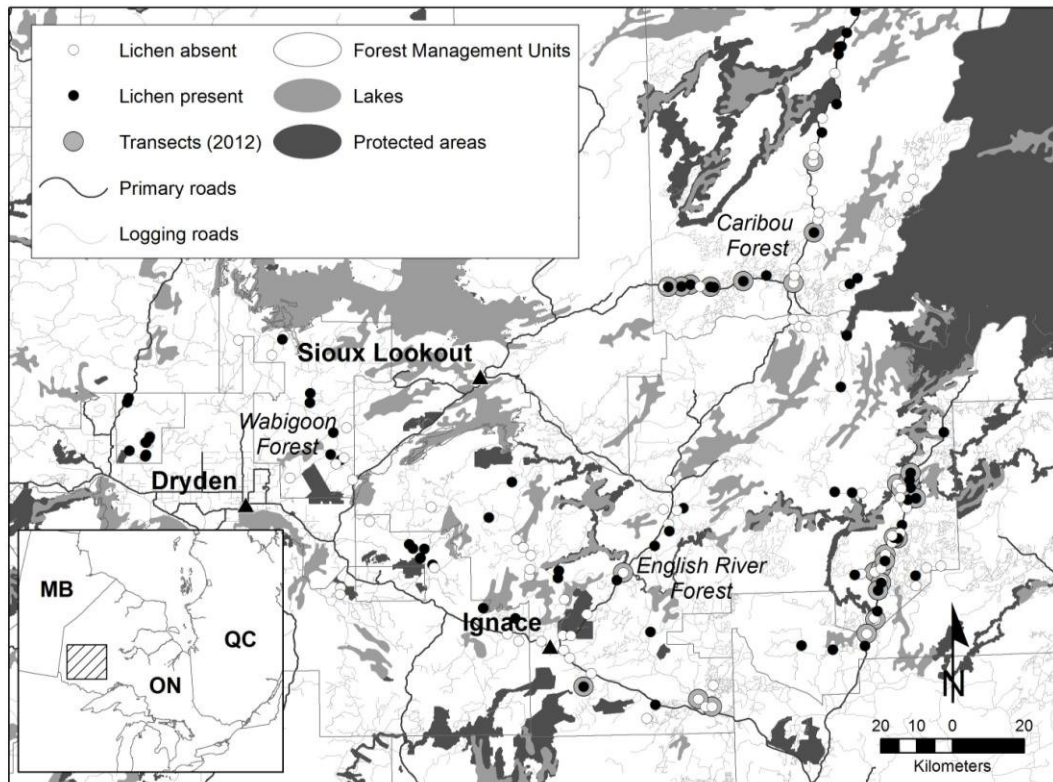
FIG. 2.1: Location of permanent growth plots (PGPs) (*n* = 152) and stand transects (*n* = 30) in northwestern Ontario, Canada.

Three forest management units overlap the study area: the Caribou and

English River forests (managed by Resolute Forest Products) and Wabigoon

forest (managed by Domtar Pulp and Paper Products Inc.). Forests in the area

include pure stands of black spruce or jack pine and mixedwood stands of white

spruce (*Picea glauca*), balsam fir (*Abies balsamea*), trembling aspen, and white

birch (*Betula papyrifera*). Tamarack (*Larix laricina*), balsam poplar (*Populus

balsamifera*), and cedar (*Thuja occidentalis*) are also present but less common.

Red pine (*Pinus resinosa*) and eastern white pine (*Pinus strobus*) are found in

isolated patches. Sands and gravels underlie the majority of the soils on the area.

Jack pine stands are extensive on the dry sand plains and rocky uplands, whereas

black spruce dominates peat-filled depressions; combinations of both species occur in stands of intermediate moisture. The majority of terrestrial lichens in my study area were *Cladonia* species: *C. mitis*, *C. rangiferina,* and *C. stellaris*. Many *Cladonia* spp. are limited to small patches on rotting wood or mineral soil.

Climate conditions vary slightly across the study area, with the northwest corner somewhat colder and drier than the southeastern corner. Monthly mean temperatures are –19 °C in January and 19 °C in July, with 204 cm average annual snowfall and 517 mm average annual rainfall (Environment Canada, 2005: Sioux Lookout, 50°7'N, 91°54'W, 1971–2000).

2.2.2 DATA SETS

I used information from 152 permanent growth plots (PGPs) that were surveyed by the Ontario Ministry of Natural Resources (OMNR) and partners between 2005 and 2010 in northwestern Ontario. Nested within the 11.28-m-radius (400 m^2) plots, *Cladonia* lichens were visually estimated as a percentage of ground cover in 5.64-m-radius (100 m^2) Forest Ecosystem Classification (FEC) subplots (Sims et al., 1997). I focused on plot measurements likely to be important in predicting terrestrial lichen cover: the conifer component (Lambert & Maycock, 1968), tree height (Lesmerises, Ouellet & St-Laurent, 2011), stand age (Morneau & Payette,1989; Arseneault et al., 1997), soil moisture (Ahti & Oksanen, 1990), and stem density (Auclair, 1985; Lesmerises, Ouellet & St-Laurent, 2011). Of the 152 field plots, 49% overlapped with the current Brightsand and Churchill caribou ranges, and approximately 30% of plots within

the caribou ranges had lichen present. All plots were within the historic range of woodland caribou.

Plot locations followed the OMNR protocol (Forest Ecosystem Science Co-operative Inc., 2010), which selects stands ≥10 ha and >100 m from any influencing feature (i.e., roads, cut areas, lakes, rivers, stand boundaries, and any change in age class). In addition, the PGP protocol explicitly requires that selected plots be representative of stand structure and composition of the entire stand (e.g., do not represent an anomaly such as a large opening in the canopy or pocket of different species). Plots were not placed along stand boundaries or in areas of transition between forest types. The diameter at breast height (DBH) of all live trees with a DBH ≥ 2.5 cm was measured in each of the 11.28-m-radius plots. Stand age was calculated by coring a maximum of 5 and a minimum of 3 trees per plot, including at least 3 larger-diameter-class trees from the dominant and/or co-dominant crown classes. If the maximum age difference among the 3 sampled trees was >10 y, an additional tree was sampled. Tree height was calculated by averaging the heights of 6 sample trees for each main canopy species, including the 4 largest-diameter trees, 1 randomly selected smaller-diameter tree >4.9 cm DBH, and 1 randomly selected tree midway between the smallest (DBH ≥ 2.5 cm) and largest diameters. Soil moisture regimes were assessed based on Forest Ecosystem Classification (FEC) standards (Sims et al., 1997) and included categories of dry, fresh, moist, and wet. I combined fresh and moist soils into a "mixed" class for the purposes of analysis. Stem density was based on the total

number of trees ≥2.5 cm DBH in the plot. PGP data were provided by the Forest Ecosystem Science Co-operative Inc.

A second set of data consisted of FRI maps for the area based on aerial photo interpretation at a scale of 1:20 000 and provided by the OMNR. For the Caribou Forest, the FRI was composed of 1996 photography and 1997 interpretation and was approved by MNR FRI branch in 1999 (OMNR, 2009b). For the English River Forest, FRI inventories were based on panchromatic aerial photography taken in 1996-1997 and field sampled in the same years. Photo interpretation, verification, and digitizing were completed in 2002-2003 (OMNR, 2007) and included use of information from a "Continuous Forest Inventory" designed in part to improve FRI accuracy. In these data, 12 prism samples were collected per 400 ha along a 2-km by 2-km grid; additional information collected at each location included height and age of trees and in some cases ecosite determination and a soil sample.

In the FRI, forest stands are delineated and tree species composition is estimated to the nearest 10%, stand age is based on logging history and/or tree heights estimated to the nearest 5-y age class, and tree height was estimated to the nearest metre for the dominant tree species. Stocking was determined based on the estimated stand basal area and interpreted directly from the aerial photographs by relating canopy cover to stocking values calculated in calibration plots. All inventories had been updated with depletions and accruals due to forest management since the time of photography; the FRI maps in my study area were updated with harvesting and wildfire records in 2010. Eight of the plots had been

previously harvested (mean age of 28 y for the harvested stands). None of the

stands selected for my study had fire or harvest events within the field data

collection period. I supplemented the FRI data with surface drainage attributes

from Northern Ontario Engineering Geology Terrain Study (NOEGTS) maps at a

scale of 1:100,000, which classified forest stands into 3 groups: dry, wet, or

mixed dry and wet. These terrain maps were based on a combination of air photo

interpretation, literature searches, and limited field work (Gartner, Mollard &

Roed, 1981). Reporting on correspondence between the 2 data sets were assessed

based on whether the FRI value was within ± 5% of the conifer composition class,

± 5 years of the age class, 2 m of the height class, and 250 trees of the density

class (FIG 2.2). FRI maps were spatially overlaid with the terrain maps and the

locations of the field-based plots using ArcGIS version 10.

Although cover assessments based on visual estimations of percent cover

have been shown to provide similar results to other sampling methods (Moen,

Danell & Holt., 2007), I undertook additional field sampling to test whether the

PGP plots reliably estimated lichen cover. Specifically, based on a stratified

random sample, I selected 30 of them (10 each for stands classified as >70%

conifer, >70% hardwood, and mixedwood) and undertook larger-scale sampling

of lichen within the corresponding FRI-delineated forest stand. Within each stand,

I used visually estimated ground lichen coverage (to the nearest 10%) within 1-m^2

plots spaced at 25-m intervals along 225-m-long transects. All ground-truth

surveys were conducted in August 2012. I used a non-parametric Wilcoxon

Signed-Rank Test to compare lichen estimates from transects with those from the

PGPs.

2.2.3 PREDICTIVE MODELS

Because of the relatively large number of stands with no *Cladonia* spp.

cover, I used logistic regression (Miller & Franklin, 2002) to examine the

relationship between lichen presence and the predictor variables. I considered

plots with ≤1% lichen cover recorded to have no lichen. I selected a subset of

ecologically relevant models *a priori* based on the literature (Burnham &

Anderson, 2002) and used information-theoretic methods based on Akaike's

Information Criterion (AIC) because they permit comparison of models with

different sets of variables (Whittingham et al., 2006). All candidate models

included at least 1 variable typically considered in caribou habitat mapping (i.e.,

conifer composition or age) and also included single-predictor and intercept only

models (Table 2.1). I identified and compared 26 main effects models for their

ability to predict *Cladonia* spp. presence, corrected for small sample sizes (AICc;

Akaike, 1973). In addition, because of potential differences in rates of stand

development, I also developed a model that tested for interaction effects between

forest type (jack pine or black spruce) and age. The model with the lowest AIC_c

was considered to be the best approximating model in the candidate set. I used

Akaike weights (Burnham & Anderson, 2002) as an additional measure of the

strength of evidence for each model and evaluated goodness-of-fit and predictive

power using an adjusted coefficient of determination (Nagelkerke, 1991). I

incorporated all models through a weighted average (model averaging) of the

models' regression coefficients to examine uncertainty in the best model

prediction (Buckland, Burnham & Augustin, 1997). I compared predictive

performance using Cohen's Kappa statistic for the top field-based and FRI-based

models and also explored sources of error by calculating false negative and false

positive rates. I used the Statistical Package for the Social Sciences (v. 19) to run

logistic regressions.

TABLE 2.1: Candidate models examined for predicting lichen presence among 152 plots in northwestern Ontario. Acronyms are: CN = % conifer in tree counts; PJ = % jack pine; SB = % black spruce; AG = stand age; HT = tree height; MS = soil moisture; DS = density[2].

Model	Variables in model
1	Intercept only
2	Stand conifer component (CN) + stand age (AG)
3	CN + tree height (HT)
4	CN + soil moisture (MS)
5	CN + stem density (DS)
6	Percentage jack pine (PJ) + percentage black spruce (SB) + AG
7	PJ + SB + AG + MS
8	CN + AG + HT + MS
9	CN + AG + MS + DS
10	PJ + SB + AG + HT + MS
11	CN + AG + HT + MS + DS
12	PJ + SB + AG + HT + MS + DS
13	HT + AG + MS + DS
14	PJ + SB + AG + HT + MS + DS + PJxAG + SBxAG

2.3   RESULTS

2.3.1   *COMPARISON OF FIELD-BASED TO FRI-DERIVED DATA*

A Wilcoxon Signed Ranks Test showed that lichen estimates from PGP

field plots did not differ significantly from ground-truthing transect plots

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[2] Stem density in field-based data is based on total tree counts.

($Z = -0.731$, $p = 0.465$), supporting my assumption that PGP plots provided accurate representation of lichen cover in the entire stand.

Among the 152 PGP plots, 45 had >1% ground cover of *Cladonia* lichens. Proportion of conifer tree species, stand age, height, density, and soil moisture were key stand characteristics that I expected would influence *Cladonia* presence; however, I found inconsistencies in the measurements of these variables in the FRI when compared with measurements of the same variables in the field (PGP) data (FIG 2.2). Assessment of conifer composition agreed between the FRI and field data when conifer cover was 81–100% (82% of these plots), but agreement between data sets decreased in mixedwood forests (e.g., only 50% of FRI data agreed with the field data in stands with 41–60% conifer component). For only those plots with *Cladonia* lichens, 40% were depicted by the FRI as having <80% conifer cover and 20% as having ≤50% conifer cover. When field-based data were used, only 13% had a conifer component <80% and none had <50% conifer (Figure 2.2), suggesting that, on the ground, only sites with very high conifer composition (>80%) support lichen. According to the field data, only 1 stand that supported *Cladonia* had wet soils. However, none of the wet soils in the FRI data corresponded with field data. The NOEGTS data included in the FRI database does not differentiate between fresh and moist soil. When fresh and moist soils were combined in the PGP, I found 67% correspondence between the 2 data sets, but only 19% agreement for dry soils. Agreement between FRI- and field-based stand age was incorrect in 62% of stands overall (evaluated within a 5-y buffer, older or younger than the age class), with the highest rate of error occurring in
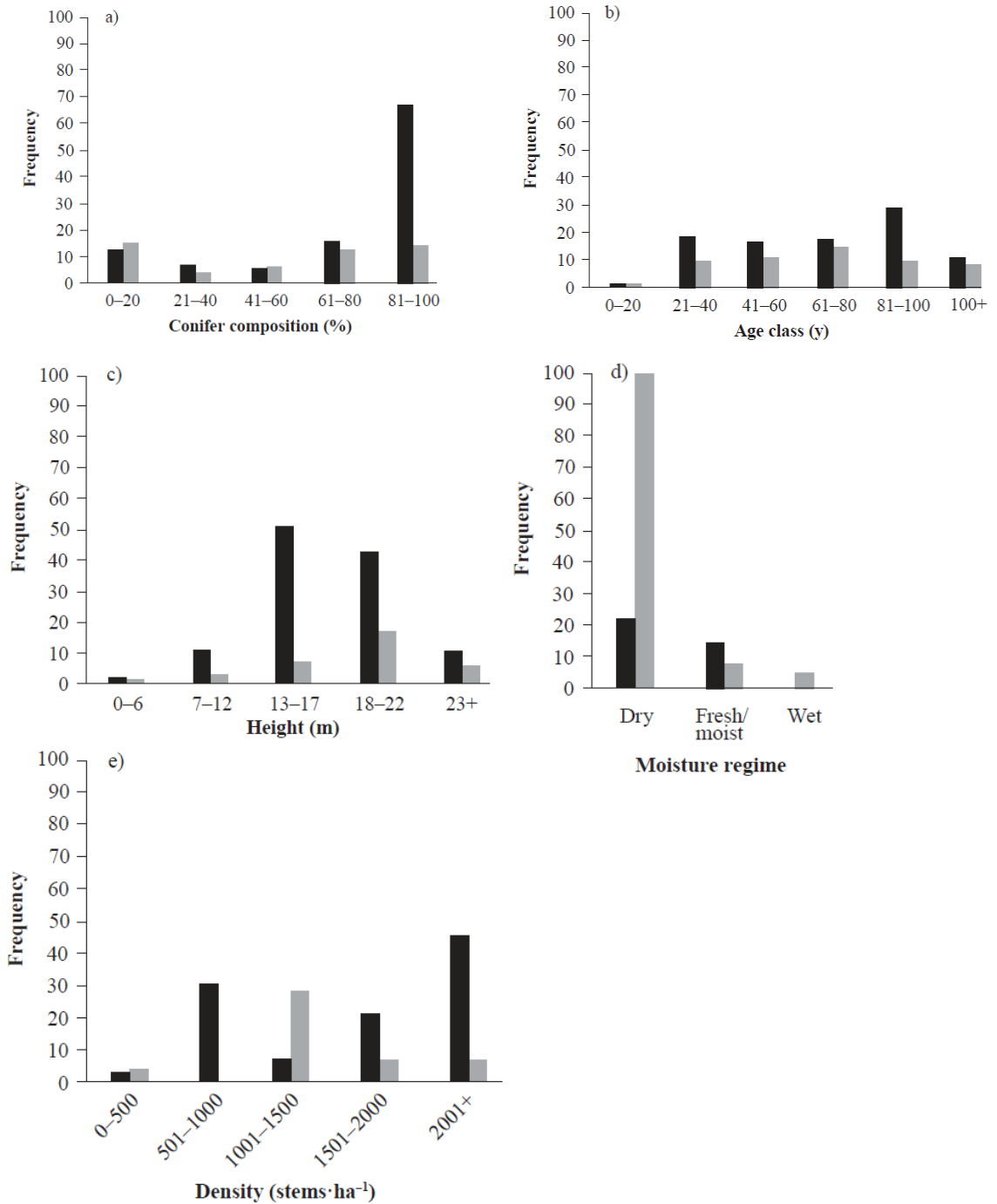
FIG. 2.2: Frequency of correspondence between field-based and FRI variables for 152 plots in northwestern Ontario, Canada, shown either as matches (black bars) or mismatches (grey bars) between the 2 data sets: a) percentage conifer, b) stand age, c) tree height, d) soil moisture, e) stand density. For parts a, b, c, and e, respectively, the 2 data sets were judged to match if they were within 5%, 5 y, 2 m, or 250 trees of each class.

 stands 61–80-y-old. The various tree height classes had similar error rates to each

other. In general, tree heights had high agreement, with mid-range tree heights

(13–17 m) having the highest agreement between the 2 data sets (88% correct).

Stem density showed strongest agreement for stands of 501–1000 stems·ha-1

(100% correct) and poorest for stands of 1001–1500 stem·ha-1 (20% correct;

Figure 2.2).

2.3.2 MODELING CLADONIA SPP. PRESENCE WITH FIELD-BASED DATA

The best-fit model using field-based data was Model 12, which was able

to predict 92% of *Cladonia* spp. absences and 62% of presences correctly (Table

2.2). The model with the lowest AIC_c included percentage of jack pine,

percentage of black spruce, tree height, stand age, soil moisture, and stem density.

By contrast, Model 11 included total conifer component rather than differentiating

between jack pine and black spruce, and had the third lowest AIC_c ($\Delta AIC_c = 3.45$;

Table 2.2). Model 10, which excluded the additional variable of density, had a

ΔAIC_c of 2.61 and an Akaike weight of 0.18. Thus, Model 12 was 3.7 times more

likely to be the best model than Model 10 (evidence ratio = 0.67/0.18). Tree

height, stand age, soil moisture, and either total conifer component or the

percentages of jack pine and black spruce were included in each of the top 4

models. Interaction effects for forest type and age were not included in top models

($AIC_c = 120.56$; $\Delta AIC_c = 14.97$).

Model averaging indicated that a dry soil moisture assignment was the

most positive and reliable predictor of *Cladonia* spp. presence (based on 95%

confidence intervals), whereas a wet soil was the strongest negative predictor of

TABLE 2.2: Number of parameters (K), Kappa, AIC$_c$ values, ΔAIC$_c$, Nagelkerke Pseudo-R^2 and w_i for top 4 models predicting lichen presence from variables in field-based plots in northwestern Ontario. Models were ranked by corrected Akaike's Information Criterion (AIC$_c$) and Akaike weights (w_i). Variable acronyms are defined in Table 2.1.

Model	K	Kappa	AIC$_c$	ΔAIC$_c$	Nagelkerke Pseudo-R^2	w_i	Predicted absence correct (%)	Predicted presence correct (%)
PJ + SB + AG + HT + MS + DS	6	0.567	-102.98	0.00	.520	0.67	91.6	62.2
PJ + SB + AG + HT + MS	5	0.540	-105.59	2.61	.517	0.18	89.7	62.2
CN + AG + HT + MS + DS	5	0.625	-106.42	3.45	.512	0.12	91.6	68.9
CN + AG + HT + MS	4	0.587	-109.47	6.49	.506	0.03	91.6	64.4

TABLE 2.3: Estimates of regression coefficients explaining lichen presence from the best-fit model (jack pine + black spruce + stand age + tree height + soil moisture + tree density) and model averages using field-based data.

Variable	β_n	Standard error (SE)	Weighted Model Averaging		Averaged β_n
Stand age (AG)	0.020	0.01	0.036	0.016	
Tree height (HT)	-0.373	0.10	-0.719	0.139	
Soil moisture (MS) Dry	1.373	0.58	2.767	0.819	
Soil moisture (MS) Mixed	0.832	0.78	1.517	1.075	
Soil moisture (MS) Wet	-3.464	1.43	-6.932	1.983	
Tree density (DS)	0.000	0.00	0.000	0.000	
Percentage jack pine (PJ)	0.047	0.02	0.055	0.017	
Percentage black spruce (SB)	0.038	0.02	0.044	0.016	
Constant	0.511	2.250			0.702

Cladonia spp. presence. Plots with a dry soil were approximately 4 times more likely to include *Cladonia* spp. (Table 2.3).

2.3.3 MODELING CLADONIA SPP. PRESENCE WITH FRI

In estimating lichen presence using FRI for the same plots, the model that included 6 parameters (percentage jack pine, percentage black spruce, tree height, stand age, soil moisture, and stocking) had the lowest AIC_c score, predicting 96% of *Cladonia* spp. absence but only 19% of *Cladonia* spp. presence correctly (Table 2.4). The fifth ranked model, which included total conifer component along with tree height, soil moisture, and stocking, predicted 13% of the plots with *Cladonia* spp. present correctly. The average predictive power for true positives for the top 5 models was only 11% for the models based on FRI data, compared to 64% for field-based data. Furthermore, there was little agreement between predicted presence for the best field-based model and the best FRI-based model (Kappa = 0.15). Of the 37 plots for which field-based data predicted *Cladonia*, the FRI data predicted only 8.

2.4 DISCUSSION

Nutritional needs, resource availability and intra- and inter-specific interactions are the foundations of habitat selection. Ungulates, including woodland caribou, use different seasonal strategies to minimize detrimental impacts to survival and reproduction (Parker, Barboza & Gillingham, 2009). While during the snow-free period the diet of woodland caribou is more varied (Bergerud, 1972), in the winter woodland caribou are habitat specialists (Antoniak & Cumming, 1998). Although the availability of *Cladonia* spp. is not considered

a key factor in the decline of woodland caribou in my study area, it is considered

an important component of habitat supply, and it likely impacts the fitness of

individuals.

TABLE 2.4: Number of parameters (K), Kappa, AIC_c values, ΔAIC_c, Nagelkerke Pseudo-R^2 and w_i for top 5 models predicting lichen presence from variables in FRI data in northwestern Ontario. Models were ranked by corrected Akaike's Information Criterion (AIC_c) and Akaike weights (w_i). Variable acronyms are defined in Table 2.1.

Model	K	Kappa	AIC_c	ΔAIC_c	Nagelkerke Pseudo-R^2	w_i	Predicted absence correct (%)	Predicted presence correct (%)
PJ + SB + AG + HT + MS + DS	6	.196	-148.74	0	.146	0.75	96.3	19.0
PJ + SB + AG + HT + MS	5	.196	-151.07	2.33	.144	0.23	96.3	19.0
PJ + SB + AG + MS	4	.067	-156.56	7.82	.115	0.01	100	4.8
PJ + SB + AG	3	n/a	-159.34	10.60	.109	0.00	100	0
CN + AG + HT + MS + DS	5	.124	-159.41	10.67	.132	0.00	96.3	13.3

Stand conifer component, stand age, tree height, and soil moisture were

variables that best predicted *Cladonia* lichen occurrence. Generally, higher

conifer dominance for this region is associated with higher nonvascular plant

cover, including lichens (Hart & Chen, 2008). Lichens mainly established on dry,

nutrient-poor sites with fresh to dry, coarse-textured mineral soils. I found that dry

plots were 4 times more likely to support *Cladonia* spp. than wetter plots. Among

my plots, 77% of stands that supported *Cladonia* spp. had >80% conifer component. However, in stands with ≥80% jack pine and/or black spruce, almost half of the stands (about 43%) >60-y-old did not support any lichen: not all mature conifer stands support *Cladonia* spp. I found tree height to be negatively correlated with *Cladonia* lichen occurrence, similar to other lichen studies (Lesmerises, Ouellet & St-Laurent, 2011), presumably a result of the reduction in light availability on the ground in stands with taller trees (Auclair, 1985). Even though conifer stands with lower stem density are elsewhere associated with increased lichen growth (Lesmerises, Ouellet & St-Laurent, 2011), also a consequence of light availability (Kershaw, 1977), stem density was not a strong predictor of *Cladonia* spp. in my analysis.

Incorrect and imprecise depictions of stand characteristics influence the ability of FRI data to accurately predict the presence of *Cladonia* spp. Providing a 5-y buffer on age, I found agreement with 67% of stands (based on 20-y incremental age classes). Age assignment from FRI data was least accurate for the 61–80 y age class (45% false positive), where *Cladonia* spp. were more probable than for younger age classes. Interpretation errors presumably account for much of the misclassification. The inconsistencies that I observed in comparing FRI and field-based data were similar to those from other studies (e.g., Dussault et al., 2001; Pinto et al., 2007; Thompson et al., 2007). I found some evidence of consistent biases: agreement was better for pure conifer stands than for deciduous and mixedwoods (Potvin, Belanger & Lowell, 1999), for older stands compared to younger stands, and for fresh / moist stands compared to dry or wet ones. Sources

of error include visibility bias in identifying tree species depending on the height

of dominant species (Biging, Congalton & Murphy, 1991), misidentification of

dominant species depending on stand age, forest stresses that alter the appearance

of a tree crown, or the angle of light at the time of the photography (Ciesla, 1990),

and consistent bias in canopy cover assessments in aerial photograph

interpretation (Thompson et al., 2007). The typical 20-y lag between complete

forest inventory updates may impact their effectiveness in modeling habitat where

stand age is an important factor. This last issue is especially relevant when age is

interpreted from tree heights in the photography, not from detailed reconstruction

of fires, logging, and other forest disturbance. Forest successional dynamics may

also cause classification accuracy to change with time since FRI production.

While stand harvest information (i.e., age) may be updated more regularly,

revisions in other map variables, such as tree height and stand conifer component,

are typically only based on expected future stand characteristics. My collection of

information on lichen cover was based on the FEC protocol, a common tool in

forest management, and showed good agreement with more exhaustive standwide

estimates. However, visual estimates are subjective, and more objective sampling

techniques might be valuable. Of special interest are estimates of lichen biomass,

as opposed to ground cover (e.g., McMullin et al., 2011).

2.4.1 MANAGEMENT IMPLICATIONS

My research shows that the current FRI performs poorly at measuring

certain aspects of woodland caribou habitat, and, as a result, I suggest that FRI

should be used to model woodland caribou winter habitat with caution. While FRI

habitat modeling may suffice in describing long-term trends in the amount of older, conifer forest cover (as shown in Thompson et al., 2007), I suggest that there are 2 circumstances where reliance on FRI may be especially detrimental to woodland caribou management. First, in ranges where the combined anthropogenic and natural disturbance exceeds or is on the threshold of the acceptable level for "self-sustaining" caribou populations as currently defined by Environment Canada (2011). Second, in forests regenerated from timber harvesting, particularly those left for natural regeneration.

Concerning the first, the critical habitat for woodland caribou is described in terms of the percentage of range needed in an undisturbed state in order to maintain that herd (Environment Canada, 2011). Critical habitat is most appropriately identified at the scale of caribou ranges and expressed relative to the probability that range conditions are sufficient to support a self-sustaining local population (Environment Canada, 2011). Of the 57 local population ranges currently delineated across Canada, 30 are assessed as "Not Self-Sustaining" (integrated probability of less than 0.5), 17 as "Self-Sustaining" (integrated probability of greater than 0.5), and 10 as equally likely to be "Self-Sustaining" or "Not Self-Sustaining" (integrated probability equal to 0.5). For example, there are 4 herds in Ontario considered to have low to moderate likelihood of self-sustainability: Berens, Brightsand, Kesagami, and Sydney. It is assumed that older, conifer-dominated stands, as depicted by forest inventory maps, should provide the winter forage and anti-predator requirements of woodland caribou. However, such assumptions of fixed habitat selection criteria have elsewhere been

criticized, in part because variation in resource availability, such as the occurrence of forage, influences resource selection (Osko et al., 2004). Trade-offs in selecting habitats will vary when resources are scarce compared to when they are not limiting (Mysterud & Ostbye, 1999). For example, Moreau et al. (2012) have built multi-level functional responses characterizing how caribou alter their selection for closed-canopy conifer forests depending upon the availability of these forests and the incidence of cutovers and roads; selection of closed-canopy conifer forests by caribou generally became stronger with increasing disturbance levels.

Concerning the second, current woodland caribou habitat strategies in areas managed for timber harvesting tend to rely on regeneration of forested habitats to provide a dynamic habitat supply. When managers determine that suitable winter caribou habitat has regenerated in an area, additional areas of a woodland caribou range can be made available for timber harvest (e.g., OMNR, 2009a). My study suggests that FRI-based models with implicit or explicit expectations of Cladonia spp. occurrence are limited by errors that originate in biased aerial photograph interpretation. The resulting uncertainty in mapping lichen is exacerbated by the fact that uncertainty itself is underestimated (Parma, 1998). My research suggests that a generalist inventory (focusing mainly on overstory) is limited, in this respect, in its ability to serve as a useful proxy for species that are habitat specialists. For this purpose, FRI may require significant ground-truthing of the understory.

Adaptive management approaches represent the foundation for woodland caribou recovery in Canada (Environment Canada, 2008), and determining the mechanisms driving caribou population dynamics in managed landscapes is considered a critical component of forest research, policy, and management (Suffling et al., 2008). The adaptive management approach requires the ability to test assumptions about mechanisms influencing complex habitat–wildlife interactions (Holling, 1978). For example, in Ontario, there are case studies underway in sites where caribou have been observed using previously harvested stands, one of which is in my study area (South Allely Lake). Abundant lichen growth is a common characteristic of these sites. Furthermore, accurate classification of stands with lichen, regardless of forage relevance, will be valuable to differentiate moose winter habitat from caribou winter habitat, with relevance to predation risk (Cumming, Beange & Lavoie, 1996), and to quantify/track management targets in habitat supply for caribou. If the tools used for planning do not allow us to test management assumptions, they will fall short of our analytical needs in an adaptive framework.

Despite the shortcoming of forest inventories, they are a central tool in forest management planning not easily replaced by alternatives, and so tools/approaches for improvement are needed. My findings regarding soil moisture and inaccuracies of FRI as a function of soil wetness warrant future research. Soil moisture conditions were a key predictor of lichens, and FRI classification accuracy was especially low for wet soil conditions. I used moisture regime data from NOEGTS; however, this mapping is developed at a relatively

coarse scale (1:100 000). Although beyond the scope of the current manuscript, it would be useful to determine if other large-scale databases, such as digital elevation models linked with hydrology and landform, could be used to enhance the predictive power of FRI information to better predict lichen occurrence and abundance. Also, the FRI used in my study was based on interpreted 1:20 000 black and white photographs. New FRIs are using 1:1000 digital colour imagery, and their interpretation, may be more consistent, and could include better information on moisture regimes. Regardless, all forest inventories are based on aerial views and thereby focus on tree cover, with understory inferences limited to the recognition of multiple-layered canopies, if visible. I argue that modelers using FRI to spatially depict wildlife habitat should recognize that FRI enables only indirect inference of understory features, and that it should be used cautiously as a result. Testing of the sensitivity and accuracy of habitat suitability models should be part of the accuracy review process in all new inventories if the intention is to use them in wildlife habitat modeling. The growing legal requirements to protect habitat for species at risk make such testing especially important.

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Chapter 3: INFLUENCE OF POST-HARVEST SILVICULTURE ON UNDERSTORY VEGETATION: IMPLICATIONS FOR FORAGE IN A MULTI-UNGULATE SYSTEM[3]

ABSTRACT:

Natural disturbance emulation has emerged as a key management approach to maintaining biodiversity in logged boreal forests. Forest managers' success in emulating understory forest ecosystem functions, e.g., for the provision of habitat even for large mammals, has not been tested due, in many cases, to incomplete records of silviculture. I examined regenerating areas of previously conifer-dominated forests in northwestern Ontario, Canada, 10 and 30 years after logging and 10 and 30 years after fire to test if understory development and moose forage abundance differed between the two disturbance types and artificial or natural regeneration approaches. In addition, I counted moose pellet groups as a measure of moose use of the region. Specific treatments included: (1) naturally regenerating, fire-origin forests, (2) post-harvest, regenerating forests with natural establishment of trees, and (3) post-harvest, regenerating forests with mechanical or chemical site preparation and planting and/or herbicide spraying. I hypothesized that the understory in post-harvest stands would support higher forage availability for moose compared to similarly-aged, fire-origin stands. Abundance of hardwoods, shrubs, and herbaceous plants was greater in naturally-regenerated post-harvest stands than in fire-origin and artificially regenerated post-harvest stands at both 10 and 30 years post-disturbance. However, post-harvest, naturally regenerating stands were not significantly associated with higher moose use, rather evidence of moose use increased as a function of the amount of naturally regenerating logged forest in the surrounding landscape. This study suggests that, relative to fire, the intensity of post-harvest silviculture influences habitat suitability for moose. The effect likely cascades to other ungulates, such as woodland caribou, and vegetation management needs to be considered at scales greater than the stand level in order to achieve habitat management for large mammals.

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3.1 INTRODUCTION

The concept of emulating natural disturbance has emerged in forestry as a management strategy that seeks to maintain economic benefits from clearcutting while sustaining the structure and composition of boreal forests (Bergeron et al., 2002). Two observations provide the rationale: (1) boreal forests experience frequent disturbances and possess inherent resilience to recover from them, and (2) boreal fauna have adapted in such a way that they can persist in this disturbance driven forest ecosystem. The emulation approach speculates, for example, that whereby wildlife species are adapted to wildfire, the predominant disturbance in unmanaged boreal forests, they should likewise adapt to timber harvesting, if practices are applied whose outcomes resemble the effects of wildfire.

This study was motivated by the considerable range recession of woodland caribou in Ontario over the past century (Schaefer, 2003). A proposed contributing cause is logging-associated increases in the extent of early successional forests that offer forage to moose and white-tailed deer (*Odocoileus virginianus* Zimm.), but, except during migration (Ferguson and Elkie, 2004) and in the spring (Hins et al., 2009) are avoided by caribou (Wittmer et al., 2007). This avoidance is likely due to an altered predator–prey dynamic created by a larger prey base (Rettie & Messier, 1998; McLoughlin et al., 2005; Briand et al., 2009) that equates functional habitat loss for caribou.

In boreal forests, significant conversion from conifer to hardwood and mixedwood stands has been documented where logging has replaced fire as the

main forest disturbance (Carleton and MacLellan, 1994). Relative to fire, disturbance from logging tends to lower dominance by conifer trees (Whittle et al., 1997). Deciduous trees can regenerate from stump sprouts and root suckers and dominate post-harvest sites. Wildfire, on the other hand, depending on its intensity, can kill or impede developing hardwood understory (Flinn & Wein, 1977) and facilitate seed dispersal in conifers (Arsenault, 2001). Condition of the seed bed also affects forest regeneration, and intense fires can expose mineral soil to improve the establishment of conifers.

Most silvicultural studies on understory species in boreal forests have focused on competition with crop trees (e.g., McDonald & Abbott, 1997). While there are claims that effects of herbicide application on moose forage quality and quantity are negligible (Cumming et al., 1995; Raymond et al., 1996), they come from studies on short-term effects (i.e., <5 years) at a small scale (i.e., the stand level). Tree planting, which has the potential to offer control over future stand density and structure, is often undertaken in productive stands where competition with shrub and hardwood species is expected, and is frequently used in combination with herbicides to control competing vegetation (Perera & Euler, 2000). Post-harvest silviculture may be able to reverse conversion from conifer to hardwood and mixedwood stands, as diversity and abundance of understory plants are strongly related to the intensity of site preparation (Newmaster et al., 2007) and to overstory composition (Hart & Chen, 2008). However, intensive silviculture is often avoided in favour of natural regeneration for ecological and economic reasons. Moreover, good records of silviculture to test long-term and

larger-scale effects on maintenance of functions like moose or caribou habitat supply have only been recently assembled in a way to field-test changes over time. I used the long-term records of silviculture on the English River and Caribou Forest Management Units (FMU) maintained by AbitibiBowater (Resolute), Inc. to track forest successional pathways to different degrees of investment in forest management. My objectives were to compare the abundance of common trees, shrubs and herbaceous plants that comprise moose forage, and to compare moose use among 10- and 30-year-old: (1) naturally regenerating, fire-origin forests, (2) post-harvest, regenerating forests with natural establishment of trees, and (3) post-harvest, regenerating forests with mechanical or chemical site preparation and planting and/or herbicide sprayed. Relative to the other treatment types, I expected that natural regeneration would result in stands with higher deciduous tree and shrub counts, and a greater percentage of herbaceous groundcover. I expected differences among fire origin, naturally regenerating and more intensively-treated forests to be greater for younger than for older stands, as increasing shade under a developing overstory will eventually limit the shrub and herb layers regardless of treatment type. I expected moose forage availability and moose pellet group counts to be highest in logged areas with natural regeneration, both at the stand and home range scale.

3.2 METHODS

3.2.1 STUDY AREA

The study took place in the English River Forest Management Unit (FMU) and in southern portions of the Caribou FMU, approximately 200 km northwest of

Thunder Bay, Ontario, and in Wabakimi Provincial Park, a large (892,000 ha)

park east and northeast of the management units where logging is not permitted

(49°47'N, 91°02'W; FIG. 3.1). Forest cover in the area consists mainly of black

spruce (*Picea mariana* [Mill.] B.S.P.) and jack pine (*Pinus banksiana* Lamb.)

growing in relatively pure stands or in mixed stands in association with white

spruce (*Picea glauca* [Moench] Voss), balsam fir (*Abies balsamea* L. Mill),

trembling aspen (*Populus tremuloides* Michx.) and white birch (*Betula papyrifera*
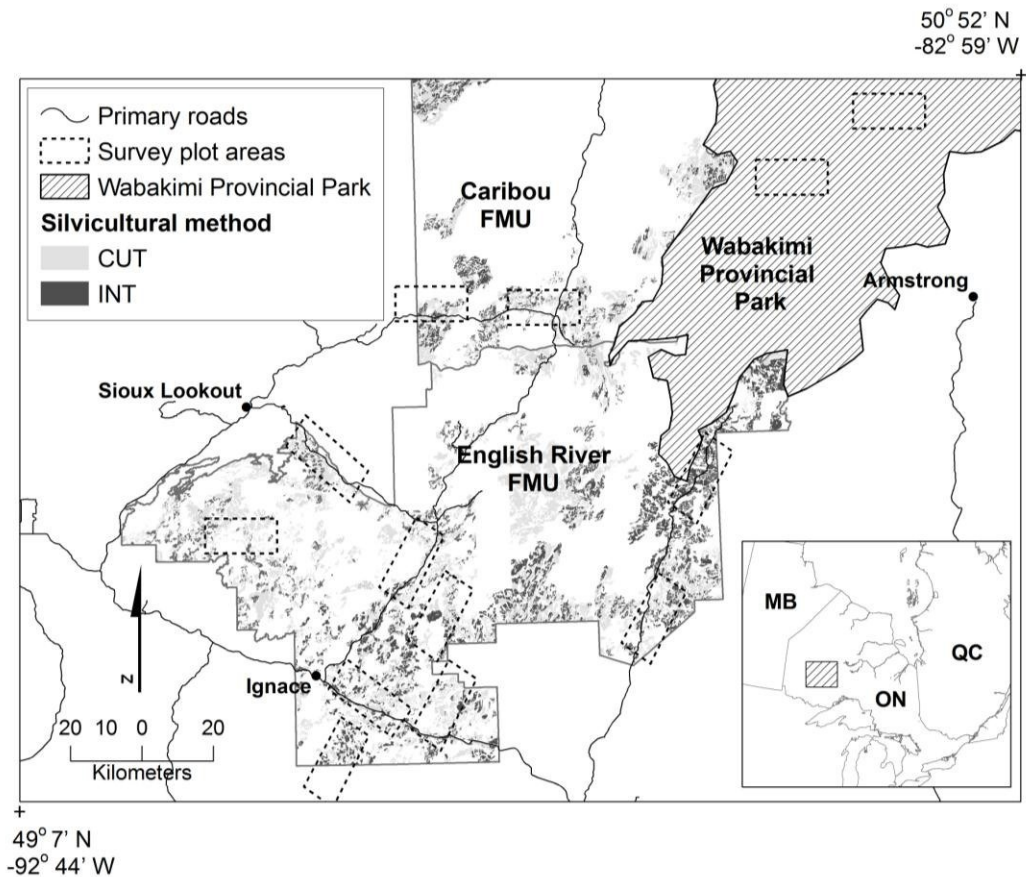
FIG 3.1: Location of study area in northwestern Ontario, Canada, showing the survey plot areas, major roads and towns, and the distributions of two treatment types (CUT = clear-cut, natural regeneration; INT = clear-cut, planted and/or sprayed) in the Caribou and English River Forest Management Units.

Marsh.). Jack pine stands are extensive on dry sand plains and rocky uplands, whereas black spruce dominates in peat-filled depressions. Monthly mean temperatures are -19 °C in January and 19 °C in July, with 204 cm average annual snowfall and 517 mm average annual rainfall (Environment Canada: Sioux Lookout 50°7'N, 91°54'W, 1971–2000).

The study area supports 0.23–0.26 moose/km^2 (McKenney et al., 1998), the dominant ungulate in the region. Moose occur in a range of forest types, especially when pre-sapling or sapling seral stages dominate (Rempel et al., 1997). Moose population growth rate is positively related to the abundance of mixed deciduous habitat (Brown, 2011). Prior to the late 1950s, woodland caribou populated the entire study area. At present, about one-half of the English River FMU and the entire Caribou FMU are north of the line of continuous caribou occupancy defined by Ontario's Ministry of Natural Resources (OMNR, 2009), and are consequently managed under provincial guidelines aimed at maintaining long-term caribou habitat. The OMNR defines caribou habitat as nearly contiguous stands >60 years old comprising 100% black spruce, eastern white cedar (*Thuja occidentalis* L.) and American larch (*Larix laricina* [Du Roi] Koch) on sites considered to have low productive capacity due to drainage and soil types, as well as stands with >70% black spruce and >20% trembling aspen and white birch (Racey et al., 1999; Ferguson & Elkie, 2004; Brown et al., 2007). Jack pine stands are eligible if they comprise >70% jack pine and <20% trembling aspen and white birch, or the trembling aspen and white birch component of the stand is <20% and the jack pine component is larger than the combined black

spruce and white spruce components. In the 1940s, white-tailed deer, with similar

general habitat requirements as moose, extended over the entire English River

(and former Brightsand) FMU, but was considered absent from the Caribou Forest

(Great Lakes Forest Products Ltd., 1975). During the 1950s and 1960s, white-

tailed deer range contracted south of the FMUs as a result of severe winters, at

which time moose populations began to rise (OMNR, unpublished data).

Currently, white-tailed deer appear to be expanding northward again, with some

recent sightings in the Caribou Forest, the northern extent of our study area.

White-tailed deer and woodland caribou are distributed more sporadically in the

study area and density estimates are not available for these species.

3.2.2 DATA COLLECTION

　　　I used 1976 and 1996 Forest Resource Inventory (FRI) maps (OMNR,

unpublished) to select jack pine and black spruce stands that were conifer-

dominated prior to disturbance. I sampled stands in three post-disturbance

regeneration types: fire (FIRE), clearcutting followed by natural regeneration

(CUT), and clearcutting followed by intensive silviculture (INT). CUT stands

typically incorporated seed trees (i.e., a small number of seed bearing trees left on

site following logging), and were generally not mechanically or chemically

treated after the harvest. Stand density and composition after the harvest were not

controlled. The INT treatment always had mechanical site preparation followed

by manual planting or spraying with herbicide, or a combination of planting and

spraying with herbicide. I amalgamated planting and herbicide combinations into

one treatment based on a pilot study in 2008 that showed no significant effects on shrub and tree composition between the two treatments. For this study, INT did not include any pre-commercially thinned stands.

I randomly selected twenty FRI-defined stands in each of the three treatment types that were approximately 10 years post-disturbance (i.e., logging/fire occurred in 1996–1999) and twenty stands at approximately 30 years post-disturbance (i.e., logging/fire occurred in 1976–1979). The equipment used for mechanical site preparation differed between the two age classes. In general, skidder-pulled passive trenchers were used on 10-year-old stands and tractor-pulled drags (barrels and chains) were used on the 30-year-old stands. The primary herbicide used on 30-year-old INT stands was 2,4-D (2,4-Dichlorophenoxyacetic acid), whereas glyphosate herbicides (Round Up[®] and Vision[®]) were introduced in the mid-1980s and applied aerially using helicopters in many of the 10-year-old INT stands. To ensure that soil types did not systematically vary among the treatments, I sampled soils with an auger to a depth of 1 m and classified each sample into a ''soil moisture regime'' based on Ontario's Forest Ecosystem Classification protocol (Sims et al., 1997).

I conducted field plot measurements between July and early September in 2008 and 2009. Using ArcView (v. 9.1), I selected a random point in each stand 100–500 m from the nearest truck-accessible secondary road to serve as the starting point of a 60-m long transect. The mean distance between stands of the same treatment was 3.2 km. Circular plots of 5.65-m radius (100 m^2) were

centered at the ends and middle of the transect (i.e., three plots per stand). Within

a plot, all individual stems >2 m in height were counted by species. These

included the woody species that are considered the most important moose forage:

mountain maple (*Acer spicatum* Lam.), white birch, beaked hazel (*Corylus*

cornuta Marsh.), balsam fir, trembling aspen, cherry (*Prunus* spp.), willow (*Salix*

spp.), and ash (*Sorbus* spp.) (Peek et al., 1976; Crête & Bedard, 1975; Irwin,

1985; Cumming, 1987). I counted stems <2 m in height using a 1-m wide bar held

at 1 m in height along two 10-m long belt transects running N–S and E–W across

each plot (20 m^2 in total) (adapted from Rodgers et al., 2008). Percent of ground

covered by vascular plants, moss, lichen, exposed soil, coniferous litter,

deciduous litter and coarse woody debris (CWD) was visually estimated in four 1-

m^2 subplots per plot. I counted moose fecal pellet groups in a random subset of

five stands per treatment, by use of five 5.65 m (100 m^2) radius circles in each

stand (Neff, 1968); i.e., an additional two plots were located 30 m perpendicular

to the original 60 m vegetation transect. A pellet group was defined as a group of

at least five pellets within one pellet distance from one another, with at least half

of the pellet group falling within the plot; this definition corresponds to estimated

moose density (Harkonen & Heikkila, 1999). Plots were located at a maximum

distance of 500 m from the nearest secondary road, a requirement due to my

interest in silviculture.

3.2.3 DATA ANALYSES

Analyses were undertaken separately for 10- and 30-year-old stands.

Composition and abundance of woody stems in tree and shrub layers and

groundcover estimates were examined by use of non-metric multidimensional

scaling (NMDS). A Sorensen (Bray-Curtis) distance was used for the ordination,

as it assigns less weight to outliers, which are common in ecological data

(Sørensen, 1948). Ordinations were developed based on plotting a measure of fit

(''stress'') to the number of solutions. I calculated Kendall's tau rank correlation

coefficients to test the strength of the association between species and ordination

axes. To test the hypothesis that no floristic differences existed among the

treatments, I used a Multiple Response Permutation Procedure (MRPP) set at the

Sorensen distance measure (in order to be consistent with the ordination). MRPP

is a non-parametric analog to Discriminant Function Analysis and determines

whether variation between treatments exceeds that expected based on the variance

within treatments. I applied Dufrêne and Legendre (1997) indicator species

analysis (ISA) to tree and shrub data and groundcover estimates to describe

differences in individual species abundances among treatments and to identify

target species that were more abundant in one or another of the treatments.

Relative abundance, RA, and relative frequency, RF, were multiplied to calculate

an indicator value, IV, for each species j in each treatment k:

$$IV_{kj} = 100 \ (RA_{kj} \ x \ RF_{kj}) \hspace{3cm} (1)$$

In addition, I applied a Monte Carlo test of significance of observed maximum indicator value, based on 1000 randomizations (McCune & Grace, 2002). Only species with alpha levels less than 0.05 and with an indicator value greater than 25 were considered indicator species for a treatment (Dufrêne & Legendre, 1997). I applied a Bonferroni correction to account for multiple comparisons in pairwise comparisons among treatments. All multivariate tests were carried out using PC-ORD ver. 5 (McCune & Mefford, 2006). Analysis of variance (ANOVA) was used to determine the relationship between moose pellet counts and treatment at the stand-level, separately, for both 10-year-old and 30-year-old stands. Examination of residuals indicated that the assumptions of homogeneity and normality were satisfied. In addition, I was interested in the degree to which variation among moose pellet counts could be attributed to the degree of regeneration in the surrounding landscape. Home ranges for North American moose can vary, on average, from 10–40 km^2 (Crête, 1988). Accordingly, I measured the area of INT, CUT and FIRE in circular regions surrounding the plot centers at three scales: 10 km^2 (1.75 km radius), 20 km^2 (2.5 km radius), and 40 km^2 (3.55 km radius) and tested the relationship with moose pellet density at each scale using regression. Since I found that the random selection of stands expanded to larger scales resulted in some spatial overlap in two home ranges of both the CUT and INT treatments, I compared moose pellet counts, silvicultural treatments and between-site distances using Focus 2.1 (Holland et al., 2004) to evaluate potential lack of spatial independence associated with multi-scale analysis.

3.3 RESULTS

3.3.1 TREE, UNDERSTORY AND GROUND-LAYER VEGETATION COMPOSITION

10-year-old stands

Soil moisture regimes did not differ significantly among treatments (Table

3.1). Differences in species composition between the treatments occurred for 10-

year-old stands, especially for jack pine and trembling aspen growth in tree and

shrub layers (Table 3.2). The NMDS ordination for shrubs and trees resulted in a

three-dimensional solution that explained

TABLE 3.1: Soil moisture regime frequencies based on soil auger sampling of 360 field plots in northwestern, Ontario according to treatment type (FIRE = fire-origin, CUT = clear-cut, natural regeneration and INT = clear-cut, planted and/or sprayed). Pearson's chi-square comparing treatment types for 10-year-old stands = 7.8, df = 4, p = 0.10; for 30-year-old stands = 8.4, p = 0.08.

Treatment		10-year-old stands (n = 180)				30-year-old stands (n = 180)			
		Dry-fresh	Moist	Wet	Total	Dry-fresh	Moist	Wet	Total
FIRE	Count	47	11	2	60	46	5	9	60
	Expected	42.3	13.0	4.7		45.3	9.3	5.3	
CUT	Count	37	14	9	60	47	9	4	60
	Expected	42.3	13.0	4.7		45.3	9.3	5.3	
INT	Count	43	14	3	60	43	14	3	60
	Expected	42.3	13	4.7		45.3	9.3	5.3	
Total		127	39	14	180	136	28	16	180

TABLE 3.2: Stand characteristics of 120 stands (360 field plots) sampled in northwestern Ontario, Canada (FIRE = fire origin, CUT = clear-cut harvested, naturally regenerated, INT = clear-cut harvested with planting, herbicide-spraying or both). Values are mean percentage tree Composition by stand (with SE in parentheses).

Origin and age class	n	Post-disturbance stand composition (%)					
		Jack pine	Black spruce	Balsam fir	Aspen	White birch	Other
FIRE							
10 years	20	79(5)	2(2)	0	3(2)	16(4)	<1
30 years	20	44(8)	35(7)	6(3)	9(5)	6(1)	<1
CUT							
10 years	20	27(8)	3(5)	3(1)	48(9)	11(2)	8
30 years	20	30(8)	28(7)	24(7)	10(4)	8(3)	<1
INT							
10 years	20	73(7)	8(5)	3(1)	11(4)	4(3)	<2
30 years	20	29(6)	44(6)	6(3)	9(3)	11(3)	<1

85% of the variation in the data (final stress = 13.8), a reliable solution for ecological data (McCune & Grace, 2002). Examination of the third axis showed little evidence of variation related to the treatments, so only Axes 1 and 2 are presented (FIG 3.2A). Axis 1, which explained 39% of the variation in the data, was most positively correlated with shrubs considered preferred moose forage, including, serviceberry (tau = 0.456), mountain maple (tau = 0.419), trembling aspen (tau = 0.387), and beaked hazel (tau = 0.277). This axis was most negatively correlated with jack pine (tau = -0.660), which is more associated with caribou habitat. Axis 2, which explained 29% of the variation in the data, was most positively correlated with beaked hazel (tau = 0.379) and mountain maple (tau = 0.331) and most negatively correlated with black spruce (tau = -0.431). There was strong differentiation between CUT stands and the other two stand types (FIRE and INT) due to relatively high densities of deciduous shrubs in the former (upper right quadrant); differentiation between the latter two stand types was not as evident.

The MRPP permutation procedure ($p < 0.01$, T = -12.09) led to a small A value (A = 0.087) indicating differences among the FIRE, CUT and INT groups. The greatest difference in community composition and abundance, based on pairwise comparisons, was between CUT and FIRE ($p = 0.001$, T = -11.22, A = 0.09) followed by CUT and INT ($p = 0.001$, T = -9.97, A = 0.08) and FIRE and INT ($p = 0.01$, T = -4.94, A = 0.04). Several species were significantly more
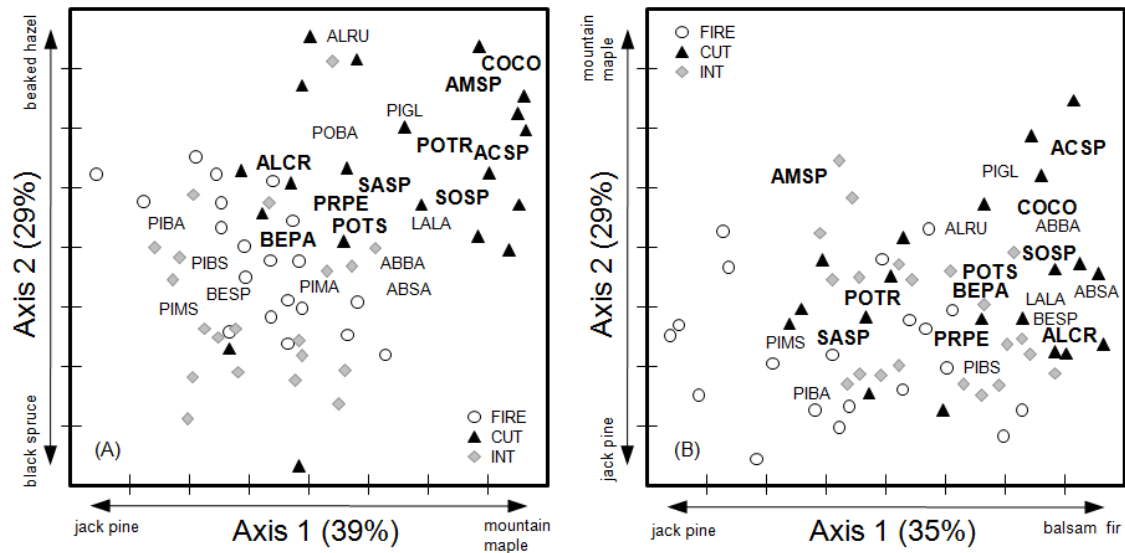
FIG. 3.2: Non-metric multidimensional scaling ordination for tree (taller than 2 m) and shrub species (including trees shorter than 2 m) composition on (A) 10-year-old stands (n = 60), and (B) 30-year-old stands (n = 60) in northwestern Ontario, Canada. Axes 1–3 had an R^2 of 0.845 cumulatively (0.388, 0.291, and 0.167, respectively) for 10-year-old stands, and corresponding values of 0.816 (0.351, 0.287, and 0.180) for 30-year-old stands. Acronyms are: ABBA (*Abies balsamea*), ABSA (*Abies balsamea* shrub), ACSP (*Acer spicatum*), ALRU (*Alnus rugosa*), ALCR (*Alnus crispa*), AMSP (*Amelanchier spp.*), BEPA (*Betula papyrifera*), BESA (*Betula papyrifera* shrub), COCO (*Corylus cornuta*), LALA (*Larix laricina*), PIGL (*Picea glauca*), PIMA (*Picea mariana*), PIMS (*Picea mariana* shrub), PIBA (*Pinus banksiana*), PIBS (*Pinus banksiana* shrub), POTR (*Populus tremuloides*), POTS (*Populus tremuloides* shrub), PRPE (*Prunus pensylvanica*), SASP (*Salix* spp.), and SOSP (*Sorbus* spp.). Important species for moose forage shown in bold type.

frequent and abundant in the FIRE and CUT treatments in the 10-year-old stands, based on the ISA (Table 3). Jack pine, white birch, black spruce and jack pine and white birch shrubs were significantly associated with FIRE stands. In contrast, trembling aspen, serviceberry, beaked hazel, willow and mountain maple were significantly associated with CUT stands.

The NMDS ordination on ground cover in the 10-year-old stands yielded an optimum solution in three dimensions with a final stress of 10.813 (FIG 3.3A).

Axis 1, which explained 52% of the variation in the data, was most positively

correlated with vascular plants (tau = 0.462), and most negatively correlated with

CWD (tau = -0.702). Axis 2, which explained 26% of the variation in the data,

was most positively correlated with litter/exposed soil (tau = 0.696) and most

negatively correlated with moss (tau = -0.277). FIRE stands were strongly

distinguished from INT and CUT stands due to their high relatively high CWD,

although several of the CUT sites in the top right of the figure grouped separately

from the other two stand types due to high percent cover of soil/litter.
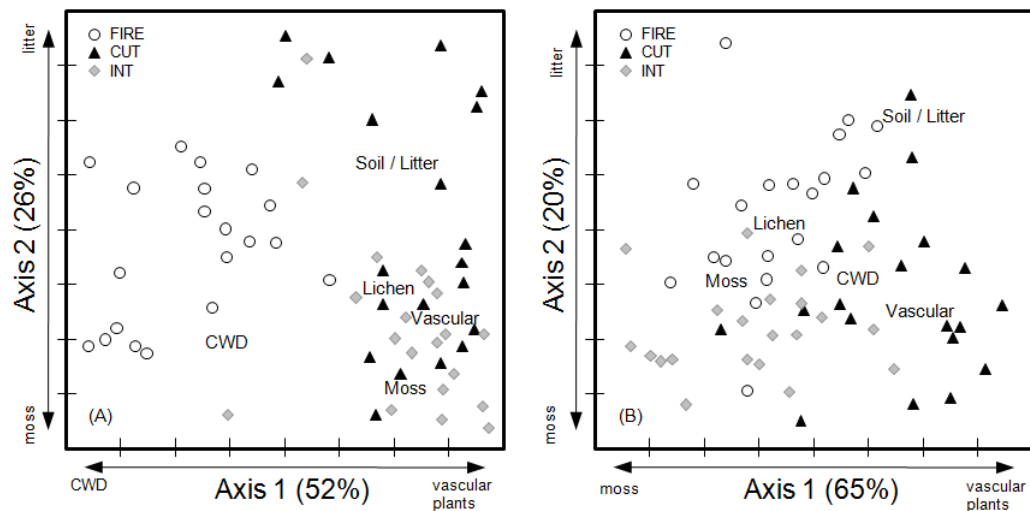
FIG. 3.3: As Fig. 2 except that ordination is for percent groundcover composition on (A) 10-year-old stands ($n = 60$), and (B) 30-year-old stands ($n = 60$) in northwestern Ontario, Canada. Groundcover classes were: vascular plants, moss, lichen, rock, exposed soil/litter, and coarse woody debris (CWD). Axes 1–3 (NMS 3-dimensional solution) had an R^2 of 0.931 cumulatively (0.504, 0.220 and 0.207, respectively) for 10-year-old stands and Axes 1 and 2 (NMS 2-dimensional solution) had an R^2 of 0.857 cumulatively (0.265 and 0.591, respectively) for 30-year-old stands.

In the MRPP permutation procedure ($p < 0.001$, T = -11.64, A = 0.135),

the greatest difference in community composition and tree and shrub abundance,

based on pairwise comparisons, was between CUT and FIRE ($p < 0.001$, T = -12.01, A = 0.16), followed by INT and FIRE ($p < 0.001$, T = -7.10, A = 0.09) and INT and CUT ($p = 0.002$, T = -4.47, A = 0.05). CWD was an indicator of FIRE stands ($p < 0.001$), whereas lichen ($p < 0.001$) and moss ($p = 0.02$) were indicators of INT stands, and herbaceous plants ($p = 0.01$) were an indicator of CUT stands.

30-year-old stands

Again, soil moisture regimes did not differ significantly among treatments (Table 3.1). The NMDS ordination resulted in a three dimensional solution that explained 82% of the variation in the data (final stress = 12.2). Axis 1, which explained 35% of the variation in the data, was similar to the case for 10-year-old stands: most positively correlated with shrubs considered preferred moose forage, this time including mountain maple (tau = 0.421), balsam fir (tau = 0.420) and green alder (tau = 0.419), and most negatively correlated with jack pine (tau = -0.466, Fig. 2B). Axis 2, which explained 29% of the variation in the data, was most positively correlated with mountain maple (tau = 0.372) and beaked hazel (tau = 0.347) and most negatively correlated with jack pine (tau = -0.532). Strongest differentiation among the treatments was shown along the first axis, with CUT tending to have high values, INT having intermediate values, and FIRE the lowest values.

The MRPP had a T value of 6.16 ($p < 0.01$), indicating weaker separation among treatments compared to the 10-year-old stands. In pairwise comparisons,

the greatest difference was between CUT and INT ($p = 0.01$, T = -4.90, A = 0.04),

followed by CUT and FIRE ($p = 0.01$, T = -4.21, A = 0.03) and FIRE and INT ($p = 0.01$, T = -4.02, A = 0.03). Three shrub species were significantly associated

with CUT stands by ISA: green alder, beaked hazel and mountain maple (Table

2.3).

TABLE 3.3: Significant indicator species based on age class and treatment in northwestern Ontario, Canada (FIRE = fire-origin stands and CUT = clear-cut harvested, naturally regenerated). See text for details.

Species	Treatment	Observed indicator value	Indicator Value from randomized groups		
			Mean	S. dev.	*p*
10-year-old sites (*n* = 60)					
Pinus banksiana	FIRE	58.1	38.9	4.54	<0.01
Betula papyrifera	FIRE	50.4	30.7	5.20	<0.01
Pinus banksiana shrub	FIRE	60.1	31.2	5.60	<0.01
Picea mariana shrub	FIRE	57.9	31.4	4.91	<0.01
Betula papyrifera shrub	FIRE	38.4	38.4	7.79	0.02
Populus tremuloides	CUT	44.8	31.7	6.48	0.05
Amelanchier spp.	CUT	37.5	19.3	6.93	0.01
Corylus cornuta	CUT	44.8	14.4	5.27	<0.01
Salix spp.	CUT	49.9	36.3	6.43	0.04
Acer spicatum	CUT	49.9	14.0	5.83	<0.01
30-year-old sites (*n* = 60)					
Alnus crispa	CUT	44.9	26.3	6.34	0.01
Corylus cornuta	CUT	45.0	11.6	4.56	<0.01
Acer spicatum	CUT	35.0	10.1	4.41	<0.01
Abies balsamea	CUT	39.2	10.3	4.61	0.04

Groundcover differed between treatments in 30-year-old stands (FIG.

3.3B), although there was weaker separation evident among the treatments

relative to 10-year-old stands (stress = 3.18, 2- dimensional solution). Axis 1,

which explained 65% of the variation in the data, was most positively correlated

with vascular plants (tau = 0.542), and most negatively correlated with moss (tau

= -0.662). Axis 2, which explained 20% of the variation in the data, was most

positively correlated with litter/exposed soil (tau = 0.743) and most negatively

correlated with moss (tau = -0.401). Groundcover also differed among the FIRE,

CUT and INT stands based on the MRPP permutation procedure ($p < 0.001$, T = -

6.14, A = 0.072). The greatest difference, based on pairwise comparisons, was

between CUT and INT ($p > 0.001$, T = -7.40, A = 0.11), followed by CUT and

FIRE ($p = 0.006$, T = -3.63, A = 0.042) and INT and FIRE ($p = 0.05$, T = -1.94, A

= 0.023). CWD ($p = 0.02$) and lichen (p= 0.02) were indicators for FIRE stands,

moss (p = 0.02) was an indicator for INT stands (Fig. 3.3).

3.3.2 MOOSE PELLET COUNTS

Moose pellet counts were variable and low in both 10-year-old (mean

[±standard error of the mean (SEM)] 0.17 [0.07] pellet groups per 100 m^2) and

30-year-old stands (mean [±SEM] 0.09 [0.05] pellet groups per 100 m^2).

Differences in pellet counts among the silvicultural treatments in each age class

were not significant at the stand level ($F_{1,9} = 1.23$, $p = 0.30$). The percentage of

the landscape around the plots that was harvested and naturally regenerated

(CUT) at a scale of 10 km^2 was significantly, positively correlated with moose

pellet counts in 10-year-old stands ($F_{(1,7)} = 20.7$, $p = 0.004$, $R^2 = 0.74$). The same

was true for areas of 20 km^2 ($F_{1,7} = 13.2$, $p = 0.011$, $R^2 = 0.63$) and 40 km^2 ($F_{1,7}$

= 9.6, $p = 0.021$, $R^2 = 0.55$). The percentage area of INT and FIRE were not

correlated with moose pellet counts at these scales (10 km^2, p = 0.18, p = 0.47; 20

km^2, $p = 0.17$, $p = 0.32$; 40 km^2, $p = 0.45$, $p = 0.42$). Moose pellet counts and the

percentage of the landscape harvested were not significant for 30-year-old stands

for FIRE (10 km^2, $p = 0.28$, 20 km^2, $p = 0.43$; 40 km^2, $p = 0.61$), CUT (10 km^2, $p = 0.29$, 20 km^2, $p = 0.26$; 40 km^2, $p = 0.24$) or INT (10 km^2, $p = 0.36$, 20 km^2, $p = 0.42$; 40 km^2, $p = 0.51$).

3.4 DISCUSSION

Silvicultural investment was important in determining understory, a critical component of habitat for ungulates. Planting and herbicide-spraying accelerate succession toward conifer-dominance by establishing conifer stock and killing competing vegetation (Bell et al., 1997). Stands where the overstory had a higher abundance of deciduous trees also had higher deciduous and total shrub abundance, consistent with other studies (e.g., Legare et al., 2002). Age and post-harvest treatment both influenced groundlayer vegetation, but differences relating to disturbance type and post-harvest treatment may have been more a result of the influence of silviculture on overstory composition. Stands with low non-vascular plant abundance in the composition were likely due to higher leaf litter associated with higher deciduous tree and shrub composition (Beatty & Scholes, 1988). Previous research has shown that deciduous trees (e.g., aspen and birch) are associated with high transmission of light filtering to the understory, high foliar nutrient content, and high pH and base cations, which support greater understory richness and diversity (Paré & Bergeron, 1996; Messier et al., 1998). Pre-established rhizomatous species are more likely to persist after harvesting compared to fire, as logging mainly results in removal of the overstory (Hart & Chen, 2008). In addition to competition for light and moisture, allelopathic effects

likely contribute to lower vascular plant cover as a result of conifer-dominance associated with more intensive silviculture. I propose that two mechanisms are driving differences among the two age classes. For 10-year-old stands, a higher legacy of the pre-disturbance vegetation remains and can explain why the groundcover of harvested treatments differed from groundcover in fire-origin stands. For 30-year-old stands, allelopathic suppression due to the acidity of conifer litter (Mallik, 2008) can explain why post-harvest, naturally regenerating stands were most different from fire-origin and intensive silviculture. Lichen was not abundant and rarely present in young fire-origin stands, consistent with other understory studies in boreal forests (Hart & Chen, 2008).

During the stand initiation phase, i.e., for the young forests I assessed, treated areas were closer to emulating natural disturbance in terms of understory composition than the older forests I assessed. This result suggests two possibilities: (1) the difference in the silvicultural treatment, primarily the type of herbicide sprayed, between the 30- and 10-year-old stands was less effective for the 30-year-old stands or (2) the advantage of using intensive silviculture to emulate vegetation composition post- disturbance is largely lost by 30 years. Both possibilities are supported by previous research. For example, Kennedy & Jordan (1986) found gyphosate-treated areas support half as much moose forage as 2,4-D-treated stands. Likewise, some convergence in forest successional pathways in burned and treated stands is expected, as previously reported for Alaska (Rees & Juday, 2002) and Quebec (Bergeron & Dubuc, 1989). Over time, the influence of herbicide applications on forest understory can be diminished due to persistence

of seeds in the seed bank, seed sources adjacent to the harvested area and the sprouting capacity of competing vegetation (Freedman et al., 1994). Lower abundance of most woody forage species by 30 years in my study is likely explained by the lower light transmission occurring during competitive stem exclusion processes (Ross et al., 1986), which I expect to occur regardless of the disturbance origin and regeneration method.

The potential impact of understory vegetation on ungulates is direct. For the same region, moose, white-tailed deer and wolf populations were largest, and woodland caribou populations smallest, in forests with a higher deciduous component (Bowman et al., 2010), suggesting a link between the increased prevalence of deciduous cover and increased predator abundances. Woodland caribou have been found to use less young, shrub-rich habitat than what is available to them (Hillis et al., 1998); they also avoid mixed and deciduous stands (Courtois et al., 2008). Conversely, both moose and white-tailed preferentially occupy deciduous forests (Krefting and Phillips, 1970), where higher food availability of forage results in earlier sexual maturity and more frequent multiple births (McNicol & Timmermann, 1981). Briand et al. (2009) showed that woodland caribou avoided forest with a dense shrub layer and consequently separated themselves from areas attractive to moose. For moose, trembling aspen, white birch, willow, mountain maple, mountain ash, beaked hazel, green alder, serviceberry and pin cherry are used for forage throughout the year (Peek et al., 1976; Irwin, 1985) with the addition of balsam fir and balsam poplar in the winter (Thompson & Vukelich, 1981; Cumming, 1987). I found stands left for natural

regeneration after clear-cut harvesting supported higher abundance of all of these species compared to planted, herbicide-sprayed and post-fire stands.

Thompson et al. (2003) developed aspatial models based on estimated probabilities of habitat use for a range of boreal wildlife species: in 5–10-year-old conifer-dominated stands, they predicted that moose were three times as likely to use stands harvested and left for natural regeneration than stands with more intensive silviculture; for mixedwoods of the same age, moose use was six times as likely. For stands 10–30-years-old, the same prediction was reduced to twice as likely for both conifer-dominated and mixedwoods stands. Although I found that post-disturbance treatments influence moose forage availability, my estimates of moose use were not correlated to silvicultural treatments at the stand level. As suggested by other studies (e.g., Dussault et al., 2006), moose habitat suitability may be more accurately assessed at scales larger than the forest stand. When I investigated post-disturbance treatments at scales of 10–40 km^2, I found support for the relationship I was expecting (i.e., increased moose use as the amount of CUT forest increased), consistent with forage studies at the moose home range scales (e.g., van Beest et al., 2010). Other factors also may affect habitat use, including cover, human impacts, time lags, and proximity of nearby populations (Gasaway et al., 1989; Rempel et al., 1997; Herfindal et al., 1999; Nikula et al., 2004), factors that I did not investigate in my study. In addition, Laurian et al. (2000) found less moose use $\leq$500 m from roads which may explain relatively low pellet counts on all of my treatment stands.

3.4.1 MANAGEMENT IMPLICATIONS

My study supports the conclusion that post-harvest, vegetation

management influences moose forage, and that vegetation changes associated

with silviculture during stand initiation can impact moose use. Stands left to

regenerate naturally after harvest were most likely to support increases in moose

densities, as a result of associated increases in mixed deciduous habitat abundant

in forage (Brown, 2011). Predetermined financial allocations for silviculture have

been a factor limiting past application of intensive silviculture, although other

factors include ease of access to a site for planting and availability of natural seed

on-site. Regeneration is usually the highest cost in stand management and has the

longest return time on investment (Brace and Bella, 1988). While there are

economic advantages in support of higher quality and quantity of merchantable

wood associated with higher silvicultural investment, these investments are

significant, ranging from $10/ha for natural regeneration to upwards of $1300/ha

for intensive renewal (Arlidge, 1995). Pre-commercial thinning, which I did not

include in my investigation, can also result in diverse understory and overstory

vegetation conditions, as moose forage and moose use may be higher following

this additional investment (Sullivan et al., 2007; McLaren et al., 2000).

Forest regeneration has important implications for both woodland caribou,

which is protected under the Endangered Species Act, and moose, an

economically important species that can also reach levels that eliminate benefits

of silvicultural investments (Thompson & Curran, 1993; McLaren et al., 2000).

However, research linking woodland caribou recovery to silvicultural strategies

has concentrated on improving lichen biomass in mature forests (e.g., Stone et al., 2008), and current management practices potentially underestimate the importance of forest composition; particularly understory composition, in the short to medium terms. Across Canada, guidelines have been implemented to ensure that harvesting in caribou range is aggregated to minimize habitat fragmentation due to harvesting blocks and road building. However, even where the amount and configuration of harvesting achieve patterns similar to fire, the potential for shrub-rich regeneration can create conditions less suitable for woodland caribou. Thus, I recommend forest managers consider moose forage abundance in younger forests as an important monitoring criterion in evaluating silviculture effectiveness in multiple-ungulate systems where caribou occur or may recover.

Geographic Information Systems (GIS), satellite imagery and computer modeling capabilities allow for rigorous evaluation of landscape scale forest dynamics over time and space. There is now opportunity to improve integration of information between the landscape and stand scales, including historical silviculture. The influence of silvicultural treatments on wildlife habitat needs to be better understood within a larger landscape disturbance and regeneration pattern. To improve natural disturbance emulation, an important next step is to integrate the effect of forest regeneration resulting from stand-level silviculture and aggregations of silvicultural treatments over the landscape with population densities of moose, woodland caribou, and their predators.

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CHAPTER 4: FOREST OVERSTORY AND AGE AS HABITAT? DETECTING THE INDIRECT AND DIRECT EFFECTS OF PREDATORS IN DEFINING HABITAT IN A HARVESTED BOREAL LANDSCAPE.[4]

ABSTRACT:

Given the importance of wildlife habitat protection in meeting land use management objectives, criteria for "habitat" identification are surprisingly amorphous. For example, while much current habitat modeling has tended to avoid the term "niche modeling", niche assumptions are implicit – meaning the presence of predators and competitors is essential to whether or not a species uses, or will use, an area. In this chapter, I examine environmental variables associated with woodland caribou (*Rangifer tarandus caribou*) presence in the boreal forests of northwestern Ontario, Canada. Based on winter aerial surveys conducted in 2010-2013, I used logistic regression to identify important habitat characteristics (and/or their surrogates) and structural equation modeling (SEM) to explore causal and indirect caribou habitat relationships, at broad and fine scales. The best-fit regression model (> 10,000 ha) to explain caribou presence, at the broad scale, included the presence of moose (*Alces alces*), wolves (*Canis lupus*), logging roads and primary roads, and all top models included wolves. In contrast, at the fine scale (< 1,000 ha), older, conifer forest was included in all of the top models of caribou presence. Using SEM, at broad scales, I found significant effects of increases in logging road density resulting in a direct increase in wolf presence, and indirectly in a decrease in caribou presence. However, at fine scales, I found significant direct positive effects between moose browse and moose presence, with indirect negative effects on caribou presence. I provide evidence that, at broad scales, habitat identification that includes logging roads and wolves provides a better measure of suitability of an area for caribou occupation than does forest cover alone. I suggest modeling of present or future habitat for woodland caribou will only be marginally effective if additional covariates of predation risk are not inclusive to the quantification of habitat supply.

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4.1 INTRODUCTION

The loss or degradation of habitat is the central cause of declining numbers for many species (Kerr and Deguise, 2004), making wildlife habitat protection an important goal in sustainable land use management. Clearly, where protection of habitat is intended to support species' persistence, habitat and fitness (i.e., higher survival and reproduction rates) are necessarily linked. Habitat has been defined as an area with the combination of resources (e.g., food, cover, water) and environmental conditions (e.g., temperature, precipitation, presence or absence of predators and competitors) that promotes occupancy by individuals of a given species and allows those individuals to survive and reproduce (Morrison & Hall, 2002). Habitat quality varies, ranging from low (i.e., supports survival), to medium (i.e., supports reproduction), to high (i.e., supports population persistence; Hall et al., 1997). Habitat selection is a hierarchical process that involves both innate and learned behavioral decisions made by an animal regarding what habitat to use (Johnson, 1980), and selection is ultimately based on survival and subsequent reproductive success (Hildén, 1965). Differential habitat selection is a fundamental aspect of species coexistence (Rosenzweig, 1981). In practice, researchers infer preference and selection based on habitat use, assuming species select habitat (i.e., use some resources disproportionally over others) where their fitness is higher.

Grinnell (1924) considered the niche to be the ultimate unit of habitat. However, current habitat modeling has tended to avoid the term "niche modeling," owing largely to concerns over data limitations. Nonetheless, niche

assumptions are implicit. Spatial models are not applicable over time and space

unless one assumes that environmental predictors estimate, however imperfectly,

an underlying biological phenomenon (Warren 2012). Without the niche

assumption, there is no apparent reason to expect that the present and future

distribution of a species should be linked through a set of environmental

predictors (Warren, 2012). Modeling an organism's niche is required if we are to

explain, and most importantly predict, habitat use and distribution limits

(Kearney, 2006).

Nonetheless, there are species for which important elements of niche are

not generally associated with legal interpretations of their "habitat." Woodland

caribou (*Rangifer tarandus caribou*) are one such example. Woodland caribou

declines have been reported across Canada (Environment Canada, 2008): caribou

and their habitat are protected by federal and provincial laws. Most current

research supports the hypotheses that higher predation is the key factor in decline

and that larger wolf (*Canus lupus*) populations are due to increased abundance of

early seral-stage, forage-rich hardwood and mixedwood forests, created largely by

logging, and supporting additional prey for wolves, including moose (*Alces alces*

L.: e.g., Courtois et al., 2008). While predation and apparent competition appear

to play a primary role in habitat selection by caribou (Seip, 1992; Hillis et al.,

1998; Gustine et al., 2006; Wittmer et al., 2007; Bowman et al., 2010), habitat

modeling generally relies on forest overstory composition as a surrogate for

predator avoidance. At present, caribou habitat quantification by resource

managers is largely limited to defining one surrogate: older, conifer forests.

Here, my objectives were to (1) examine environmental variables expected to be linked to the caribou niche, including the presences of moose and wolves, and (2) explicitly integrate indirect relationships between activities anticipated to decrease caribou use, specifically road building, timber harvesting and post-harvest regeneration, and their effects on moose and wolf presence in my study area. I hypothesized that winter habitat models that predicted caribou use best would include variables that increase the likelihood of moose and wolf activity. Further, I predicted (1) that forest overstory composition and age alone will not provide strong prediction of caribou presence, rather, that the presence of both wolves and moose will strongly predict a decrease in caribou use, and (2) that the indirect effects of the amount of timber harvesting, percentage of area harvested and left for natural regeneration and presence of logging roads will result in an increase in the likelihood of wolf and moose presence. Furthermore, I predicted that these relationships will be scale-dependent. The fitness costs and benefits of habitat selection change with scale; habitat selection may correspond to different limiting factors at different scales (Mayor et al., 2009; Johnson, 1980). I expected that at broader scales, woodland caribou will select areas with lower moose, wolves, road densities and young seral forest. At finer scales, woodland caribou will select habitats with forest stands likely to provide more winter forage (e.g., older, conifer forests expected to support higher lichen abundance, an important winter food for caribou), as forage availability is expected to be less likely than predation to limit woodland caribou at the population scale (Rettie & Messier, 2000). In this Chapter, I demonstrate an application of structural equation

modeling (SEM) in my assessment of the direct and indirect relationships between environmental predictors and habitat use by woodland caribou. The results of my analyses have important implications for the identification and quantification of habitat for woodland caribou and other species at risk. If environmental variables other than forest overstory describe habitat more accurately in the context of the resources and conditions required for species' survival, then the lack of inclusion of these variables may overstate the amount of habitat available now and into the future.

4.2 METHODS

4.2.1 STUDY AREA

Data collection took place in the English River Forest and Caribou Forest Management Units, approximately 200-600 km northwest of Thunder Bay, Ontario (FIG. 4.1). Forest cover consisted mainly of black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) growing in relatively pure stands or in association with white spruce (*Picea glauca* [Moench] Voss), balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides* Michx), and white birch (*Betula papyrifera*). Jack pine stands are extensive on the sandy plains and rocky uplands, whereas black spruce dominates in peat-filled depressions. Monthly mean temperatures are -−19 °C in January and 19 °C in July, with 204 cm average annual snowfall and 517 mm average annual rainfall (Environment Canada, 2005: Sioux Lookout 50°7′N, 91°54′W, 1971-2000). The study area includes portions of two caribou management ranges defined by the Ontario Ministry of Natural Resources (Ontario's Brightsand and Churchill ranges) and

four Wildlife Management Units (15A, 15B, 16A, 16C). My study area included

areas both occupied and unoccupied by caribou, as well as a gradient of

anthropogenic disturbance. Caribou density estimates for these ranges were not

available at the time of my research; however, wolf density for the study area is

estimated to be 6.0 – 7.5 wolves per 1000 km^2, with approximately 140 moose per

1000 km^2 (Rodgers et al., 2009).
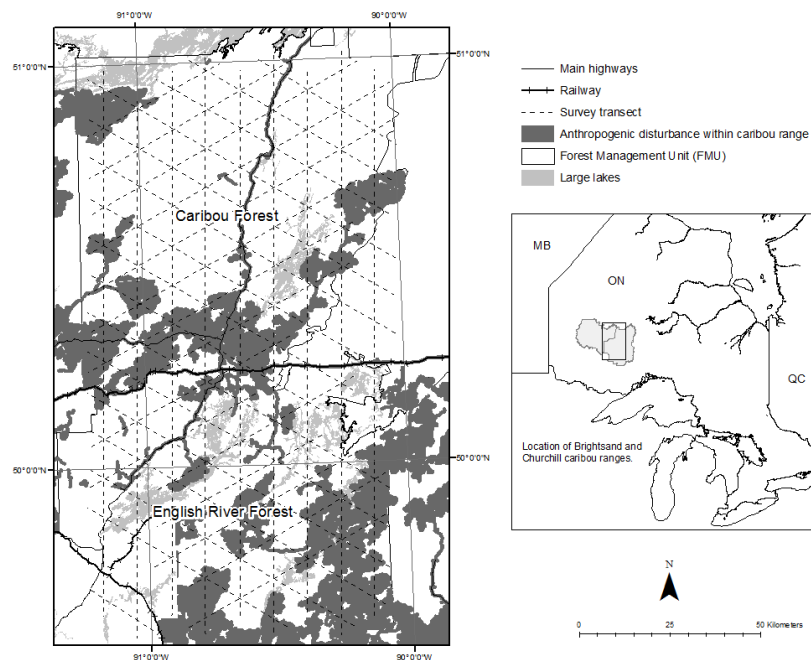
FIG. 4.1: Location of study area in northwestern Ontario, Canada showing aerial survey transects (2010, 2011 and 2013) as dotted lines.

4.2.2 *AERIAL SURVEYS*

I conducted woodland caribou, moose and wolf surveys during January

27-February 18, 2010, February 2-29, 2012 and February 13-March 7, 2013 using

a Cessna 172 fixed-wing airplane (cruise speeds of approximately 120 km/h,

mean altitude 150 m). A systematic sample was produced by flying transects

approximately 10 km apart over an area of 11,000 km^2 (transects totaled c. 3,740

km). I followed north–south and diagonal (northwest–southeast and southwest–

northeast) fly routes through the centers of 6000 m radius hexagon cells (adapted

from Magoun et al., 2007). Surveys were conducted 1-–4 days after a "track

obliterating" snowfall (fresh snowfall of at least 5-–10 cm). I used both track

identification and animal sightings to establish presence.

The aerial surveys resulted in presence/absence data for 130 (~10,000 ha)

hexagons (each hexagon was surveyed during each of the 3 years). For my study,

I assumed that occupancy and detection probabilities were constant across both

space and time (Mackenzie, 2005), based on the following rationale: (1) caribou

are highly mobile, and daily winter movement rates were expected to be

consistent with woodland caribou in other parts of the boreal forest (e.g., 0.64 ±

0.13 km/day; Stuart-Smith et al., 1997). Consequently, I assumed that the high

likelihood of animals using adjacent lakes and rivers (both frequent and dispersed

throughout my study area) where detectability is very high compensated, in part,

for potential missed detection due to canopy cover. (2) Woodland caribou tend to

group together during winter months (Darby and Pruitt, 1984), and are, as a result,

generally considered conspicuous during winter surveys. By revisiting transects

over 3 years we were confident in a high probability of detection due to multiple

opportunities for observation. (3) Previous studies in eastern Manitoba and

Ontario found little to no discernible difference in caribou distribution in the

winter from year to year (Stardom, 1977; Cumming et al., 1996). If my

assumptions were incorrect, I could be omitting areas used by caribou.

4.2.3 COVARIATES

I calculated 8 environmental variables at multiple scales based on my *a priori* hypotheses: moose presence, wolf presence, a conventional habitat model (i.e., amount of caribou preferred winter habitat based on forest composition and age), amount of moose dormant season browse, density of logging and primary roads, area harvested and left for natural regeneration and the amount of edge habitat (Table 4.1). The presence of moose and the presence of wolves were considered environmental variables for all analyses (i.e., the presence of predators and apparent competitors). I calculated primary and logging road density using a combination of available data (OMNR, 2009; Minutillo and Marleau, 2005) and updates, where required, based on new interpretation of satellite imagery (ESRI, 2012). We used Ontario's Landscape Tool (Elkie et al., 2013) and Forest Resource Inventories (FRI) to generate continuous coverage of the relative amount of moose dormant season browse and caribou winter habitat. Using FRI, moose dormant season browse was based on a 50 m grid the amount of predicted browse (kg/ha) based on ecosite, development stage, stand age, overstory tree species composition and canopy closure (see details in Elkie et al., 2009). Caribou preferred winter habitat also was determined from FRI-based forest age and tree composition (Elkie et al., 2010). Edge density was calculated as the number of kilometers per hexagon where areas expected to be food-rich habitats for moose (moose dormant season browse) were juxtaposed with habitat providing shelter against predation risk during the winter and/or where snow depth was expected to be less. I defined this "dormant season cover" as conifer and mixedwood stands

with an average canopy height of >6 m. Lastly, previous research found that,

relative to fire, the intensity of post-harvest silviculture influenced habitat

suitability for moose, with increased moose use associated with greater amounts

of naturally regenerating logged forest in the surrounding landscape (Boan et al.,

2011). Therefore, I included area harvested and left for natural regeneration (5-25

years) in each hexagon in my analyses. Unfortunately, FRI information was not

available for the large wilderness-class park in the study area (Wabakimi

Provincial Park) or for the private land holdings that overlapped with my study

TABLE 4.1: Description of variables used to model caribou presence within the Caribou and English River forests, Ontario, Canada. Presence was determined by track or animal sighting in at least one year of observation.

Acronym	Description	Unit of measurement	Supporting Literature
MS	Moose presence recorded through winter aerial surveys (2010-2013)	0/1	Fuller et al. 1992
WF	Wolf presence recorded through winter aerial surveys (2010-2013)	0/1	Bowman et al. 2010
PR	Primary roads considered permanent infrastructure	km/km^2	Dyer 1999; Whittington et al. 2004
LR	Logging roads built for accessing timber and other post-harvesting treatments	km/km^2	Mladenoff and Sickley 1998; James and Stuart- Smith 2000; Dyer et al. 2002
CUT	Area harvested for timber and left for natural regeneration (i.e. no herbicide spraying or planting)	Percentage of sample unit	Boan et al. 2011
MBROW	Moose dormant season browse	Percentage of sample unit	Bowman et al. 2010
EDGE	Distance of MBROW boundary adjacent to conifer-dominated (>70%) or mixedwood forest, height > 6m	Km/km^2	Hamilton et al. 1980
CHAB	Area of conifer-dominated (>70%) forest greater than 60 years old.	(Area CHAB/Area sample unit)*100	Elkie et al. 2010

area, so these areas were omitted from my final analyses (22 hexagons with a

6000 m radius, $n = 130$).

4.2.4 STATISTICAL APPROACH

I used logistic regressions and structural equation modeling (SEM) to test

a set of proposed explanatory models to assess to what extent timber harvesting

and road building explain presence or absence of moose and wolves and the

subsequent presence or absence of caribou in the hexagon cells. Logistic

regression allowed me to calculate how a change in environmental covariates

affected the odds of caribou being present, and rank best -fit models. However,

subsequent SEM allowed me to test indirect relationships, a key component of

current hypotheses regarding woodland caribou habitat use. We were able to take

best-fit models a step further and test potential causal relationships among

variables. Multicollinearity was tested using Spearman's correlation, and none of

the relationships between the variables was significant at $p < 0.05$, except for

those between logging and primary roads ($r = 0.310$, $p = 0.01$) and between

wolves and logging roads ($r = 0.238$, $p = 0.01$). We considered the differentiation

of logging and primary roads to be of importance to the analysis, so we

maintained both variables. Additionally, we deemed the correlation between

wolves and logging roads to represent an important mechanism in explaining

caribou presence, therefore biologically meaningful and not redundant, so we also

kept both of these variables in the analyses.

4.2.5 SCALE SENSITIVITY

My approach to scale selection for modeling was iterative. I initially identified hexagons with 5000 m radii (DeCesare et al., 2012) to test hypotheses of broad scale habitat selection where I expected predator presence, directly, and greater moose presence/moose browse, indirectly, to determine caribou presence. Further, I tested additional scales, evaluating increments of 250 m radii larger and smaller than the original (e.g., 4500 m, 4750 m… etc). Using a stepwise selection method with entry testing based on the significance of the score statistic, and removal testing based on conditional parameter estimates (Conditional Forward Selection), I selected 6000 m radius and 2000 m radius hexagons for final analyses, as at these two scales I found highest predictive results, as well as evidence of significant change in the importance of environmental parameters.

4.2.6 LOGISTIC REGRESSION

I used information-theoretic methods based on Akaike's Information Criterion (AIC) because they permitted comparisons of models with different sets of variables. I compared 11 candidate models based on combinations of environmental covariates that both included and excluded presence of moose and wolves and also included single-predictor (caribou preferred winter habitat) model, including the null model (intercept only) and global model (which included all covariates), for their ability to predict caribou presence in winter, corrected for small sample sizes (AIC$_c$; Akaike, 1973).

I used Akaike weights (Burnham and Anderson, 2002) as an additional measure of the strength of evidence for each model and evaluated goodness-of-fit

and predictive power using an adjusted coefficient of determination (Nagelkerke,

1991). The model with the lowest AIC_c was considered to be the best

approximating model in the candidate set. I incorporated all models through a

weighted average (model averaging) of the models' regression coefficients to

examine uncertainty in the best model prediction (Buckland et al., 1997). I

compared predictive performance using Cohen's Kappa statistic for top models

(with $\Delta AIC_c \leqslant 5$ compared to the model with the lowest AIC_c). I used the

Statistical Package for the Social Sciences (v. 17) to run logistic regressions

(SPSS, 2008).

4.2.7   *STRUCTURAL EQUATION MODELING*

In addition, I tested models with the lowest AICc scores, at both broad and

fine scales, using structural equation modeling (SEM). SEM can evaluate

complex ecological processes where multiple and concurrent interacting processes

are hypothesized to take place (Grace, 2006). Unlike the variables in the logistic

regressions, SEM variables can be both dependent and independent, which

allowed investigation of indirect effects and potential causality; SEM could

evaluate both direct (e.g., presence of wolves) and indirect effects (e.g., logging

roads facilitating wolf access which effects the presence of caribou), explicitly. In

this sense, I considered it an approach to test the mechanisms behind the

correlations in the environmental factors explaining caribou presence.

As each of the dependent variables (caribou, moose and wolf presence)

were measured dichotomously (i.e., having only two possible values:

present/absent), traditional methods for structural equation models that assume

continuous dependent variables and linear relationships were problematic.

Therefore, I used probit models which assume that the dichotomous dependent

variable is the realization of an unobserved (i.e., latent) continuous variable

(Finney and DiStefano, 2006). In the context of my data, this unobserved

continuous variable is analogous to the propensity to observe caribou in a given

area.

At the broad scale (6000-m radius), the SEM model included the indirect

effect of logging roads and primary roads (through wolf presence), and the direct

effect of wolf and moose presence on caribou presence. At the fine scale (2000-m

radius), models included the indirect effects of moose dormant season browse,

and area harvested and left for natural regeneration and the direct effects of moose

presence, and caribou preferred winter habitat on caribou presence. I tested model

fit using a Chi-square goodness of fit statistic and the root mean square error of

approximation (RMSEA). For Chi-square, a non-significant p-value (> 0.05) of a

proposed model suggests that the model and data structures do not differ

significantly and therefore that the proposed model is a plausible representation of

the relationships among variables. RMSEA also considers model parsimony and $<$

0.05 indicates a good fit (Browne and Cudeck, 1993). RMSEA is appropriate in

confirmatory context (Rigdon, 1996). For the SEM, Mplus software was used

(MPLUS version 6.11, 2011).

4.2. SPATIAL AUTOCORRELATION

Spatial autocorrelation is an underlying characteristic of bio-geographical data. However, it can increase the chance of a Type I error, and lead to a conclusion that there is a pattern when, in fact, one does not exist (Boyce, 2006). To test for spatial autocorrelation, I used Moran's *I*. Values of Moran's *I* are assessed by a test statistic (the Moran's I standard deviate) which indicates the statistical significance of spatial autocorrelation in model residuals.

I found spatial distribution of values in the dataset more spatially clustered than would be expected if underlying spatial processes were random (Moran's index = 0.53; Z = 9.01; $p < 0.01$). To test the effect of the lack of spatial independence associated with the contiguous sampling for the broad scale analysis (i.e., all hexagons directly adjacent to other hexagons), I reran logistic regressions using stratified samples from the data set to increase spatial separation. I tested multiple subsets of hexagons ($n = 20$) a minimum of 10 km apart and we compared Kappa values (the proportion of correctly predicted presence after the probability of chance agreement is removed).

4.3   RESULTS

4.3.1   *LOGISTIC REGRESSIONS*

The best-fit model at the 6000 m radius scale was Model 3, which was able to predict 80% of caribou absences and 73% of presences correctly (Akaike weight = 0.43). This model included information on the presence of moose, wolves, logging roads and primary roads, all of which were correlated with decreases in caribou observations (Table 4.2). The second best model was Model

TABLE 4.2: Candidate models for predicting woodland caribou (Rangifer tarandus caribou) presence in the English River and Caribou Forests in northwestern Ontario. Acronyms are: MS = moose presence, WF = wolf presence, PR = primary road density (km/km^2), LR = logging road density (km/km2), CUT = harvested and left for natural regeneration, MBROW = dormant season winter moose browse, EDGE = km of MBROW adjacent to conifer-dominated or mixedwood forest (ht > 6 m), CHAB = caribou preferred winter habitat. Models were ranked by corrected Akaike's Information Criterion (AIC$_c$) and Akaike weights. Models with ΔAIC$_c$ < 5 are in bold.

	Model Number	Model description	2000 m radius			6000 m radius		
			ΔAIC$_c$	Akaike weights (all models)	Nagelkerke Pseudo-R^2	ΔAIC$_c$	Akaike weights (all models)	Nagelkerke Pseudo-R^2
	0	Intercept	18.05	0	0	46.80	0	0
Preferred winter habitat only	1	CHAB	**4.45**	**0.07**	**0.20**	31.39	0	0.18
Alternate Prey with Predator	2	MS + WF	10.53	0	0.16	30.46	0	0.21
	3	MS + WF + PR + LR	8.16	0.01	0.23	**0.00**	**0.43**	**0.52**
Alternate Prey Habitat with Predator	4	MS + WF + CUT	11.87	0	0.17	30.08	0	0.24
	5	MS + WF + CUT + MBROW + MBROWxEDGE + CHAB	**3.98**	**0.09**	**0.32**	7.09	0.01	0.50
Alternate Prey Habitat without Predator	6	MS + CUT + MBROW+ CHAB	**0.00**	**0.64**	**0.31**	6.98	0.01	0.46
Predator Efficiency	7	WF + PR + LR	15.75	0	0.15	**1.65**	**0.19**	**0.49**
	8	WF + CHAB + PR + LR	**3.72**	**0.10**	**0.28**	**2.02**	**0.15**	**0.50**
Alternate Prey Habitat and Preferred Habitat	9	MS + CUT + MBROW + MBROWxEDGE	**4.31**	**0.07**	**0.31**	8.69	0.01	0.47
Alternate Prey / Habitat and Predator Efficiency	10	MS + WF + CUT + PR + LR	8.88	0.01	0.25	**1.48**	**0.20**	**0.52**

10, which included the additional variable of area harvested and left for natural

regeneration (ΔAIC_c = 1.48, Akaike weight = 0.20).

Moose browse and the interaction between moose browse and edges were

not included in any of the top models. Caribou preferred winter habitat was

present in one of the top models (Model 8, ΔAIC_c = 2.02, Akaike weight = 0.15),

along with wolf presence and roads. Percent of variation explained approached

50% for all models (R^2 = 0.49-0.52). Model averaging (Table 4.3) indicated that

logging roads were the strongest negative predictor of caribou presence (based on

a 95% confidence interval).

TABLE 4.3: Estimated logistic regression coefficients explaining caribou presence from best-fit model (moose + wolves + primary roads + logging roads) and model averages (based on top 4 broad scale models with ΔAIC_c < 2).

Variable	β_n	Standard error (SE)	Weighted Model Averaging	
			Averaged β_n	Averaged SE
Moose presence (MS)	-1.630	0.878	-1.933	0.951
Wolf presence (WF)	-1.493	0.540	-2.029	0.751
Primary road (PR)	-0.567	0.623	-0.806	0.849
Logging road (LR)	-3.025	0.703	-6.105	1.012
Area harvested and left for natural regeneration (CUT)	--	--	0.004	0.007
Caribou preferred winter caribou habitat (CHAB) – conventional model	--	--	0	0
Constant	4.727	1.139	9.551	1.402

In analyses at the 2000-m radius scale, caribou preferred winter habitat was included in all of the top AIC models (Table 4.2), but overall these models had lower prediction success for the presence of caribou. The best-fit model at the 2000-m radius scale was Model 6, and included moose presence, caribou preferred winter habitat, area harvested and left for natural regeneration and moose dormant season browse (Akaike weight = 0.64). R^2 values approached 0.30 for all models that included caribou preferred winter habitat.

4.3.3 STRUCTURAL EQUATION MODELS

At the broad scale, for Model 3, two direct effects were significant (Fig. 4.2). Areas with wolves were associated with fewer caribou observations (β = −1.042, SE = 0.411, p = 0.01). Additionally, increases in logging road density led to a higher presence of wolves. There was also a significant indirect effect of logging roads on caribou presence. Increase in logging roads were associated with
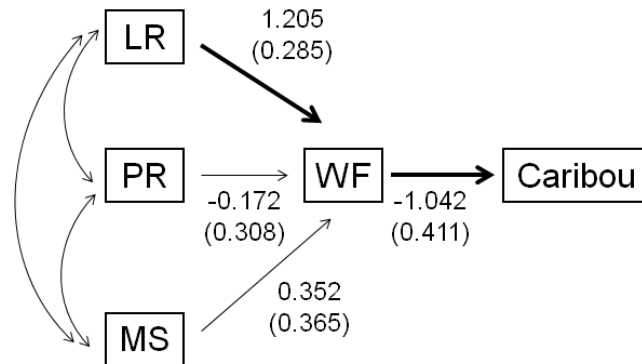

FIG. 4.2: Two-path diagram of probit coefficients and their respective standard errors at a scale of 6000 m radius hexagons (for a model relating MS + WF + LR + PR). Significant direct effects include logging roads on wolf presence (p < 0.05), and wolf presence on caribou presence (p < 0.001). Significant indirect effects include logging roads on caribou presence (p < 0.05).

fewer caribou observations ($\beta = -1.255$, SE $= 0.535$, $p = 0.02$). However, the

model statistic suggested the overall model fit was not strong ($\chi^2 = 19.326$,

$p < 0.001$, RMSEA $= 0.224$).

At the finer scale, for Model 6, which included moose presence, moose

dormant season browse, caribou preferred winter habitat, and areas harvested and

left for natural regeneration, several paths were significant (Fig. 4.3). First, areas

with moose presence were associated with fewer caribou observations

($\beta = -0.532$, SE $= 0.206$, $p = 0.01$). Second, increases in caribou preferred winter

habitat were associated with more caribou observations ($\beta = 0.013$, SE $= 0.004$, p

$= 0.01$). In addition, increases in moose browse were associated with more moose

observations ($\beta = 0.002$, SE $= 0.001$, $p = 0.01$). The moose dormant season

browse measure also had a significant indirect effect on caribou. Increases in

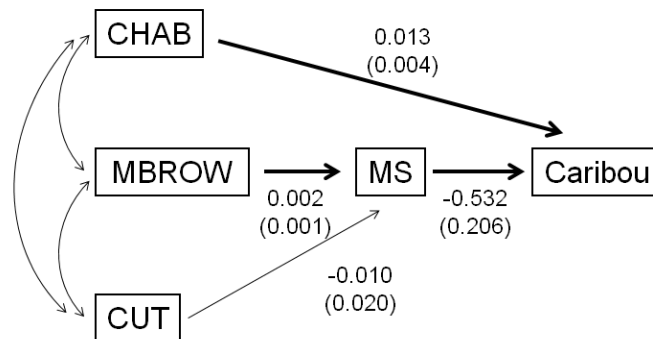moose browse were associated with fewer caribou observations ($\beta = -0.001$,

FIG. 4.3: Two path diagram of probit coefficients and their respective standard errors at a scale of 2000 m radius hexagons (MS + CHAB + MBROW + CUT). Significant direct effects include 1) moose presence on caribou presence ($p < 0.05$), 2) winter caribou habitat on caribou presence ($p < 0.01$), 3) moose browse on moose presence ($p < 0.01$). Significant indirect effects include moose browse on caribou presence ($p < 0.05$).

SE = 0.001, p = 0.04). In this case, the model statistic suggested an adequate fit

(χ^2 = 4.231, p = 0.24, RMSEA = 0.065).

4.4   DISCUSSION

Woodland caribou habitat selection occurs at multiple scales (Rettie and

Messier, 2000; DeCesare et al., 2012), and multiple scales of modeling may be

required to characterize the full context of habitat relationships (Boyce, 2006). I

did find that caribou presence in the study area appeared to correspond to limiting

factors at scales of importance. Wolf presence was included in all of the top

models at the 6000-m radius scale, whereas surrogates for forage were included in

the top models at the 2000-m radius scale. These results support the hypothesis

that limiting factors are driving selective behavior at increasingly finer scales until

it is overcome by the next most dominant limiting factor supersedes selection

(Rettie and Messier, 2000).

At the broad scale, each of the best-fit AIC models included wolves and

roads, suggesting that the presence of predators and their ability to move

relatively efficiently across the landscape and/or perceived predation risk are

important in the identification of areas of caribou use at this scale. In contrast, the

model based only on overstory tree composition and forest age – the more

conventional depictions of caribou habitat - was not a strong predictor of caribou

presence (Table 4.2). This outcome is consistent with conclusions for other

species, where the inclusion of additional predictor variables representing the

presence–absence of known competitors and/or predators has been shown to

significantly increase the predictive power of models (e.g., Guisan and Thuiller,

2005, Poley et al., 2014). Factors with greater potential to reduce individual

fitness are expected to be avoided at broad spatial scales. Avoiding the factors that

are most limiting at each successive scale will maximize an individual's fitness.

As such, caribou exhibit strongest selection at the scale that permits them to avoid

the effects of predation (Rettie and Messier, 2000). While the causes for the range

recession are likely multifaceted, studies have shown a close correlation between

the recession of woodland caribou and the northward progression of timber

harvesting and associated road development in the province (Schaefer, 2003).

Reduced availability of forage and increased distribution and abundance of

predators are considered limiting factors most closely related to timber harvesting

(Johnson et al., 2004). Previous research has argued that commercial timber

harvesting increases abundance of other ungulate prey that use early seral-staged

forests (e.g., moose) and supports the contention of asymmetric predator-mediated

apparent competition and caribou declines. However, my models demonstrated a

greater importance of the road network as a negative indicator of caribou presence

than the presence of early seral stage forests at the broad scale, similar to

Bowman et al., 2010. While, an active approach to post-harvest regeneration (e.g.,

herbicide spraying and planting versus post-harvest, natural regeneration) a

strongly discriminating factor explaining spatial separation among wolf prey in a

multi-ungulate system (Boan et al., 2011), I found that the addition of the

proportion of post-harvest regeneration is an important contribution only in my finer scale models.

SEM at the broad scale did not result in strong model fit for a number of reasons. While ideally, as a reflection of strong predictive power, model fit statistics based on the Chi-square distribution will be non-significant, in many applications this does not hold true. For example, Chi-square will increase with non-normally distributed data, as was the case with my data. However, I think the significant indirect effects show the value of the SEM approach, overall. In addition, I expect there are other variables not included in my models that may increase model fit. For example, animal perceptions of predation risk are often the result of interactions between predator abundance and behavior, availability of alternative prey, landscape context and habitat structure, and environmental predictors of predators vary significantly both temporally and spatially. Risk of interaction with humans and/or territorial boundaries may further explain wolf presence, and result in better overall model fit.

4.5 MANAGEMENT IMPLICATIONS

In light of the costs required to monitor animals, maintaining a specific amount and configuration of a vegetation type(s) is often assumed to meet the legal direction for management: to prevent wildlife species from being extirpated or extinct, and provide for the recovery of wildlife species that are extirpated, endangered or threatened as a result of human activity. For example, it is the maintenance of overstory forest cover types that is most closely monitored and

reported through forest management planning (Thompson et al., 2007). In addition, land managers are expected to manage not only the current habitat of a species, but also to model future habitat conditions. Such modeling is used as a tool to assess potential impacts in land-use decisions and establish conservation priorities. In forest management, habitat is often considered synonymous with vegetation type; forest age and overstory tree composition are considered surrogates for caribou habitat (Schaefer and Pruitt, 1991), yet, the determination of factors responsible for the presence of a population of animals in an area and its habitat use are complicated, interrelated and not completely apparent (Morrison et al., 2006). Accurate species-environment relationships are critical, particularly as a result of legal implications associated with the protection of habitat for species at risk. A reliance on assumed understanding of ecological processes and patterns could result in misplaced resources, or worse from a conservation perspective, harmful management actions (Loiselle et al., 2003).

Overstory tree composition and age, alone, were not the strongest surrogates for predicting woodland caribou use during the winter. As such, we argue that legislation, policy and research defining habitat should explicitly consider the presence of predators and competitors. Managers must understand fitness consequences of management decisions by quantifying more than the amount and/or configuration of a vegetation feature. Since the goal of protection of habitat is the survival and recovery of a species, habitat should be explicitly tied to fitness. While this study did not endeavor to calculate demographic changes, we did take the first step at expressing a mechanistic analysis of how

environmental factors (e.g., the presence of predators and their alternative prey) influence the presence of caribou. In conclusion, an understanding of the niche is critical when ecologists attempt to predict an organism's future distribution (Kearney, 2006). Modeling future habitat for woodland caribou in winter, a critical season to their survival, will only be marginally effective if additional covariates of predation risk are not inclusive to the quantification of habitat supply.

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CHAPTER 5: CONCLUSIONS AND RECOMMENDATIONS

More than 200 peer-reviewed studies have been published on woodland caribou in Canada in the past decade. An overarching theme expressed through this body of research is the premise that, while predation is likely the proximate cause of population decline, alterations to habitat that support predator increases is the ultimate cause. My research is consistent with those findings, and suggests that, as a result of changes to habitat introduced through anthropogenic disturbance, the use of forest overstory and age as surrogates for woodland caribou habitat is limited.

However, there are two important considerations in the interpretation of my results: (1) I used presence of caribou as an indicator of habitat quality, which has the potential to mislead as caribou may be present in areas that have negative impacts on their fitness (e.g., habitat sinks), and (2) I relied strictly on winter observations, which potentially belies the overdispersed arrangement of females at calving and post-calving, and does not illuminate habitat relationships with the mounting evidence of the importance of black bear predation on caribou (Pinard et al., 2012). First, forest management plans that rely on habitat characteristics to infer habitat quality are quite speculative, both with regard to population persistence and pertaining to predictability of species densities based on habitat characteristics (Van Horne 1983). As such, correlating my results explicitly with survival and reproduction characteristics would contribute substantially to ensuring my proposed model covariates indeed improve the delineation of habitat.

While outside of the scope of my research, one could apply demographic information, including adult survival rates and / or calf recruitment, on the Brightsand caribou range when OMNR's range assessments become publicly available (not available at time of writing). Further, conducting similar analyses to compare ranges in decline and those that are stable in northwestern Ontario would advance my assessment of the efficacy of conventional caribou habitat models. Second, in regard to the seasonal focus of my model, winter provides the best conditions for detecting animal tracks via aerial survey. However, the same covariates I modeled for winter could be tested with caribou and wolf collaring data, in place of presence-absence data recorded through my aerial surveys, to provide information on habitat during seasons where caribou are more difficult to detect visually. Nonetheless, other studies have shown that caribou avoid recently harvested areas during calving, summer and the fall rutting period (e.g., Hins et al., 2009).

IMPLICATIONS FOR FOREST MANAGEMENT IN ONTARIO

Prior to the 1800s, the range of woodland caribou spanned much of North America, including parts of northern United States (Banfield 1961). Subsequent range recession and population decline have received much attention (Vors et al., 2007), with approximately half of the historic range of the forest-dwelling ecotype being lost over the past 100 years. The result has been that woodland caribou are now protected by federal and provincial legislation. Protection of habitat is a key management goal linked to conservation of the species. However, publicly-owned forests in Ontario, which comprise the vast majority of land within current

caribou range in this province, are subject to a complicated array of definitions of habitat. For example, Ontario's evolving forest management policy under the Crown Forest Sustainability Act (1994), Ontario's Endangered Species Act (2007), and Environment Canada's (2008) definition of critical habitat each have distinct definitions of habitat with important implications for woodland caribou. The following is a brief consideration of the extent to which these definitions are consistent with the evidence and implications of my findings.

The Ontario Crown Forest Sustainability Act (1994) requires that Forest Management Plans (FMP) identify threatened and endangered species as "featured species", and provide for their protection within the area covered by the plans. The management emphasis is on making efforts to mitigate impacts. In addition, the Province has introduced policy, the Caribou Conservation Plan (CCP; OMNR 2009a), that provides broad policy direction regarding woodland caribou conservation and recovery in forest management planning, among other planning initiatives. The most significant direction in the CCP as it pertains to FMP is to provide for the maintenance of a continuous and predictable supply of mature conifer forest through forest renewal, both for "quality caribou habitat" and to provide "a reliable source of wood" for the forestry sector (OMNR, Winter 2012, p. i).

Ontario has committed to conducting and reporting on range assessments for the caribou ranges within the province (CCP). In Ontario, range condition and population risk for caribou are determined by: 1) assessing the amount of disturbance and evidence of caribou population size and trend, and 2) combining

this assessment with an evaluation of the amount and distribution of habitat in comparison with an estimated natural condition (Elkie et al. 2012). At the time of writing this thesis, no range condition reports were available in Ontario. The Forest Management Planning Manual provides direction to maintain a continuous supply (spatially and temporally) of habitat for woodland caribou (OMNR, 2009b), and management objectives are required to consider the Endangered Species Act, 2007, including any applicable habitat regulations and relevant policy direction.

In practice, "habitat" is calculated as the amount and configuration of older, conifer forests, and compared to historical and simulated amounts and configurations of older, conifer forests. This definition of habitat is based on the implicit assumption that overstory tree composition and age depicted in FRI provide a good surrogate for "area on which [the caribou] depend, directly or indirectly, to carry on its life processes." However, in my research, I found that models to quantify habitat based solely on forest overstory and age performed poorly compared to those that included other indirect and direct effects of logging. This performance review suggests that the value of conifer to caribou depends not only on its age, but also the ability of surrounding landscape to facilitate hunting by wolves, either through provision of adjacent adjacent young forest or road access. Further, I showed that post-harvest understory characteristics related to ungulate forage and that potential caribou refuge habitat from their predators and alternate prey varied significantly depending on post-harvest regeneration approach. Abundance of hardwoods, shrubs, and herbaceous

plants was greater in naturally-regenerated post-harvest stands than in fire-origin

and artificially regenerated post-harvest stands at both 10 and 30 years post-

disturbance. Moose use increased as a function of the amount of naturally

regenerating logged forest in the surrounding landscape. The intensity of post-

harvest silviculture influences habitat suitability for moose, and based on current

knowledge of spatial separation, the effect likely cascades to other ungulates, such

as woodland caribou.

In addition, while undertaking my research, Ontario passed a new

Endangered Species Act (ESA, 2007), which updated previous legislation (1971).

The new law recognized that recovery of species required not only protection of

the species themselves, but also of their habitat (Ontario's Endangered Species

Act, 2007). The ESA prohibits damage or destruction to the habitat of endangered

and threatened species. Once a species is listed as endangered or threatened on the

Species at Risk list, timelines are set to define the habitat for the species in a

habitat regulation. Ontario's Endangered Species Act (2007) defines "habitat" as:

> (a) with respect to a species of animal, plant or
> other organism for which a regulation made under
> clause 55 (1) (a) is in force, the area prescribed by
> that regulation as the habitat of the species, or,
>
> (b) with respect to any other species of animal, plant
> or other organism, an area on which the species
> depends, directly or indirectly, to carry on its life
> processes, including life processes such as
> reproduction, rearing, hibernation, migration or
> feeding,
> and includes places in the area described in clause
> (a) or (b), whichever is applicable, that are used by
> members of the species as dens, nests, hibernacula
> or other residences; ("habitat").

Under the Act, "general habitat" is an area on which a species depends, directly or indirectly, to carry out its life processes. For woodland caribou, habitat is defined based on the estimated tolerance of the species to alteration before the feature's function, or usefulness, in supporting a species, is compromised. Category 1 (habitat characteristics where caribou are assumed to have low tolerance to changes in the amount or quality and may have potentially strong population-level implications) includes "high use areas", or sub-range habitat features that exhibit repeated, intensive use by individuals or multiple caribou, and include "nursery areas" (generalized features in which individual or multiple adult female caribou select during late parturition, give birth, and raise their calves during the spring, summer and early fall), "winter use areas" (generalized features associated with soil and forest cover conditions that provide abundant ground lichen for winter forage, and tend to have lower average snow depths that may facilitate easier movement than in surrounding areas) and "travel corridors" (generalized habitat features that caribou may use to move between nursery areas and winter use areas). Category 2 (where caribou are assumed to have moderate tolerance to alteration) includes "seasonal ranges", or sub-range habitat features that encompass the majority of caribou distributions during all seasons within the range. Category 3 (where caribou are assumed to have the highest tolerance to alteration) have the biophysical features and forest composition consistent with seasonal ranges, yet are currently young or disturbed (< 40 years old).

In regard to winter use area, my research suggests there are significant limitations in use of forest resource inventories (FRI) in detecting "winter use areas." To the best of my knowledge, I have not seen these features identified using any other approaches in forest management. My research shows that FRI was not capable of accurately predicting understory vegetation, specifically *Cladonia* lichen species, in spite of the strong prediction provided by field-based data using the same attributes (e.g., soil moisture, age, conifer canopy cover, tree density and height). The best model for field-based data, which included percentage of jack pine and black spruce in the tree canopy, tree height, stand age, soil moisture, and stem density, correctly predicted 92% of cases where *Cladonia* species were absent ($n = 107$ plots) and 62% of cases where they were present (i.e., cover > 1%; $n = 45$ plots). FRI performed poorly by contrast, with only 19% of plots with lichen present identified correctly. FRI thus provided weak support for identifying winter forage availability for woodland caribou. These findings have important implications for predictions of herd productivity as the FRI cannot differentiate between sites with winter forage and those without, and suggest that improved remote-sensing capabilities are required in order to assess woodland caribou winter habitat.

Lastly, recent research has provided evidence of a relationship between disturbances (both anthropogenic and natural) and caribou population persistence (Environment Canada, 2008), indicating total disturbance as the best predictor of caribou recruitment levels. Populations that experience more forest disturbances (natural and anthropogenic) are shown to experience lower recruitment (ratio of

calves/per 100 females), an indicator of the decline of populations. Environment

Canada determined that a recruitment rate of approximately 29 calves per 100

females is the threshold that separates a growing population from one in decline

(Environment Canada 2008). This calf recruitment threshold falls into the "non-

self-sustaining" domain at approximately 38% total disturbance, which references

a precautionary risk zone indicating where a population may begin to decline
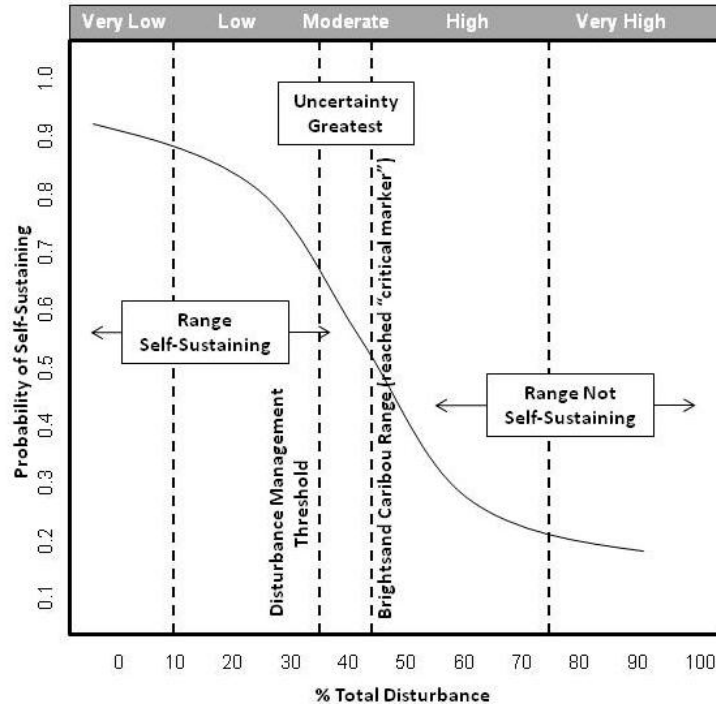
(FIG. 5.1, Environment Canada 2008).

FIG. 5.1: Tiered management thresholds for managing risk associated with recovery planning for boreal caribou critical habitat (modified from Environment Canada 2011). The "critical marker" indicates the point at which conditions suggest the likelihood of meeting the recovery objective is low (i.e., 45% disturbance). Disturbance above this marker means that resistance and resilience may have been compromised. The Federal Recovery Strategy states that, at this level of disturbance, the management emphasis is on restoring conditions to support self-sustaining populations.

These findings can assist in understanding the amount of stress on a range by identifying the total disturbance footprint, and obtaining a recruitment estimate by proxy.

According to OMNR (2013), the Brightsand range, the focus of my research, experienced a rate of 45% disturbance within the range. While my research is not linked to population trends, I did find that older conifer forests, as depicted in Ontario's FRI, did not provide good predictive capabilities of caribou presence at broad scales, rather covariates associated with Environment Canada's definition of "disturbance," specifically the existence of logging roads (an indicator of disturbance at broad scales), and recently disturbed young forests (an indicator of disturbance at fine scales), were associated with caribou use.

In conclusion, if protecting habitat for the purpose of sustaining woodland caribou is a goal of forest management, then habitat based on forest overstory and age (for example, conventional habitat models based on FRI) should be re-evaluated. The limitations of FRI in predicting winter forage, the changes in forest composition as a result of post-harvest regeneration, and the direct and indirect effects of roads and wolves on the landscape suggest that revisions to conventional habitat models are required. Modeling future habitat for woodland caribou in winter, a critical season to their survival, will only be marginally effective if additional covariates of predation risk are not part of the quantification of habitat supply. This issue is likely of greatest concern in caribou ranges where anthropogenic disturbance has replaced fire in terms of its impacts on shaping the forest structure and composition.

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