Modelling scenarios for forest conservation through restoration following moose (*Alces alces*) disturbance

by

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ABSTRACT

Hyper-abundant ungulates can act as a disturbance and hinder natural forest regeneration when they severely overbrowse vegetation. In Newfoundland (Canada), hyper-abundant moose have suppressed balsam fir advanced regeneration producing alternate stable states. I integrated data from field observations and experiments, aerial photographs and drone imagery to parameterize mathematical models of boreal understory and canopy regeneration in Newfoundland. I used simulations to evaluate several restoration scenarios for moose impacted forests, including reduced browsing pressure and seedling planting. Model outcomes suggest active restoration via planting birch and balsam fir seedlings is required to restore the understory and canopy vegetation to its natural state in large canopy gaps, and any planting should be done under low moose browsing pressure or within moose exclosures. The study found that Markov models parameterized by aggregate data with simulated herbivory can be used to support experimental studies and strengthen evidence for restoration planning.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1: GENERAL INTRODUCTION

The continued degradation of forests due to natural and anthropogenic disturbance has led to an overall loss in ecosystem function, a reduction in biodiversity and in extreme cases, has resulted in the extinction of endemic species (Wade et al., 2003; Betts et al., 2017). Global change drivers, such as climate and land-use change, are accelerating the degradation of forests by increasing the frequency of disturbances (Kurz et al., 2008; Moritz et al., 2012; de Groot et al., 2013), decreasing forest resilience to disturbance (Bourque et al., 2005) and increasing the fragmentation and destruction of forests through the encroachment of agriculture, infrastructure and forest industry (Trumbore et al., 2015; Hansen et al., 2013; Haddad et al., 2015). Within degraded landscapes, forests are failing to naturally regenerate, resulting in a loss of key species and producing persistent open canopied patches within previously closed canopied systems (Beguin et al., 2016; Barrette et al., 2017). With the increasing pressure on forest ecosystems, it is of the upmost importance to identify key factors preventing the regeneration of forested landscapes and develop effective restoration protocols to restore ecological health and prosperity within these systems (Aronson and Alexander, 2013; Hobbs and Norton, 1996).

One factor resulting in failed regeneration is the hyper-abundance of ungulates that directly and indirectly alter forest regeneration trajectories (Persson et al., 2000; Côté et al., 2004; Mysterud and Østbye, 2004; Côté et al., 2014; Barrette et al., 2017; Schmitz et al., 2018). Ungulates can indirectly alter regeneration trajectories by trampling vegetation and altering nutrient cycling with the removal of nutrients through selective feeding and the heterogeneous input of nutrients through urination and defecation (Hobbs and Norton, 1996; Persson et al., 2000). Direct effects of ungulates on forest regeneration occurs through the overbrowsing and grazing of vegetation, altering the morphology, productivity and distribution of vegetation (McInnes et al., 1992; Persson et al., 2005).

This failed regeneration due to hyper-abundant ungulates is an increasingly prevalent issue in many biomes. For example, on Anticosti Island (Quebec, Canada), white tailed deer (*Odocoileus virginianus*) overbrowse balsam fir (*Abies balsamea*) seedlings and saplings suppressing their regeneration, and in some areas, causing mortality of the balsam fir advanced regeneration layer (Tremblay et al., 2007). This overbrowsing effectively prevents the recruitment of balsam fir into the canopy after stand replacing disturbance. As balsam fir is one of the dominant canopy species in this boreal forest, the suppression of balsam fir advanced regeneration results in changes to canopy composition and can form persistent gaps within the crown (Tremblay et al., 2007; Côté et al., 2014). The impacts of ungulates are not always as evident as they are on Anticosti Island as ungulates may overbrowse rare canopy trees instead of dominant canopy species (Mysterud and Østbye, 2004). However, the ramifications of overbrowsing rare species are equally as important. In Norway, the European yew (*Taxus baccata*) was listed as an endangered species and reserves were established to protect the remaining trees from harvesting (Mysterud and Østbye, 1995; Mysterud and Østbye, 2004) which harvesting was thought to be the main factor reducing yew canopy abundance. However, once the reserves were established it was clear that they were largely ineffective as roe deer (*Capreolus capreolus*) overbrowsing was preventing yew regeneration within the reserves (Mysterud and Østbye, 1995; Mysterud and Østbye, 2004). Examples like these span the globe, from hyper-abundant elk in the Rocky Mountains reducing aspen (*Populus tremuloides*) abundance (Ripple and Larsen, 2000); deer and feral goats preventing forest regeneration across New Zealand (Wardle et al., 2001); sika deer (*Cervus nippon*) preventing forest regeneration after clear cutting in Japan (Takatsuki, 2009; Yamagawa et al., 2010); white tailed deer reducing understory biodiversity after disturbance in North American temperate forests (Nuttle et al., 2013); introduced Sitka black tailed deer (*Odocoileus hemionus*) reducing red cedar (*Thuja plicata*) recruitment in Haida Gwaii (Martin and Baltzinger, 2002); moose in Fennoscandian boreal forest suppressing rowan and birch growth (Speed et al., 2013; Kolstad et al., 2018) and the creation of moose spruce savannas in Isle Royale and Newfoundland due to hyper-abundant moose populations (Brandner and Peterson, 1990; Gosse et al., 2011). The causes of hyper-abundant herbivores are many but mostly depend on the increasing human footprint that is providing ideal conditions for herbivores to thrive (Côté et al., 2004; Estes et al., 2011). Specifically, humans are introducing herbivores into novel environments (Martin and Baltzinger, 2002; Gosse et al., 2011; Hidding et al., 2012), removing top predators (McLaren et al., 2004; Estes et al., 2011), creating agricultural mosaics (Côté et al., 2004) and altering forest succession through forestry (Fisher and Wilkinson, 2005).

Moose are an invasive species in Newfoundland, originally introduced to develop recreational hunting and provide an additional food source (McLaren et al., 2009). They were introduced twice, once in 1878 and again in 1904. In 1932 wolves were extirpated from the island, removing their main predator. The removal of natural predators paired with increases in human disturbances (e.g., forest harvesting) and periodical natural disturbances (e.g., spruce budworm (*Choristoneura fumiferana*) outbreaks) on the island provided optimal conditions for moose abundance to increase. As a result, the moose population on the island reached peaks of over 150,000 moose in 1960 and 1990 (McLaren et al., 2004; McLaren et al., 2009). Moose abundances have recently declined but there are still over 112,000 moose with variable local densities depending on habitat quality (Government Newfoundland, 2015). The density of moose in high quality habitat, such as protected parks, is still considered to be above carrying capacity as the vegetation they browse is not only failing to regenerate but also disappearing from the canopy and understory (Mercer and McLaren 2002; McLaren et al., 2004). As such, moose alter plant diversity, modify forest composition, cause localized extinctions of palatable species, reduce vegetation biomass and alter regeneration trajectories, resulting in alternate stable states (Gosse et al., 2011; Ellis and Leroux, 2017).

Natural disturbance from wind and insects, such as hemlock looper (*Lambdina fiscellaria*) and spruce budworm, play an important role in balsam fir dominant boreal forests, facilitating balsam fir dominance in small and medium canopy gaps and increasing canopy and understory diversity in large canopy gaps (McCarthy, 2001; Arsenault et al., 2016). Prior to disturbance, balsam fir seedlings and saplings form a layer of advanced regeneration (Messier et al., 1999). After a small or medium scale disturbance, the advanced regeneration rapidly grows to fill the canopy gap. Within these medium sized gaps, yellow birch growth is at its peak due to the increased light availability and reduced competition between shade intolerant shrubs as compared to large canopy gaps (Salmon et al., 2016). The seedbed is typically dominated by mosses (specifically feathermoss), with an understory comprised of shade tolerant and moderately shade tolerant herbs, shrubs and saplings (McLaren and Janke, 1996). Within large canopy gaps the layer of balsam fir advanced regeneration does not fill the entire gap as it loses some of its competitive edge against the shade intolerant shrubs and saplings (Ulanova, 2000). Consequently, the canopy will be diverse, comprised of both shade tolerant and intolerant species, with an understory comprised of shade intolerant shrubs, herbs and saplings (Messier et al., 1999). In these gaps birch typically grows around the perimeter as it is outcompeted by shade intolerant shrubs in the completely open areas (Prévost and Charette, 2015).

Moose and Forest Dynamics in Newfoundland

In Newfoundland spruce budworm outbreaks re-occur approximately every thirty years which leads to increased understory biomass through the facilitation of rapid sapling and shrub growth within the canopy gaps (Arsenault et al., 2016). This along with the lack of predators and disease led to the ideal conditions for moose to reach hyper-abundance (McLaren et al., 2004; McLaren et al., 2009). Following canopy removal through natural and anthropogenic disturbance in balsam fir dominant boreal forest hyper-abundant moose suppress forest regeneration leading to alternate stable states shifting the balsam fir dominant boreal forest to moose spruce savannas (McLaren et al., 2004; Figure 1.1).

Alternative stable states such as these are alternate conditions of an ecological system that remain stable after small perturbations (Scheffer et al., 2001; Beisner et al., 2003; Scheffer et al., 2009). Alternate stable states can be reached through large perturbations and once entered can be extremely difficult to return to the prior state.

Within these alternative stable states systems experience changes in composition and diversity which can cause altered ecosystem function (Scheffer et al., 2001; Beisner et al., 2003; Scheffer et al., 2009). Empirical evidence of alternative stable states has been documented in several systems including freshwaters (Carpenter et al., 2001; Scheffer et al., 2003), forests (Dublin et al., 1990; Holling and Meffe, 1996; Xu et al., 2015) and oceans (McCook, 1999; de Roos and Persson, 2002; Vergés et al., 2016). Moose hyper-abundance causes the development of alternate stable states in Newfoundland through the overbrowsing on the layer of balsam fir advanced regeneration, birch saplings and shrubs after initial canopy removal via natural (e.g., spruce budworm) or human (e.g., forest harvesting) disturbance (Gosse et al., 2011). The overbrowsing severely suppresses the growth of these saplings, preventing canopy closure resulting in an open canopied system with an altered seedbed quality (Brandner et al., 1990; Kneeshaw and Bergeron, 1998). Further, the interspecific competition between species is altered, resulting in less abundant unpalatable species such as spruce becoming more abundant within these alternate states (Chen and Taylor, 2012). This alternate stable state has been named a spruce moose savanna, as the canopy remains open after canopy disturbance with intermittent spruce scattered in the gap and a dry, unfavourable seedbed that prevents the natural regeneration of other species (Pastor et al., 1988; McLaren et al., 2004; Gosse et al., 2011) (See Appendix A). The understory vegetation in spruce moose savannas in Newfoundland are usually dominated by grasses and unpalatable shrubs such as mountain laurel (*Kalmia latifolia*) and sheep laurel (*Kalmia angustifolia*). Although this alternate trajectory induced by moose overbrowsing has been identified and classified by several papers, little is known about the impacts this alternate trajectory has on the biomass and diversity of seedbed, herbs and shrubs in Newfoundland balsam fir dominant boreal forests.

The negative effects of moose hyper-abundance are not limited to selectively browsed vegetation, rather, moose hyper-abundance can cause cascading effects on the abundance and diversity of soil microbes, lichens, birds and arthropods (Suominen et al., 2008; Rae et al., 2014; Ellis and Leroux, 2017; Kolstad et al., 2018). For example, in Western Newfoundland, Canada, Rae et al. (2014) observed that ground nesting and insectivorous birds are negatively affected by moose hyper-abundance. Specifically, moose overbrowsing reduced vegetation biomass, which decreased arthropod abundance and the availability of suitable ground nesting materials (Rae et al., 2014). Furthermore, overabundant moose can reduce lichen diversity by decreasing the diversity of micro habits within the balsam fir dominant boreal forest (Boudreault at al., 2002; McLaren et al., 2004). It is important to note that the effects of moose overbrowsing on diversity are complex. Even if overall diversity is not decreased with hyper-abundant moose, moose can still homogenize the environment by causing shifts from specialist to generalist species (Kolstad et al., 2018). Therefore, the effects of moose can span multiple trophic levels, resulting in a decrease in forest productivity and ecosystem function.

Restoring Balsam Fir Dominant Boreal Forests

Restoration ecology emerged as a discipline in the 1980’s providing a link between the management of natural resources and the science of ecology (Anderson et al., 2009; Higgs et al., 2014). Over the decades restoration ecology has rapidly developed, broadening to an adaptable approach that uses historical systems as a reference, aiming to restore ecosystem function as opposed to ecological aesthetics (Hobbs and Harris, 2001; Higgs et al., 2014). Restoration ecology is increasingly recognized as an important sub field of conservation biology through the reestablishment of ecosystem function and potential increases in multi-trophic biodiversity (Balaguer et al., 2014; Possingham et al., 2015).

As a result of the detrimental impacts caused by moose hyper-abundance, several studies have examined the effectiveness of numerous passive and active restoration scenarios for balsam fir dominant boreal forests (McLaren et al., 2009; Gosse et al., 2011; Charron and Hermanutz, 2017). Passive restoration is the removal of an environmental stressor without directly intervening with natural regenerative processes whereas active restoration is the intervention and implementation of restoration protocols that alter natural regenerative processes to aid in ecosystem recovery (Holl and Aide, 2011; Beltran et al., 2014; Zahawi et al., 2014). In most cases, passive restoration through moose reduction is deemed ineffective, as the legacy effect of moose overbrowsing prevents natural regeneration without active restoration (McLaren et al., 2009). As such active restoration protocols are required to restore balsam fir dominant boreal forests. Some examples of active restoration strategies tested include the addition of balsam fir seeds to plots (Humber and Hermanutz, 2011), planting balsam fir seedlings under variable ground preparation treatments (Charron and Hermanutz, 2017) and the removal of moose browsing pressure by placing exclosures (McLaren et al., 2009). Based on these studies, planting balsam fir seedlings without ground preparation (Charron and Hermanutz, 2017) in conjunction with moose population control is the most effective restoration protocol for increasing balsam fir recruitment and closing canopy gaps on the island of Newfoundland

(Humber and Hermanutz, 2011). Although effective restoration scenarios have been identified for balsam fir, a foundation species, studies have not examined how to restore other canopy trees, such as birch, or understory vegetation (Frerker et al., 2013).

In addition to the lack of restoration protocols addressing the restoration of non-foundation but high conservation value species, restoration studies have been largely experimental (Frerker et al., 2013). As such, restoration modelling has been used to support experimental studies but few studies have used simulation based modelling for herbivore disturbed landscapes while simulating restoration scenarios (Twilley et al., 1999; Possingham et al., 2015). Further, no studies have used aggregate data to parameterize simulation based restoration models with simulated herbivory. Where many experimental studies are constrained by time, failing to capture the long-term effects of restoration planning, models can be used to simulate forest trajectories after implementing restoration protocols. Furthermore, several simulations can be conducted simultaneously to determine which restoration scenarios will be effective within the simulated system allowing for efficient evaluation of many potential restoration scenarios. Also, restoration models can be used to corroborate experimental restoration studies and strengthen restoration results, aiding in decision making processes and restoration planning and potentially aiding in policy implementation.

I derive a Markov model of the balsam fir dominant boreal forest regeneration trajectories for the island of Newfoundland and test a suite of restoration scenarios for restoring both the understory and canopy vegetation. My specific objectives were to i) derive and parameterize a mathematical model of balsam fir dominant boreal forest dynamics using aggregate data from two Eastern Newfoundland, Canada, boreal forest sites (Nature Conservancy Canada's (NCC) Salmonier property located in the Avalon Ecoregion and Terra Nova National Park (TNNP) located in the North Shore and Central Newfoundland Ecoregion (Meades, 1989)), and use this mathematical model to identify ii) current regeneration trajectories after disturbance in balsam fir dominant boreal forest, iii) the effects of moose overbrowsing on the seedbed, herbs, understory, and canopy vegetation and iv) effective restoration scenarios to restore canopy and understory abundance and diversity. My results show Markov models parameterized via aggregate data with simulated herbivory can be used to test restoration scenarios and support experimental restoration literature.

Figure 1.1. Examples of a spruce moose savanna in Cape Breton Highlands (Nova Scotia, Canada) (left; photo credit: Ken Oakes) and the composition of the forest in closed canopy systems on Salmonier property (Newfoundland, Canada) (right; photo credit: Meghan Noonan). Note the heavily browsed dead or dying balsam fir snags in the left image.

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CHAPTER 2: MODELING SCENARIOS FOR FOREST RESTORATION AFTER MOOSE OVERBROWSING

2.1 INTRODUCTION

Human impact on the environment has facilitated ungulate hyper-abundance through the introduction of herbivores to novel environments (Martin and Baltzinger, 2002; Gosse et al., 2011; Hidding et al., 2012), removal of predators (McLaren et al., 2004; Estes et al., 2011), industrial fragmentation of habitats (Fisher and Wilkinson, 2005) and agricultural mosaics (Côté et al., 2004). The direct and indirect effects of hyper-abundant ungulates can lead to failed forest regeneration in degraded landscapes resulting in a decline of forest health and productivity (McInnes et al., 1992; Hobbs and Norton, 1996; Persson et al., 2000; Mysterud and Østbye, 2004; Persson et al., 2005; Barrette et al., 2017; Schmitz et al., 2018). Ungulate hyper-abundance can cause local extirpation of key species, reduced biodiversity and altered forest regeneration trajectories producing alternate ecosystem stable states (McInnes et al., 1992; Hobbs and Norton, 1996; Persson et al., 2005). The effects of hyper-abundant ungulates has been observed in many forests, from boreal forests in North America (McInnes et al., 1992; Ripple and Larsen, 2000; Tremblay et al., 2007; Gosse et al., 2011; Côté et al., 2014), to temperate forests in Japan (Takatsuki, 2009; Yamagawa et al., 2010), New Zealand (Wardle et al., 2001) and United States (Nuttle et al., 2013). Under the increasing pressure from global change drivers, which are accelerating the rate of forest degradation, the failed regeneration and production of alternate stable states within degraded landscapes highlights the need for effective restoration protocols to preserve and restore ecosystem function and services (Schmitz et al., 2018).

Passive restoration through herbivore reduction has had mixed results in restoring forests degraded by herbivore hyper-abundance. For example, after the eradication of introduced herbivores from Santa Cruz, USA, Beltran et al. (2014) reported an increase in woody cover three decades after herbivore removal suggesting passive restoration was successful. Whereas Royo et al. (2010) found moderate success after culling white tailed deer in the Pennsylvania, USA temperate forest, finding an increase in shrub and herb cover but no change in vegetation diversity. Further, Tanentzap et al. (2011) reported limited tree recruitment after a reduction in deer densities between 1996 and 2009 in the temperate forest of Southwestern Ontario, Canada, suggesting active restoration is required to improve tree recruitment. The failure of passive restoration in some degraded forests has been attributed to the legacy effect of herbivore hyper-abundance where altered abiotic and biotic conditions can limit the regenerative capacity of vegetation with limited resilience to severe browsing pressure (Tanentzap et al., 2012).

Active restoration may be required in severely degraded ecosystems where passive restoration has failed to reach restoration goals (Gosse et al., 2011). Several methods of active restoration within forest systems have been studied including direct seeding, seedling planting, ground preparation treatments and canopy removal (McLaren et al., 2009; Wright et al., 2012; Faure-Lacroix et al., 2013; Charron and Hermanutz, 2017). The success of active restoration protocols varies based on restoration targets and forest properties. For example, seeding is a cost-effective restoration protocol that has successfully restored oak in Southern Scandinavia and restored tropical forests in Costa

Rica (Madsen and Löf, 2005; Cole et al., 2011). However, several studies have reported inefficient restoration after direct seeding due to seed and newly emerged seedling herbivory, competition, seed desiccation and the vulnerability of newly emerged seedlings indicating restoration success can be case specific (Gosse et al., 2011; Palma and Laurance, 2015). Planting seedlings has been found to be a more effective and quicker way to restore degraded forests than seeding, however additional restoration measures such as herbivore exclusion, ground treatments and planted seedling diversity varies based on forest conditions and restoration goals.

Due to the variability of restoration success in forests with different properties, local experimental studies are often relied on to determine which restoration protocols to implement (Palma and Laurance, 2015; Souza and Engel, 2018). Conducting experimental studies within unique landscapes can be cost inefficient and timely, not to mention experimental studies are often short term which can fail to capture long term forest responses to restoration. To bridge this gap, mathematical modelling may be an effective tool to aid in forest restoration planning. Such models can simulate a variety of restoration scenarios to evaluate the effectiveness of diverse restoration protocols for a given system. I derive a mathematical model informed by multiple data sources, including aerial imagery and field data, to explore boreal forest dynamics on the island of Newfoundland. My focus is to investigate several restoration scenarios for restoring degraded balsam fir dominant boreal forests that have failed to naturally regenerate due to moose hyper-abundance in Eastern Newfoundland, Canada. Specifically, the objectives of this study are to derive and parameterize a mathematical model for balsam fir dominant boreal forest understory and canopy dynamics using aggregate data from Eastern

Newfoundland. I use this model to identify a) the effects of moose on the seedbed, herbaceous layer, understory and canopy within the forest b) the current forest regeneration trajectories after disturbance and c) effective restoration scenarios to restore the vegetation abundance and diversity within the understory and the canopy. I used modified Markov models to simulate several restoration scenarios including passive restoration through moose reductions and active restoration through multispecies seedling planting. By incorporating both understory and canopy vegetation I was able to suggest restoration scenarios that will restore both the foundation canopy species and the understory vegetation whereas traditional active restoration has focused mainly on foundation species recovery.

2.2 METHODS

Study Organism and System

Study organism – Moose are a circumpolar species, occupying predominantly boreal forests in North America and Eurasia with some range expansion into temperate forests in North America (Pastor et al., 1988). Moose preferentially browse palatable shrub and hardwood species (e.g., willow spp., birch spp., and trembling aspen) as well as balsam fir, aquatic vegetation and herbaceous species (Timmermann and McNicol, 1988; McInnes et al., 1992; Molvar et al., 1993; Routledge and Roese, 2004). Both anthropogenic and natural disturbance has a positive impact on moose as the quality and quantity of available browse increases following disturbance (Lavsund et al., 2003; Fisher and Wilkinson, 2005). In locations with hyper-abundant moose, preferential browsing can lead to reduced abundance and altered diversity of vegetation causing alternate regeneration trajectories following disturbance (McLaren et al., 2004). In addition to selective browsing, moose can alter forest regeneration through several direct and indirect ways including trampling, altered nutrient cycling and dispersal of invasive species (Persson et al., 2000; Persson et al., 2005).

Moose became hyper-abundant in Newfoundland several decades after their introduction in 1878 and again in 1904 (McLaren et al., 2009; Gosse et al., 2011). Moose hyper-abundance in Newfoundland was facilitated by severe forest disturbance through cyclic spruce budworm outbreaks and intensified forest harvesting (McCarthy, 2001; Fisher and Wilkinson, 2005; Arsenault et al., 2016). Once the forest canopy has been disturbed understory vegetation rapidly grows to fill the canopy gap providing ample food for the increasing population of moose (McLaren et al., 2004; Gosse et al., 2011). Wolves, the main predator for moose on Newfoundland, were extirpated in 1932 (McLaren et al., 2004; McLaren et al., 2009). The increased food availability and extirpation of predators, in conjunction with a lack of disease and parasites affecting moose, resulted in moose becoming hyper-abundant across the island (McLaren et al., 2004; McLaren et al., 2009). Moose reached peak abundance of approximately 150,000 in the 1990's causing failed regeneration of forests. This resulted in alternate regeneration trajectories producing spruce moose savannas in some degraded forests (McLaren et al., 2004). As a result, hunting pressure was increased which combined with other drivers (e.g., reductions in forest harvesting, density dependence, no recent budworm outbreak) reduced the moose population to approximately 112,000 (Government Newfoundland, 2015). Forests, however, are still failing to naturally regenerate causing population declines of birch and shrub species as well as persistent open canopied patches (Brandner et al., 1990; Kneeshaw and Bergeron 1998). As such moose are still considered above carrying capacity due to their legacy effect on vegetation causing regeneration failure and continued depletion of their preferential browse (Mercer and McLaren, 2002).

Study site – I conducted this study in eastern Newfoundland on Nature Conservancy Canada's (NCC) Salmonier property (1.77 km^2, Newfoundland, Canada, 47°10'54.3" N, 53°23'55.7" W) and in Terra Nova National Park (TNNP; ~400 km^2, Newfoundland, Canada, 48°31'31.08" N, 53°57'55.799" W) (Figure 2.1). I used data from these two sites for model development and parameterization. The sites had similar disturbance history, forest composition and moose browsing intensity to ensure results are reflective of balsam fir dominant boreal forests.

NCC's Salmonier property is located in the Avalon Forest Ecoregion, the smallest ecoregion in Newfoundland (Meades, 1989). This ecoregion is characterized by its predominantly balsam fir canopy, interspersed with both white and yellow birch trees (Meades, 1989). The cool summers, mild winters and high levels of precipitation in the region, with over 1200 mm precipitation annually, produces high levels of fog throughout the forest (Department of Municipal Affairs, 2019). The unique nature of this ecoregion has led to high levels of plant and lichen diversity and is home to a variety of at risk lichen species, such as boreal felt lichen (*Erioderma pedicellatum)* (McMullin and Wiersma, 2017). Due to its small size, this ecoregion is relatively understudied and provides a unique opportunity to examine the effects of moose overbrowsing and disturbance.

TNNP is a National Park located on the Northeastern coast of Newfoundland within the North Shore and Central Newfoundland Ecoregions (Meades, 1989). The North Shore and Central Newfoundland Ecoregions are similar in species composition with a canopy dominated by spruce and balsam fir. Both ecoregions have been affected by fire disturbance, resulting in large dominant spruce patches throughout (Meades, 1989). Areas that have been unaffected by fire in the Central Newfoundland Ecoregion are balsam fir dominant with feathermoss seedbed. In the North Shore Ecoregion, white spruce (*Picea glauca*) is more abundant than it is in the Central Newfoundland Ecoregions and trembling aspen is less abundant. Yellow birch is not present in either Ecoregion (Meades, 1989).

Model Development

I derived a Markov model to predict regeneration trajectories within small and large forest canopy gaps. I used this model to evaluate a suite of restoration scenarios under a gradient of moose browsing pressure with simulated birch and balsam fir seedling planting. Markov models are discrete time stochastic models that use transition probabilities (p_{ij}) to predict changes from state *i* to *j* over time (Eq. 1) (Horn, 1975; Wootton et al., 2001; Appendix B). Transition probabilities are the probability that one state will change to another or remain the same after one time step (Horn, 1975). The two primary assumptions of the Markov model include time homogeneity and the Markov property. Time homogeneity means the transition probabilities are independent of the current time step (Horn, 1975). It is assumed that the environmental conditions at the start of the simulation remain constant throughout the simulated time frame. The Markov property means each transition is only dependent on the state the system was in in the previous time step (Usher, 1978).

I incorporated both understory and canopy vegetation layers by parameterizing the model using aggregate data from TNNP and Salmonier field datasets, Salmonier aerial photos and drone imaging. I built twelves states into the model creating a 12x12 baseline transition matrix (Figure 2.2, Table 2.1). The twelve states are good seedbed (SB), poor seedbed (SBB), herbaceous (H), shrub (SH), birch sapling (YBS), browsed birch sapling (YBSM), balsam fir sapling (BFS), browsed balsam fir sapling (BFSM), spruce sapling (BSS), birch tree (YB), balsam fir tree (BF) and spruce tree (BS) (Figure

2.2, Table 2.1). I chose the three canopy states (YB, BF, BS) and five sapling states (YBS, YBSM, BFS, BFSM, BSS) based on the dominant canopy species within balsam fir dominant boreal forests in the Avalon Ecoregion (Meades, 1987). I chose the two seedbed states based on which seedbeds are most suitable for balsam fir germination (Lorenzetti et al., 2008; Duchesneau and Morin, 1999). Lastly, I grouped the herbaceous species to form the herbaceous state and the shrub species to form the shrub state to capture the forest dynamics without overwhelming the model with the diversity within these two states. For example, there were over 10 shrub species and 15 herbaceous species in the TNNP and Salmonier property field data. The dynamics of the model can be described by the following equation.

$$N_j[t+1] = \sum_i N_i * p_{ij} \qquad \text{Eq. 2.1}$$

where t is time (year), N_j is the proportional cover that is state j and p_{ij} is the transition probability from state i to j.

Model analysis

To determine the forest regeneration trajectories within the balsam fir dominant boreal forest and evaluate the effectiveness of simulated restoration protocols I first built the *baseline model* with the calculated transition probabilities (Table 2.2). The *baseline model* is a simple Markov model with no weighted transition probabilities to simulate changes in moose browsing pressure, gap dynamics or restoration scenarios. As such, the *baseline model* captures the current forest landscape and dynamics, a forest that is currently experiencing the legacy effects of long term moose overbrowsing. I used the *baseline model* to i) determine forest dynamics and support model development by showcasing similarities to observed forest dynamics, ii) examine model sensitivity and iii) as the starting base for all other models (Figure 2.3).

I began my model analysis by determining the eigenvectors of the *baseline model* to determine the stable state of the model which is reflective of the forest composition at equilibrium (Wootton et al., 2001). Then I performed a local-one-at-a-time (OAT) perturbation sensitivity analysis and a global scenario based perturbation sensitivity analysis on the *baseline model* to assess the sensitivity of the model to variations in the transition probability matrix (Pianosi et al., 2016). The local and global sensitivity analysis demonstrated no substantial qualitative impact on the restoration recommendations made within this chapter (see Appendix C). Next, I used the *baseline model* as a building block for all other models. I initially added simulated moose browsing pressure on the *baseline model* to build the *moose model*. The *moose model* is a Markov model that includes the effects of moose browsing pressure on the forest regeneration trajectories by positively and negatively weighting transition probabilities, measuring the basic model dynamics with simulated herbivory without simulated gap dynamics. I then simulated small and large gap regeneration dynamics using the *moose model* to make the *small gap model* and *large gap model* (Figure 2.3). The *small gap model* and *large gap model* are Markov models that reflect the more complex dynamics of forest regeneration after simulated herbivory by showcasing the different dynamics of regeneration with a gradient of moose herbivory under differing forest gap sizes. Lastly, I evaluated all restoration scenarios (outlined below) with the *moose model*, *small gap model* and *large gap model*.

Moose and gap size

Moose Model – One key restoration option is reducing the moose population. I included moose effects on forest regeneration by multiplying transition probabilities from the *baseline model* (Table 2.3; Figure 2.3) (Dodds, 1960; Bergerud and Manuel, 1968; Taylor et al., 2017) by an independent measure of moose impact, M. M varied from 0.001 to 1 with higher values indicating lower moose impacts and a value of 1 indicating no moose browsing pressure. A key feature of the row stochastic Markov model is that each row must sum to 1 to ensure the total input into the model is equal to the total output from the model. This criterion ensures that there is 100% proportional cover of vegetation in and 100% proportional cover of vegetation out. I balanced the matrix by dividing transition probabilities that would be positively impacted by moose browsing trends ensuring each row still summed to 1 (Horn, 1975).

Moose effects and forest regeneration trajectories can vary depending on gap size (Appendix A). The classification of gap sizes is highly variable within literature, often dependent on the study conducted and the types of disturbance discussed. For the purposes of my thesis I chose to simulate regeneration dynamics within two gap sizes (small (<5 ha) and large (>5 ha) gaps) following the gap size classifications used by Charron and Hermanutz (2016) while studying restoration protocols in TNNP. These two gap sizes have unique abiotic properties, vary significantly in severity of disturbance and have distinct trends in regenerative success for various vegetation layers (see Appendix

A). Using these gap sizes also allowed for comparison of my model results to TNNP experimental findings. I simulated gap regeneration dynamics building off of the *moose model* to create a small (<5 ha) gap model and a large (>5 ha) gap model. The data used to parameterize the transition probabilities came from data for both small and large canopy gaps and both balsam fir and birch grow better in canopy gaps <5 ha (McCarthy, 2001; Houle and Payette, 1990; Salmon et al., 2016). I simulated small canopy gaps by weighting balsam fir (BF) and birch (YB) transition probabilities by a gap factor, Gf1=1.5. I simulated large canopy gap regeneration by simulating increased poor seedbed development by positively weighting transition probabilities to poor seedbed (SBB) by Gf2 (Gf2=1.5) and decreased spruce growth by negatively weighting transition probabilities to spruce (Table 2.4) by Gf3 (Gf3=0.5) (Mallik, 2003; Charron and Hermanutz, 2017). I simulated increased poor seedbed (SBB) development as large gaps cause reduced soil moisture, decreased feathermoss cover and increased herbaceous leaf litter which negatively affects balsam fir recruitment. I simulated a decrease in spruce growth as large canopy gaps have shown a reduction in spruce abundance (Table 2.4). I did not weight herbaceous (H) and shrub (SH) transition probabilities because they encompass a greater range of species within the states (Mallik, 2003). As such there are species within both states that grow better in small versus large gaps. For instance, grass, which was grouped into the herbaceous state (H), is common in large gaps that are failing to regenerate whereas other species, such as bunchberry (*Cornus canadensis*) grow better in smaller gaps due to the partial shade. Small canopy gaps were simulated by weighting balsam fir (BF) and birch (YB) transition probabilities by a gap factor (Gf1) simulating increased growth.

Restoration Scenarios

I tested nine restoration scenarios, including moose reductions and exclosures with balsam fir and birch seedling planting, on the *small gap model* and *large gap model* (Table 2.5; Figure 2.3; See Appendix D for restoration tested on *moose model*). I used three target simulated moose browsing pressures and simulated balsam fir and birch seedling planting within each of the targets to determine the effectiveness of seedling planting with small (M=0.1), medium (M=0.45) and large (M=0.8) reductions in moose browsing pressure. Starting with a severe moose browsing pressure (M=0.001). I simulated reductions in moose browsing pressure from severe moose browsing pressure (M=0.001) to reach three targets (M=0.1, M=0.45 and M=0.8) by gradually increasing the weighting on transition probabilities. First, I simulated severe moose browsing pressure within the *small gap model* and *large gap model* by running the model for 100 time steps at M=0.001. Once the 100th time step was reach I began gradually increasing the weighting, M, by intervals of approximately 0.05 until the target browsing pressure was reached (Liénard and Strigul, 2016). For instance, if I was simulating a medium reduction in moose browsing pressure (M=0.45), on the 100th time step I began increasing the weighting of M 0.05 intervals until I reached an M value of 0.45. Once the target was reached, the model continued to run at the target M value, in this case 0.45, until the 200th time step. This process was repeated for each of the target M values (0.1, 0.45, and 0.8). I simulated the placement of an exclosure by making M=1 after the first 100 times steps where the model was run at an M=0.001 ($M = 0.001$ if $t \leq 100$, $M = 1$ if $t > 100$ for exclosure plots). I did not decrease moose population slowly for the exclosure because the actual moose population is not reduced, rather an exclosure is placed and additional restoration is conducted simultaneously. The simulation of exclosures within this model may also emulate the effects of culling moose. The use of exclosures as a restoration protocol is effective when culling the herbivore population is not economically or ecologically feasible. For the purposes of this thesis the use of exclosures is suggested as a restoration strategy due to the unpredictable spatial distribution of moose herbivory and the importance of moose hunting socially and economically (Timmermann and Rodgers, 2005; Fisheries and Oceans Canada, 2011).

Next, I simulated balsam fir and birch seedling planting under the three target moose browsing pressure and within the exclosure (M=0.1, M=0.45, M=0.8 and M=1) using a restoration parameter, R_{PK} where K = L for large canopy gap, S for small canopy gap and N for non-gap specific (*moose model*). For the first 100 time steps while M=0.001, I made R_{PK}=1 indicating no restoration is taking place. After the first 100 time steps, I increased R_{PK} to simulate planting (R_{PL}=1 if $t \leq 100$, R_{PL}=2 if $t > 100$; R_{PS}=1 if $t \leq 100$, R_{PS}=1.33 if $t > 100$) and ran the model for an additional 100 time steps with M gradually increasing as outlined above. I placed restrictions on the R_{PK} value to ensure none of the transition probabilities are greater than 1 (Appendix E). As such, an R_{PK} value of 2 was chosen for the non-gap specific model (*moose model*) and large canopy gap model and a value of 1.33 was used for the *small gap model*. I applied the R_{PK} values to the seedbed to birch sapling, seedbed to balsam fir sapling, birch sapling to birch tree and balsam fir sapling to balsam fir tree transition probabilities to simulate the effects of planting seedlings on seedling and sapling growth (Table 2.6). To ensure the specific value of R_{PK} did not impact restoration conclusions each restoration scenario was run under a several R_{PK} values (Appendix E). In addition, I ran each restoration scenario again while just applying the R_{PK} value to the seedbed to birch sapling and seedbed to balsam fir sapling transition probabilities (Appendix E). Reducing the R_{PK} value only changed restoration conclusions when the R_{PK} value was nearly 1 ($R_{PL} \leq 1.25$ and $R_{PS} \leq 1.08$), where an R_{PK} of 1 is the equivalent of no seedling planting. When R_{PK} approached 1 the effectiveness of the R4 restoration scenario (see Figure E. 1) was increased relative to the seedling planting scenarios. Furthermore, applying R_{PK} to just the seedbed to sapling transition probabilities did not change the rank of effectiveness and thus restoration suggestions remain the same (Appendix E).

Model Parameterization

I parameterized the models using several data sources including NCC Salmonier property aerial imagery (Figure 2.1; Figure 2.4; Appendix F), NCC Salmonier property drone imagery, TNNP field data and NCC Salmonier property field data to fit the Markov model to balsam fir dominant boreal forests and incorporate seedbed, understory and canopy dynamics (Table 2.1). The Salmonier property data sources are ideal to fit the model to the target balsam fir dominant forest, however, I did not have all of the data needed to parameterize the understory dynamics using only Salmonier property data. As such, I supplemented the Salmonier property field data with TNNP data to build the 9x9 understory matrix and to estimate the transition probabilities for understory dynamics. I used the Salmonier aerial and drone imagery to build the 3x3 canopy matrix and to estimate the transition probabilities for canopy dynamics. Any canopy gap that regenerates is filled rapidly by growing saplings; as such I considered each open to tree transition a sapling to tree transition, merging the 3x3 canopy matrix with the 9x9 understory transition creating the final 12x12 matrix (Table 2.2). I used the Salmonier property field data to inform understory and canopy transition probabilities. The following outlines all of these data components (Figure 2.5).

Photo analysis – I used five aerial photos and one drone project to determine the canopy tree transitions (Figure 2.4). The five aerial photos were from taken in 1969, 1978, 1985, 1995, 2009 (Figure 2.6). The drone imaging was captured in August 2018 for approximately 1/3rd of the Salmonier property and was flown by NCC staff with appropriate training.

I georeferenced all of the aerial images to a 2008 aerial photo from the Salmonier property with the coordinate system NAD 1983. Each aerial photo then underwent an additional georeferencing to the 2009 photo, ensuring each photo was precisely aligned prior to analysis within the Salmonier property boundaries. I then applied a 15 m x 15 m grid to the aerial photos and categorized each cell within the boundary as either birch, bog, conifer, open or road based on the dominant cover type.

I chose the five categories based on visibility limitations. Deciduous trees were easily identifiable and based on the ecoregion the deciduous canopy trees would be predominantly white and yellow birch. However, given the resolution of the photos I was unable to differentiate between balsam fir and spruce trees. As such, all conifers were placed into the conifer category and were refined into balsam fir and spruce using TNNP data, Salmonier property field data, drone imaging and literature during data processing. The bog and road categories were included to ensure proper alignment between the images. The open category was any area, besides road and bogs, that did not have a canopy. I classified grid cells into one of the five categories based on percent cover within the cell. A cell was assigned to the category with the highest percent cover within the cell. I only retained conifer, birch and open cells for canopy transition probability calculations.

To capture recent imagery of the property a drone was flown over a third of the NCC Salmonier property (Appendix G). Drone imagery was required as several windthrow events have happened between 2009 and 2018 producing new gaps within the property and expanding old canopy gaps. The location of the flights was determined in advance based on the disturbance and canopy composition. The site I chose had a large patch of birch and large persistent canopy gap. I processed the drone imagery using Pix4D mapper and I imported the drone imagery into ArcGIS where geolocation accuracy was compared to the 2009 aerial photo. The same gridding and categorizing methods were used as described above for the drone imagery.

I determined the canopy transition probabilities from the aerial and drone imagery by first counting all the transitions between each pair of aerial photos for each grid cell (n = 5 pairs of aerial imagery). Since trees are not spontaneously replaced by other tree species, rather they fall, creating open seedbed, and a sapling growing nearby replaces them, each transition from birch to conifer or conifer to birch was broken down to two transitions: conifer/birch to open and open to birch/conifer (Beaudet and Messier, 1998; Dumais, 2014). To determine the transition probabilities from state i to state j (p_{ij}), I estimated the total number of transitions from i to j (N_{ij}) divided by the total number of transitions from state i ($\sum_j N_{ij}$) (Hill et al., 2004; see Appendix H for an example using this equation). Specifically,

$$p_{ij} = \frac{N_{ij}}{\sum_j N_{ij}} \qquad \text{Eq. 2.2}$$

After determining the transition probabilities (Eq. 2.2) for the conifer, birch and open categories, creating five 3x3 matrices (i.e., one transition matrix for each aerial photo pair), I split the conifer transition probabilities (conifer-conifer, conifer-open, open-conifer) into balsam fir and spruce using balsam fir (BF) and spruce (BS) percent cover data from Salmonier property field data, balsam fir dominant TNNP sites and literature (BF-BF, BF-Open, Open-BF, BS-BS, BS-Open, Open-BS). Based on TNNP and Salmonier property field data analysis spruce comprised an average of 8% of the canopy which is similar to other estimates from the Avalon Peninsula (Meades 1987; 1989). I used the 8% spruce proportional cover to split the conifer transition probabilities into spruce and balsam fir canopy transition probabilities creating five 4x4 matrices. Once each 4x4 matrix per aerial photo pair (n = 5) were calculated, I averaged the five matrices to make the complete canopy matrix. I then normalized the matrix by row to ensure each row summed to 1, completing the 4x4 canopy transition matrix (Horn 1975).

TNNP Field analysis – I used TNNP field data to parameterize the understory transition probabilities for the model and inform canopy transition probabilities because Salmonier property did not have any time series data required to calculate transition probabilities for the understory vegetation (Figure 2.5). I used 5 sites from TNNP (i.e., Bread Cove, Ochre Hill, Outport Cove, Halls Beach and Minchins Cove) that were most similar to the Salmonier property. TNNP data were collected from these sites every six years within the park between 1998-2016 (Hermanutz, unpublished data; Parks Canada, unpublished data). Each site had paired plots, an exclosure and a control, with 5 subplots within each plot. Within each of the five subplots percent cover data were estimated for each species present.

I used the percent cover data from the control plots on each of the five sites. I processed the data by grouping species based on the vegetation layers for each subplot. I split seedbed into two categories, good seedbed and poor seedbed, based on its suitability for balsam fir and birch germination (Lorenzetti et al., 2008; Duchesneau and Morin, 1999). In addition, grass and fern were considered part of the herbaceous layer. To incorporate a lag effect, I added two vegetation layers, browsed birch saplings and browsed balsam fir saplings. I split balsam fir and birch saplings into browsed and non-browsed vegetation layers using the ratio of browsed to non-browsed saplings from the TNNP data and Salmonier property field data **(**Figure 2.5; see Appendix F for Salmonier property data collection methods). Next, I calculated the proportional percent cover of each of the vegetation layers within each subplots using the raw species percent cover subplot data (n = 25). To estimate transition probabilities for the understory I used a decision tree to convert the macro data into micro data within each of the subplots for each year of data (1998, 2004, 2010, 2016; Appendix H) (Lee et al., 1970; Baltzer, 2000; Storm et al., 2014). Micro data are point source data where transitions for each state can be observed over time (e.g., drone imagery, tagged trees). With macro data, the exact state transitions are not observed, only the starting proportions and final proportions are known (e.g., field data percent cover). After transforming the data, I created a count matrix to determine the number of each transition type (N_{ij}) across all of the subplots and data collection years (Appendix H). Using the count matrix, I used Eq. 2.2 to calculate the transition probabilities for a 9x9 understory matrix. Any canopy gap that regenerates is filled rapidly by growing saplings; as such each open to tree transition was considered a sapling to tree transition, merging the 3x3 canopy matrix with the 9x9 understory transition creating the final 12x12 matrix (Table 2.2).

Initial States – I used restricted random number generation to create the initial states for the models while maintaining a total percent cover of 100% (SB= 17.91, SBB= 18.45, H= 17.44, SH= 17.80, YBS=2.89, YBSM=3.17, BFS=6.86, BFSM=7.90, BSS=3.97, YB=0.85, BF=2.08 and BS=0.68). I restricted the random number generation to make the initial states reflective of a canopy opening dominated by seedbed, herbs and shrubs (i.e., reflective of a heavy moose browsing legacy). The initial states were kept the same for each model and simulated restoration scenario.

Assessing Restoration Success

Prior to moose hyper-abundance, balsam fir was the dominant canopy species, with large patches of birch in the canopy in productive boreal forest locations (Meades, 1987; Meades, 1989). Shrubs also formed a thick layer, with significant amounts of tamarack, aspen and maple (Heringa, 1981; Meades, 1987; Meades, 1989). Large gaps were the ideal location for promoting understory heterogeneity as it reduced the competitive advantage of advanced balsam fir regeneration (Messier et al., 1999; Ulanova, 2000). Therefore, I ranked restoration scenarios by their effectiveness on reaching restoration targets of a) the reestablishment of balsam fir in the canopy and understory, b) the reestablishment of birch in the canopy, c) the reestablishment of shrubs in the understory and d) the closure of canopy gaps after disturbance. Additionally, I used old aerial photos to develop some baseline estimates for canopy composition prior to severe canopy compositional changes due to moose hyper-abundance. Based on the 1969 photo of the Salmonier property the target forest should have approximately 35% birch and 65% conifer (Figure 2.6). I compared restoration protocols that successfully recruit birch against this target composition, and the restoration scenarios that approach this composition will be the scenarios deemed successful for birch recruitment.

2.3 RESULTS

***Baseline model* dynamics**

The dominant eigenvector provides the stationary distribution of the baseline Markov model predicting a system dominated by good seedbed (32%) followed by spruce trees (15%), herbs (15%) and shrubs (9%) (Figure 2.7). The saplings are dominated by spruce, with 57% of the saplings spruce, 21% balsam fir and 22% birch saplings. The canopy is 66% spruce, 26% balsam fir and 8% birch. The stationary distribution of the *baseline model* shows the effect of moose on the regeneration trajectories within the forest which results in failed regeneration of both birch and balsam fir. The stationary distribution of the *baseline model* also indicates good seedbed resilience despite altered regeneration trajectories. Based on the *baseline model* results, in severely degraded landscapes there will still be a shift to spruce dominance with minimal balsam fir and birch recruitment due to the lasting legacy effect of moose overbrowsing (Figure 2.7) (See Appendix D for *moose model* results).

Effects of moose browsing (M) on regeneration trajectories

Large gap model – Large gaps (>5 ha) do not sufficiently regenerate under any level of simulated moose browsing pressure resulting in persistent open canopied patches and a loss of diversity within the system (Figure 2.8). Under high levels of simulated moose overbrowsing (M=0.001), spruce is the only tree present in the canopy and comprises 63% of the saplings in the understory. The percent of poor seedbed greatly increases in the large gaps under high browsing pressure, comprising 36% of the seedbed as compared to the 24% in the small gaps under the same browsing pressure. Within the understory there are only herbs, spruce and some balsam fir saplings present. Both shrubs and birch saplings are lost from the understory and canopy, only beginning to return once simulated moose browsing pressure is reduced to a medium level of browse. Birch trees are essentially nonexistent in the canopy for all levels of browse, only reaching 2% of the forest composition under the lowest levels of simulated moose browsing pressure (Figure 2.8). The diversity in the understory is sufficient once simulated moose browsing pressure is low (M=0.9) with all vegetation layers present in the understory (Figure 2.8). Tree recruitment into the canopy is not sufficient under any level of simulated browse as the canopy only represents 13% of the vegetation under the lowest level of browse (M=0.9; Figure 2.8).

Small gap model – Small gaps (<5 ha) do not sufficiently regenerate under high simulated moose browsing pressures (M=0.001; M=0.1; M=0.2), with birch and shrubs disappearing from the system and balsam fir being severely suppressed resulting in a lack of balsam fir recruitment into the canopy and suppressed saplings in the understory (Figure 2.9). Under severe simulated moose browsing pressure (M = 0.001), the amount of poor seedbed, dominated by herbaceous and deciduous leaf litter, increases as canopy recruitment fails. Spruce dominates the canopy, accounting for >80% of canopy trees and 16% of the overall forest composition. The understory lacks diversity, with only herbs (i.e., bunchberry and ferns), balsam fir saplings and spruce saplings present (Figure 2.9). When I simulated a reduction in moose browsing pressure to a medium level of simulated browse (M=0.5), shrubs and birch emerge in the understory (Figure 2.9). Balsam fir recruitment to the canopy increases and represents 30% of the canopy (M=0.5). The understory diversity is increased with the addition of birch saplings and shrubs; however, both are present at small abundances representing only 2% and 3% of forest composition (Figure 2.9). There is less than 1% birch recruitment to the canopy under medium browsing pressure. When I simulated a further reduction in moose browsing pressure to a low level of browsing shrubs abundance increased, representing 7% of the forest (M=0.8; M=0.9). The amount of birch saplings increased to 4% and a couple birch trees make it to the canopy, representing 13% of the canopy trees, 4% of the overall forest composition. Balsam fir recruitment is sufficient to close the canopy gap. The overall diversity of the forest is highest at the lowest simulated browsing pressure (M=0.9). Although the canopy closure is sufficient and understory diversity is present under low simulated browsing pressure, birch recruitment to the canopy does not meet the historical birch canopy percent cover of 35% in the Avalon forest in 1969 (Figure 2.6).

Restoration Scenarios (Seedling planting (R_{PK}) and reduced browsing pressure (M))

Large gap – Nine restoration scenarios were simulated using the large canopy model (Figure 2.10, 2.11; Table 2.6). Restoration scenarios are labeled R1 through R9, in ascending order of restoration effectiveness for large canopy gaps (i.e., R9 most effective, R1 least effective) at meeting the above targets (Figure 2.10; Table 2.7). Restoration scenarios that did not meet restoration targets include the planting of balsam fir and birch seedlings under small and medium reductions in simulated moose browsing pressure (R1:R3, R5; See Appendix I). Additionally, planting balsam fir seedlings under a high reduction in moose browsing pressure is ineffective in recruiting birch to the canopy, with only 1% birch in the canopy. Placing an exclosure without planting any seedlings was also largely ineffective in recruiting birch and balsam fir to the canopy but was effective for increasing shrub abundance in the understory. Shrubs increase by 8% within the exclosure simulation (R4) compared to the second most effective restoration scenario for shrub growth (R7). Out of all nine restoration scenarios three met all targets; planting balsam fir seedlings in a moose exclosure (R7), planting balsam fir and birch seedlings under a large reduction in simulated moose browsing pressure (R8) and planting balsam fir and birch seedlings in a moose exclosure (R9; Table 2.7).

Planting balsam fir seedlings in an exclosure (R7) and planting both birch and balsam fir seedlings in an exclosure (R9) are the two most effective scenarios for canopy closure and balsam fir recruitment (Figure 2.10). Both have diverse understories with an abundance of shrubs, 9% and 8%. Birch sapling and tree percent cover is the highest in R9 out of all the restoration scenarios with a 5% saplings and 7% trees, with a relative increase of 20% in birch saplings and 43% in birch trees from the second most effective restoration protocol (Figure 2.11). Furthermore, with birch representing 22% of the canopy trees, this is the closest simulated restoration scenario to reaching the target of 35% birch canopy cover based on the forest composition in 1969. Planting balsam fir and birch seedlings under low levels of browsing (R8) is effective at restoring understory diversity (Figure 2.11). The canopy in mostly closed, with the canopy representing 25% for restoration protocol R8. Under this restoration the second largest amount of birch is recruited to the canopy, 5%, which is 18% of the canopy (Figure 2.10). Therefore, birch seedlings must be planted in large canopy gaps to increase birch canopy recruitment and meet restoration targets. Poor seedbed, good seedbed, herbs and spruce saplings are at the lowest percent covers under the restoration scenario with an exclosure and the planting of both birch and balsam fir seedlings (R9), leading to a more balanced and diverse understory.

Small gap – The ranking of effective restoration protocols is the same for small gaps as it is for large canopy gaps with the exception of restoration protocol R4, the exclosure without planting (Figure 2.12). For small canopy gaps restoration protocol R4 is a more effective restoration protocol than R5, planting both balsam fir and birch seedlings under a medium reduction in simulated moose browsing pressure. As with the large canopy gap, the restoration scenarios with planting of balsam fir and birch seedlings under small and medium reductions in simulated moose browsing pressure are ineffective at meeting restoration targets (R1:R3, R5; Figure 2.12). Unlike the large canopy gap, planting balsam fir under high reductions of moose browsing pressure (R6) is effective in recruiting balsam fir to the canopy and increasing shrub abundance and moderately successful for recruiting birch to the canopy with birch comprising 9% of the canopy compared to 1% in the large gaps for the same protocol.

2.4 DISCUSSION

Reduced forest regeneration in the presence of herbivore hyper-abundance highlights the need for effective restoration protocols especially in the face of increased rates of forest degradation due to global change drivers (Wade et al., 2003; Barrette et al., 2017; Betts et al., 2017). I used a modified Markov model parameterized with multiple data sources to predict effective restoration protocols under a gradient of moose browsing intensities within two canopy gap sizes for balsam fir dominant boreal forests. My model predicted that active restoration is required in severely disturbed forests after overbrowsing by hyper-abundant moose. Furthermore, my model predicted that planting more than just the foundation species is important to restore the forest to a similar composition and function as the historical reference forests and what comes back depends on having sufficient seed sources.

Many of the regeneration trajectories observed from my model output (Figure 2.9 and Figure 2.10) are consistent with experimental studies indicating the model captured the dynamics of forest regeneration under simulated moose browsing pressure relatively well. Consistent with field observation and long-term data collection in Newfoundland (Charron and Hermanutz, 2016; Ellis and Leroux, 2017) and Isle Royale (Krefting, 1974; Rotter and Rebertus, 2014), regenerative trajectories (Figure 2.8) indicate a lasting effect of moose on forest composition resulting in failed natural regeneration of balsam fir and birch which lead to the development of moose spruce savannas. Furthermore, my model indicates that even with the removal of moose browsing as a stressor (M), the current state of the forest in large canopy gaps is not sufficient to naturally regenerate to historic forest compositions (Figure 2.6). Empirical research also has found that even after the moose populations have declined from peak abundances in Newfoundland and Isle Royale, some forests are either failing to regenerate producing moose spruce savannas or regenerating but have altered forest composition due to the lack of preferentially browsed species regeneration and a lack of available seed sources (e.g., birch, palatable shrubs; Mercer and McLaren 2002; McLaren et al., 2004; Rotter and Rebertus, 2014). Although my simulations indicate the forest is transitioning to a sparsely populated canopy with spruce dominance, my model also predicted seedbed resilience to moose overbrowsing, a result supported by empirical studies conducted in TNNP where seedbed and soil properties showed a similar resilience even in large disturbed canopy gaps (Charron and Hermanutz, 2016; Ellis and Leroux, 2017). Seedbed resilience is important for passive restoration efforts and may make active restoration efforts more efficient as time consuming and cost prohibitive soil treatments would not be required.

Restoration simulations indicate that in large canopy gaps (>5 ha) passive restoration via moose reduction is an insufficient strategy for recruiting birch and balsam fir to the canopy and increasing birch and balsam fir abundance in the understory (Figure 2.9; Figure 2.11). This result is supported by empirical literature where passive restoration as a strategy to restore forests disturbed by herbivory has had mixed results, with numerous studies reporting sub-optimal or failed restoration after reducing herbivory (Royo et al., 2010; Tanentzap et al., 2011; Beauchamp et al., 2013; Nuttle et al., 2014). This failed restoration has been attributed to several factors including the loss of key species through selective herbivory, the loss of seed sources, altered abiotic conditions and the development of alternate stable states (Duncan and Chapman, 1999; Verheyen and Hermy, 2001; McLaren et al., 2009). Within my simulated balsam fir dominant boreal forest, the failure of passive restoration is likely a combination of the legacy effects of moose through the development of moose spruce savannas and the local extirpation or loss of seed sources for birch and shrubs. This is further supported by the exclosure simulation still did not allow for sufficient birch and balsam fir canopy recruitment, which strongly indicates active restoration will be required within large canopy gaps. This is an important finding that supports Nuttle et al. (2014) who found historic, not current, ungulate densities are better indicators of long-term forest composition. This indicates passive restoration would be ineffective and that exclosures would only be effective if placed prior to severe overbrowsing to avoid the legacy effect on preferentially browsed vegetation.

The lack of success of passive restoration in large canopy gaps indicates active restoration is crucial for restoring severely disturbed forests with hyper-abundant ungulates. Several studies have suggested the combined efforts of passive and active restoration through the reduction in herbivores and active management of forest vegetation (McLaren et al., 2009; Royo et al., 2010; Gosse et al., 2011; Humber and Hermanutz, 2011). Similar to literature suggestions, I found the two most effective restoration scenarios for meeting each of the restoration targets (increased shrub abundance, re-establishment of balsam fir and birch in the canopy and canopy gap closure) was planting balsam fir and birch seedlings after intensive reductions in moose browsing pressure and within moose exclosures (Figure 2.11). Several empirical studies have reported restoration success using seedling planting as an active restoration technique (Cole et al., 2011; Omeja et al., 2011; Faure-Lacroix et al., 2013**;** Charron and

Hermanutz, 2017). One of the criticisms of seedling planting is that many studies only focus on planting one species, generally a foundation species or quick growing species to close the canopy gaps (Corbin and Holl, 2012; Palma and Laurance, 2015). However, planting only one species in large canopy gaps can produce an even aged homogenous forest with the continued failed regeneration of vegetation that has lasting legacy effects from herbivores and has the potential to have lasting anthropogenic effects on forest composition (Corbin and Holl, 2012). My model results support this notion, as the results indicate that canopy diversity may only be restored if both balsam fir and birch seedlings are planted. As such, restoration modelling could be used to assess the regeneration capacity of species of interest under several restoration scenarios to determine whether planting seedling of each species is required to restore natural ecosystem function.

Unlike large canopy gaps, model simulations predict that small canopy gaps (<5 ha) can naturally regenerate under passive restoration through reductions in moose browsing intensity (Figure 2.10). This result is supported by Charron and Hermanutz (2016) who found active restoration was not required in small canopy gaps. However, birch abundance in the canopy remains relatively low unless actively restored and birch and shrubs fail to naturally regenerate under medium and high levels of moose browsing pressure (Figure 2.10). As such, small gaps may need active restoration if moose abundance is not properly managed. Being as previous studies have suggested moose are still above carrying capacity in Newfoundland, shrubs and birch may continue to fail to regenerate suggesting a reduction in moose population abundance or the use of active restoration may be required in small gaps to ensure birch and shrub persistence (Mercer and McLaren 2002). Results indicate that within small canopy gaps passive restoration via moose reduction produces comparable results to active restoration scenarios aside from the multispecies seedling planting within moose exclosures, which increases birch canopy recruitment substantially. Passive restoration is often preferential if results are similar to active restoration as passive restoration can be more cost effective and human intervention is limited (Holl and Aide, 2011; Zahawi et al., 2014; Charron and Hermanutz, 2016).

The strengths of my approach for restoration modelling is the incorporation of herbivores as a disturbance and the combination of multiple forest layers into Markov models. The effects of herbivores on forest regeneration trajectories are well documented from seed predation by rodents, sapling overbrowsing by ungulates to insect herbivory on canopy foliage (Angelstam et al., 2000; Mysterud and Østbye, 2004; Smith et al., 2010; Hidding et al., 2013; Madsen and Löf, 2015). As such, it is a natural extension to include herbivory effects in restoration modelling as herbivores can alter the effectiveness of restoration protocols. This task, however, has rarely been done (but see Schippers et al., 2014: De Jager et al., 2017). Aside from Markov models, which can be easily modified to reflect herbivory, other spatially explicit simulation platforms such as LANDIS II are options for restoration planning with simulated herbivory (De Jager et al., 2017). The data required to parameterize a model for multiple forest layers and herbivore impacts can be daunting and perhaps this underlies the reason for the paucity of models. To circumvent the data hungry modelling approach, I integrated several data sources from field vegetation surveys to aerial photographs to drone imagery. Technological advances will facilitate this kind of data collection and integration by capturing both understory and canopy imagery as three-dimension forest data acquisition capabilities expand (Eichhorn et al., 2017; Bagaram et al., 2018). This integration has the potential to enhance restoration planning by allowing ecologist to develop models that better capture natural complexity. Inclusive restoration protocols that address more than just foundation species is crucial for restoring ecosystem function and conserving essential species important for the maintenance of biodiversity (Chazdon, 2008; Holl and Aide, 2011).

It is important to note that the aggregate macro data approach used here is both an advantage and a disadvantage of the model. The use of macro data requires several assumptions in order to estimate transition probabilities, including the use of thresholds to transform macro data into micro data (Appendix H; Lee et al., 1970). Another assumption that had to be made to combine the micro (aerial imagery, canopy data) and macro data (understory, field data) include the assumption that all open to tree transition in aerial imagery was a transition of a sapling to tree. Qualitative patterns are key, not quantitative per se, when evaluating Markov models (Balzter, 2000). Despite relatively strict model assumptions, my sensitivity analysis demonstrates that the qualitative patterns predicted by the model are robust to variations in transition probabilities and model parameters.

Based on the model results my management recommendations include 1) herbivore population management as a primary goal with active restoration undertaken in large canopy gaps (> 5 ha) or if indicated through local species extinctions or continued failed regeneration in small canopy gaps, 2) active restoration through multi-species seedling planting and 3) the placement of exclosures if herbivore populations cannot be sufficiently reduced to facilitate natural regeneration or successful active restoration. Models are an important tool that can aid in restoration planning by testing restoration scenarios of systems of interest. However, any implementation of models should be carefully monitored and data should be fed back into a model under an adaptive management framework (Walters, 1986).

Future work should attempt to improve the integration of multiple data sources and use this modelling approach to simulate restoration under various global change drivers. The improved integration of data can be done by further developing the link between sapling to tree growth in simulation modelling or by focusing on micro data sources. For example, recent LiDAR advances allow for three-dimensional forest imagery that captures both the canopy and understory vegetation which allowed Eichhorn et al. (2017) to determine the effects of deer on forest structure in UK woodlands. The ability to calculate transition probabilities for all forest vegetation layers with micro data would significantly enhance the models predictive power. In addition, simulating global change drivers can improve restoration planning by incorporating the effects of environmental change on restoration protocols to determine restorative success under various conditions, including, but not limited to, increased temperature, altered precipitation and increased fire frequency (de Groot et al., 2013; Trumbore et al., 2015; Liénard & Strigul, 2016). Determining the effectiveness of restoration protocols in the face of global change is of increasing interest for restoration biologist and policy makers to ensure restoration protocols meet restoration targets and resources are used effectively (Palma and Laurance, 2015; Trumbore et al., 2015). By developing a model that incorporates the effects of herbivory on restoration success effective restoration protocols can be identified for severely degraded systems and can support empirical studies to aid in restoration planning. By combing experimental and modelling studies restoration protocols catered towards systems of restorative interest can be developed aiding in the timely and cost-effective restoration of degraded landscapes.

Table 2.1. States used in Markov model to incorporate each forest layer.

Forest Vegetation	Vegetation Layer	Vegetation Definition	Model State	State Abbreviation	Example
Forest Floor	Seedbed	Layer in which seeds germinate	Good seedbed	SB	Feathermoss
			Poor seedbed	SBB	Herbaceous leaf litter
Herbaceous	Herbaceous	Non-woody plants	Herbaceous	H	Bunchberry (*Cornus canadensis*), twinflower (*Linnaea borealis*)
Understory	Shrub[1]	Woody, bushing plants	Shrubs	SH	Mountain maple (*Acer spicatum*), Sheep laurel (*Kalmia angustifolia*)
	Saplings	Coniferous and hardwood species under 2 m in height	Birch saplings (browsed and not browsed states)[2]	YBS/YBSM	Not browsed and browsed yellow birch (*Betula alleghaniensis*) and white birch (*Betula papyrifera*)
			Balsam fir sapling (browsed and not browsed states)	BFS/BFSM	Not browsed and browsed balsam fir (*Abies balsamea*)
			Spruce sapling	BSS	Black spruce (*Picea mariana*) white spruce (*Picea glauca*)
Canopy	Trees	Coniferous and hardwood species greater than 2 m in height	Birch	YB	Yellow birch (*Betula alleghaniensis*) and white birch (*Betula papyrifera*)
			Balsam fir	BF	Balsam fir (*Abies balsamea*)
			Spruce	BS	Black spruce (*Picea mariana*) white spruce (*Picea glauca*)

[1] In Newfoundland, many species such as red maple (*Acer rubrum*) are lower and bushier than mainland Canada

[2] Browsed and not browsed categories were used to incorporate a legacy effect for birch and balsam fir regeneration

Table 2.2. *Baseline model* developed with the transition probabilities for all vegetation layers within the boreal forest. Transition probabilities were calculated using field data from Terra Nova National Park (Newfoundland, Canada) and field data and aerial imagery from Nature Conservancy Canada's Salmonier property (Newfoundland, Canada) (Figure 1). As per Markov model restrictions, each row sums to 1 and each transition probability is non-negative. Bolded transition probabilities represent self-replacement probabilities. Good seedbed (SB), poor seedbed (SBB), herbaceous (H), shrubs (SH), birch saplings (YBS), browsed birch saplings (YBSM), balsam fir (BFS), browsed balsam fir saplings (BFSM), spruce saplings (BSS), birch trees (YB), balsam fir trees (BF) and spruce trees (BS). See text for details.

	To:											
From:	SB	SBB	H	SH	YBS	YBSM	BFS	BFSM	BSS	YB	BF	BS
SB	**0.162**	0.159	0.188	0.182	0.088	0	0.076	0	0.145	0	0	0
SBB	0.750	**0.250**	0	0	0	0	0	0	0	0	0	0
H	0.406	0	**0.594**	0	0	0	0	0	0	0	0	0
SH	0.625	0	0	**0.375**	0	0	0	0	0	0	0	0
YBS	0.690	0	0	0	**0.050**	0.027	0	0	0	0.233	0	0
YBSM	0.690	0	0	0	0	**0.077**	0	0	0	0.233	0	0
BFS	0.358	0	0	0	0	0	**0.134**	0.044	0	0	0.464	0
BFSM	0.358	0	0	0	0	0	0	**0.178**	0	0	0.464	0
BSS	0.141	0	0	0	0	0	0	0	**0.423**	0	0	0.436
YB	0.368	0	0	0	0	0	0	0	0	**0.631**	0	0
BF	0.227	0	0	0	0	0	0	0	0	0	**0.773**	0
BS	0.227	0	0	0	0	0	0	0	0	0	0	**0.773**

Table 2.3. The transition probabilities that were negatively affected by moose were multiplied by M while positively affected transition probabilities were decreased through proportional allocation. Simulations were run with increasing M (0.001, 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, 0.8, 0.9 and 1), simulating a decrease in browsing pressure where M=0.001 is severe simulated moose browsing pressure and M=1 is no simulated browsing pressure.

Effect of Moose	**Transition Probabilities**
Positive	$p_{SB,SB}$, $p_{SB,SBB}$, $p_{SB,H}$, $p_{YBS,SB}$, $p_{YBS,YBSM}$, $p_{YBSM,SB}$, $p_{BFS,SB}$, $p_{BFS,BFSM}$, $p_{BFSM,SB}$
Negative	$p_{SB,SH}$, $p_{SB,YBS}$, $p_{SH,SH}$, $p_{YBS,YBS}$, $p_{YBS,YB}$, $p_{YBSM,YBSM}$, $p_{YBSM,YB}$, $p_{BFS,BF}$, $p_{BFSM,BF}$

Table 2.4. Positively and negatively weighted transition probabilities were balanced against all other transition probabilities within the row through proportional allocation. In large canopy gaps positively weighted transition probabilities were multiplied by 1.5 (Gf3) and negatively weighted transition probabilities were multiplied by 0.5 (Gf2). In small canopy gaps the positively weighted transition probabilities were multiplied by 1.5 (Gf1).

Gap Size	**Positively Weighted Transition Probabilities**	**Negatively Weighted Transition Probabilities**
Large	$p_{SB,SBB}$, $p_{SBB,SBB}$	$p_{SB,BSS}$, $p_{BSS,BS}$
Small	$p_{SB,YBS}$, $p_{SB,BFS}$, $p_{YBS,YB}$, $p_{YBSM,YB}$, $p_{BFS,BF}$, $p_{BFSM,BF}$	

Table 2.5. The transition probabilities that were positively affected by restoration were multiplied by R_{PK} while the transition probabilities that would be negatively affected were decreased through proportional allocation. In large canopy gaps R_{PL}=2 and in small canopy gaps R_{PS}=1.3. See Appendix E for more information on the restoration parameter (R_{PK}).

Restoration	**Positively Weighted Transition Probabilities**
Positive	$p_{SB,YBS}$, $p_{SB,BFS}$, $p_{YBS,YB}$, $p_{YBSM,YB}$, $p_{BFS,BF}$, $p_{BFSM,BF}$
Negative	$p_{SB,SBB}$, $p_{SB,SBB}$, $p_{YBS,SB}$, $p_{YBS,YBS}$, $p_{YBS,YBSM}$, $p_{YBSM,SB}$, $p_{YBSM,YBSM}$, $p_{BFS,SB}$, $p_{BFS,BFS}$, $p_{BFS,BFSM}$, $p_{BFSM,SB}$, $p_{BFS,BFSM}$

Table 2.6. Description of restoration scenarios simulated in large and small canopy gaps by weighting the Markov model transition probabilities. The intensity of moose browsing pressure decreases as the value of M increases. Specifically, M=0.001 is severe moose browsing pressure, M=0.8 is low moose browsing pressure and M=1 is no moose browsing pressure.

Moose browsing pressure	Seedling planting	Restoration scenario
M=0.001	No planting	**R0**[1]
M=0.1	Balsam fir seedlings	**R1**
	Balsam fir and birch seedlings	**R2**
M=0.45	Balsam fir seedlings	**R3**
	Balsam fir and birch seedlings	**R5**
M=0.8	Balsam fir seedlings	**R6**
	Balsam fir and birch seedlings	**R8**
M=1	No planting	**R4**
	Balsam fir seedlings	**R7**
	Balsam fir and birch seedlings	**R9**

[1] Restoration scenario R0 is the *large gap model* with no restoration. The model reflects the forest dynamic under severe moose browsing pressure and was used to compare to the restoration scenarios to determine changes in forest composition and regeneration trajectories after simulating restoration.

Table 2.7. Restoration scenario effectiveness for meeting each of the restoration targets in large canopy gaps. The targets used include the closure of canopy gaps after disturbance (Closed canopy), the reestablishment of birch in the canopy (Birch recruitment), the reestablishment of balsam fir in the canopy and understory (Balsam fir recruitment) and the reestablishment of shrubs in the understory/understory diversity (Understory diversity/Shrub recruitment). These restoration targets are based on historic reference ecosystem composition and suggested indicators of restoration success according to the SER Primer of Ecological Restoration (SER, 2004). The targets were developed to aid in restoration protocol assessment where successful restoration protocols would restore ecosystem function rather than replicate exact historical systems. As such, restoration targets were considered met based on a presence/absence basis opposed to exact values with the exception of canopy closure, which was based on the canopy proportional cover equal to or greater than the canopy proportional cover for small canopy gaps under low browsing pressure (M=0.9). See Table 2.6 for restoration scenario details.

Restoration scenario	**Closed canopy**	**Birch recruitment**	**Balsam fir recruitment**	**Understory diversity/ Shrub recruitment**
R1	No	No	No	No
R2	No	No	No	No
R3	No	No	Yes	Yes
R4	No	Yes	Yes	Yes[1]
R5	No	Yes	Yes	Yes
R6	No	No	Yes	Yes
R7	Yes	Yes	Yes[2]	Yes
R8	Yes	Yes	Yes	Yes
R9	Yes	Yes[3]	Yes	Yes[4]

[1] Most effective restoration scenario for shrub percent cover
[2] Most effective restoration scenario for balsam fir canopy recruitment
[3] Most effective restoration scenario for birch canopy recruitment
[4] Most effective restoration scenario for canopy closure

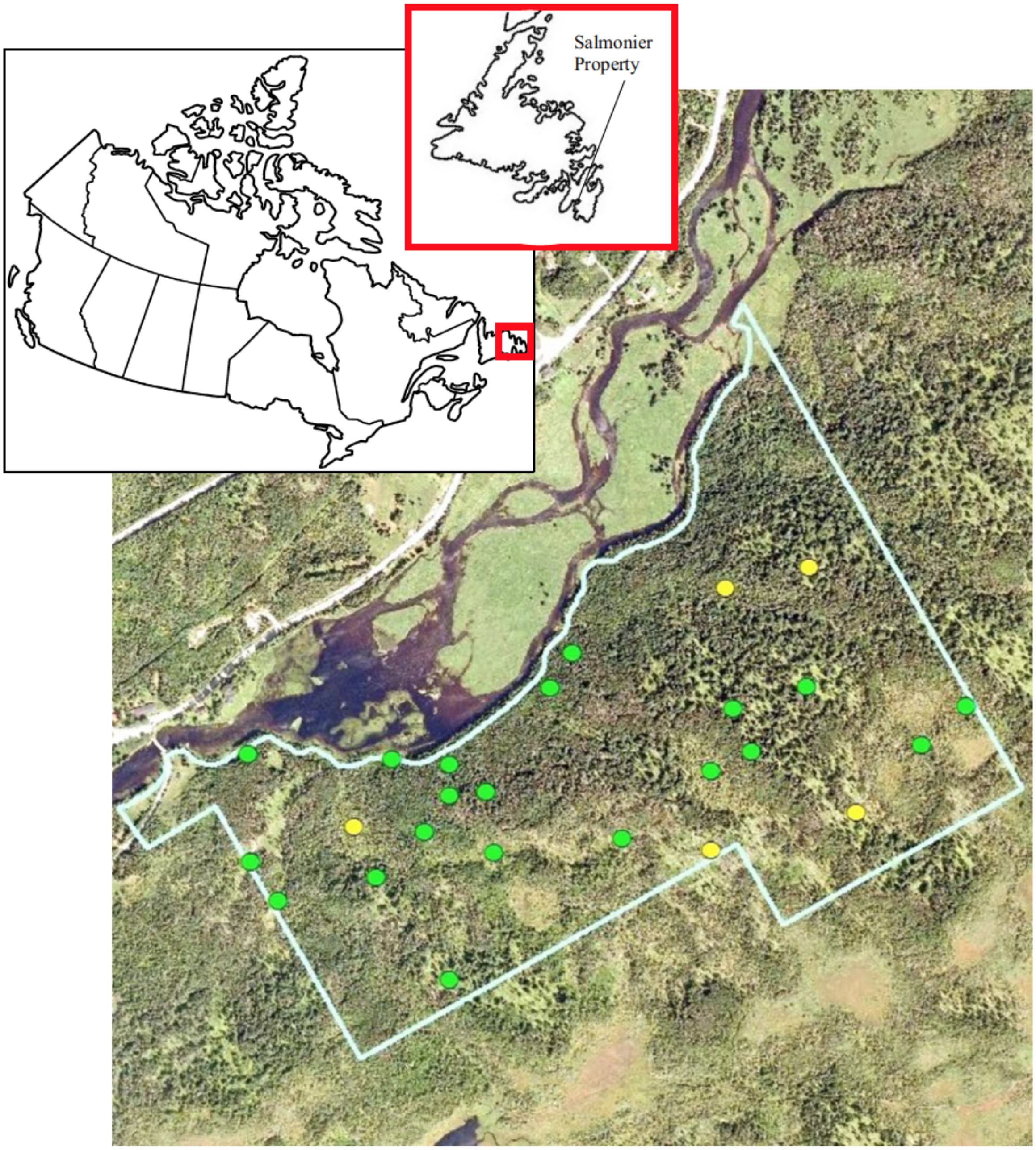

Figure 2.1. The locations of 2016 field plots (green) and the additional plots sampled in 2018 (yellow) on the Salmonier property within the Avalon Forest Ecoregion (Newfoundland, Canada).

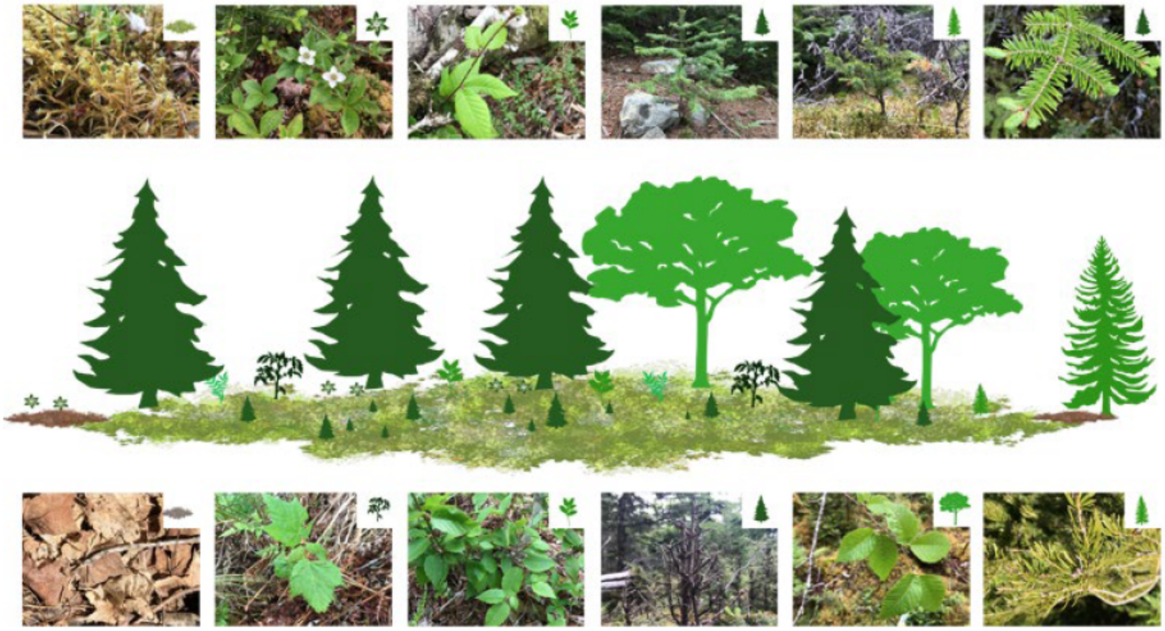

Figure 2.2. Balsam fir dominant boreal forest diagram for all 12 states incorporated in the modified Markov model. States from left to right, top to bottom: Seedbed (SB; e.g., feathermoss), herbaceous (H; e.g., bunchberry, *Cornus canadensis*), birch saplings (YBS), balsam fir saplings (BFS), spruce saplings (BSS), balsam fir trees (BF), poor seedbed (SBB; e.g., deciduous leaf litter), shrub (SH; e.g., red maple, *Acer rubrum*), browsed birch saplings (YBSM), browsed balsam fir saplings (BFSM), birch trees (YB) and spruce trees (BS).

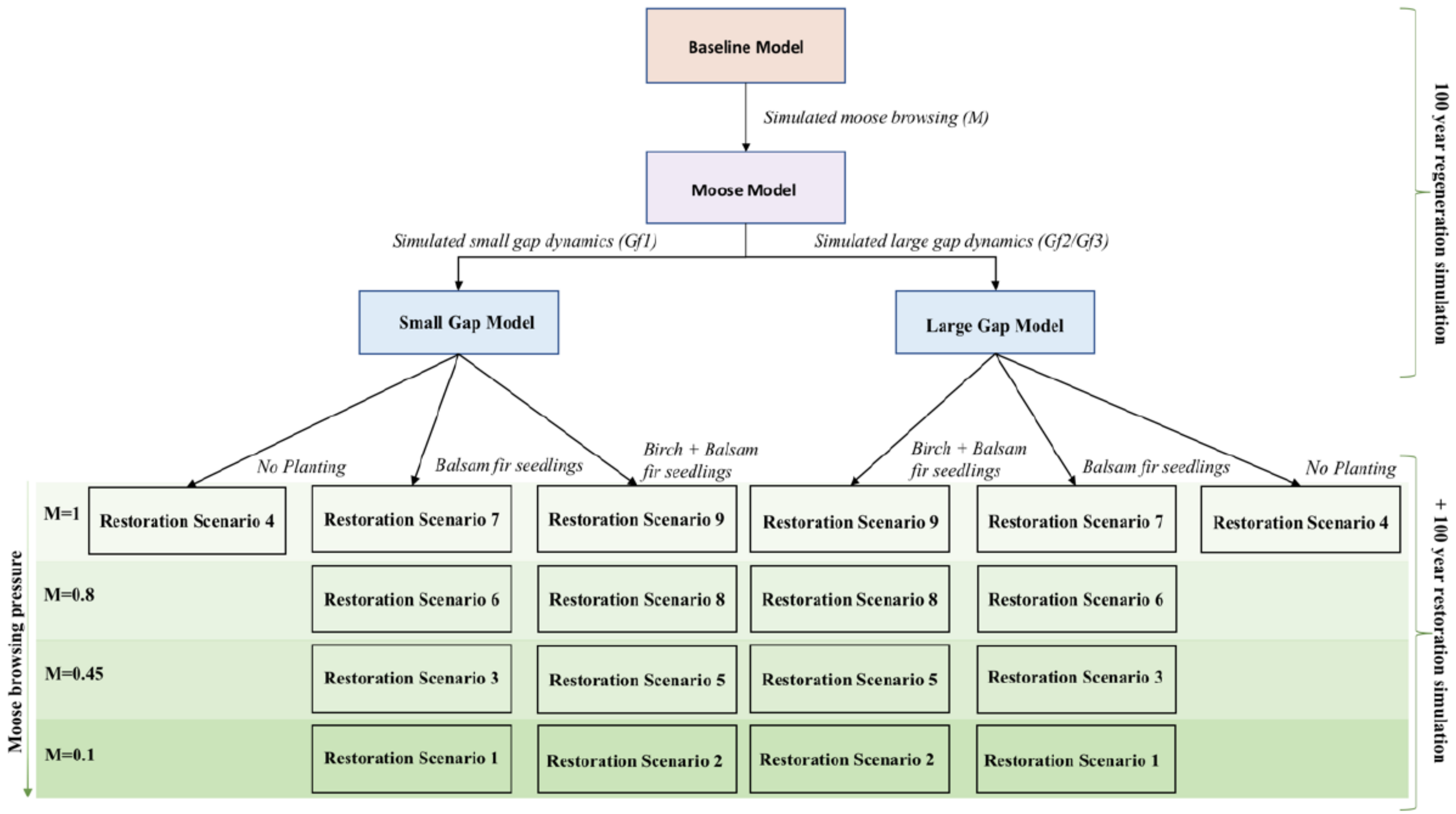

Figure 2.3. Flow diagram of model development from the initial baseline model (transition matrix) to the restoration scenarios tested on each gap size. Moose browsing pressure (M), large gap dynamics (Gf2, Gf3) and small gap dynamics (Gf1) are parameters used to weight the model based on adding these additional components. Note, for the first 100 time steps, each restoration scenarios (green boxes) was run at M=0.001 in large and small canopy gaps prior to adding restoration scenarios and increasing M for the final 100 time steps.

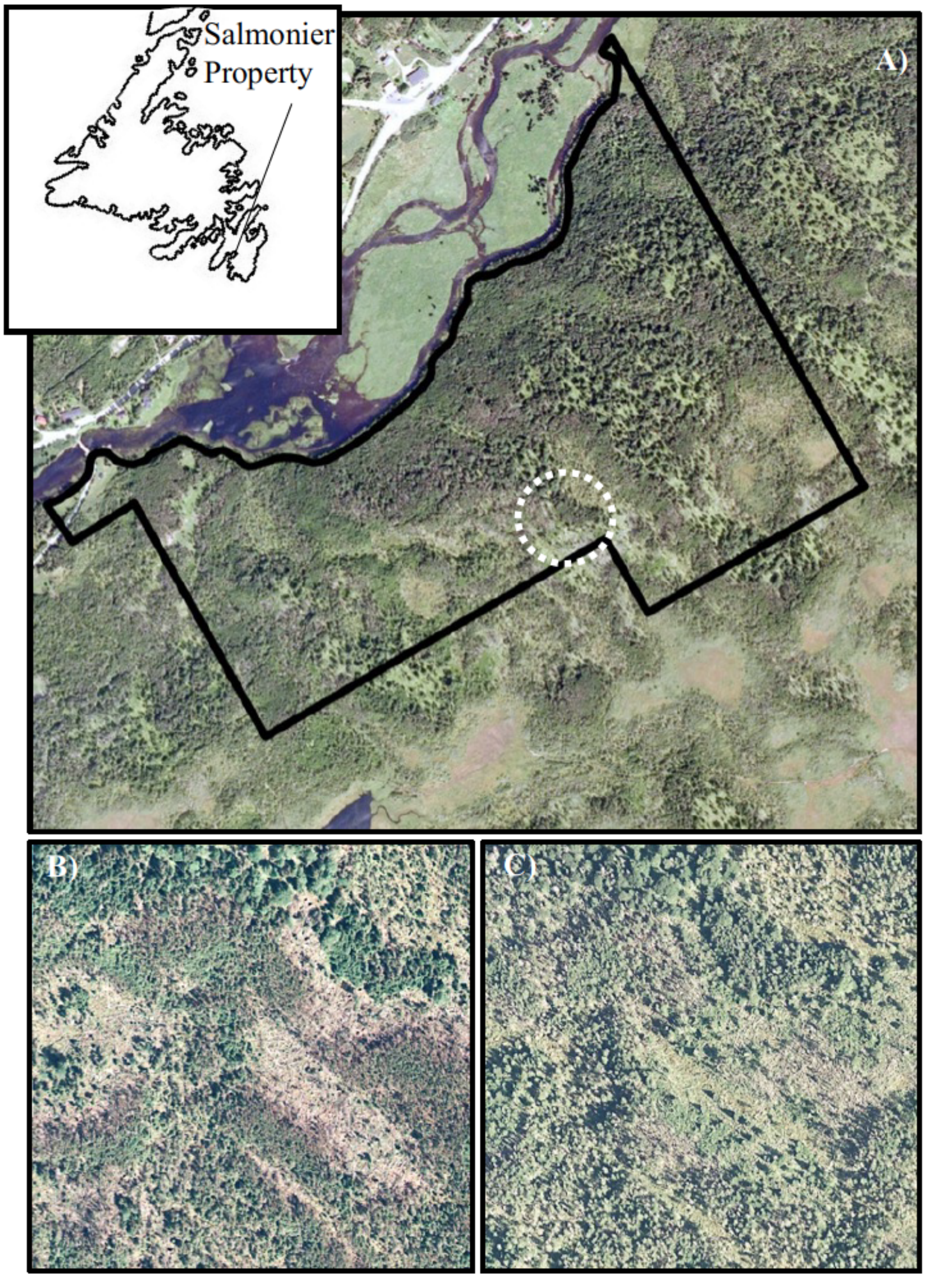

Figure 2.4. Aerial photos of the Salmonier property showing the lack of regeneration within a sizeable canopy gap. A) Aerial photo from 2008 showing the Salmonier property border, outlined in black, and the large canopy gap, circled in white. B) An aerial photo of the Salmonier property from 1996 zoomed in on the large canopy gap shortly after severe disturbance. C) An aerial photo of the Salmonier property from 2009 showing the large canopy gap has failed to regenerate and has expanded in size. As suggested by model results, this location will require active restoration.

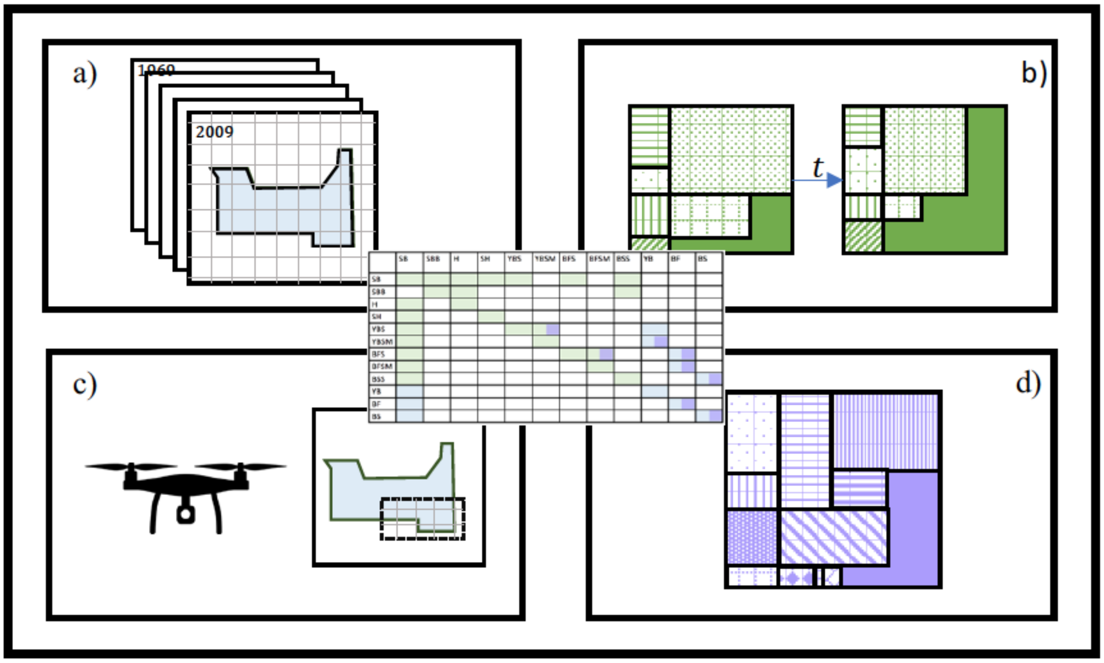

Figure 2.5. Conceptual diagram of the four data sources, a) Salmonier aerial photos b) Terra Nova National Park field data c) Salmonier drone images and d) Salmonier field data. Colours in the table correspond to which data source is used to calculate the corresponding transition probability. Transitions with dual colours indicate transitions that were calculated using multiple data sources. Understory transition probabilities were calculated by transforming macro field data from 1998 – 2010 into micro data through the use of a decision tree (see Appendix H). State changes between each data collection year were used to calculate transition probabilities. Canopy transition probabilities were calculated by gridding and identifying state changes between each grid cell for each aerial photo.

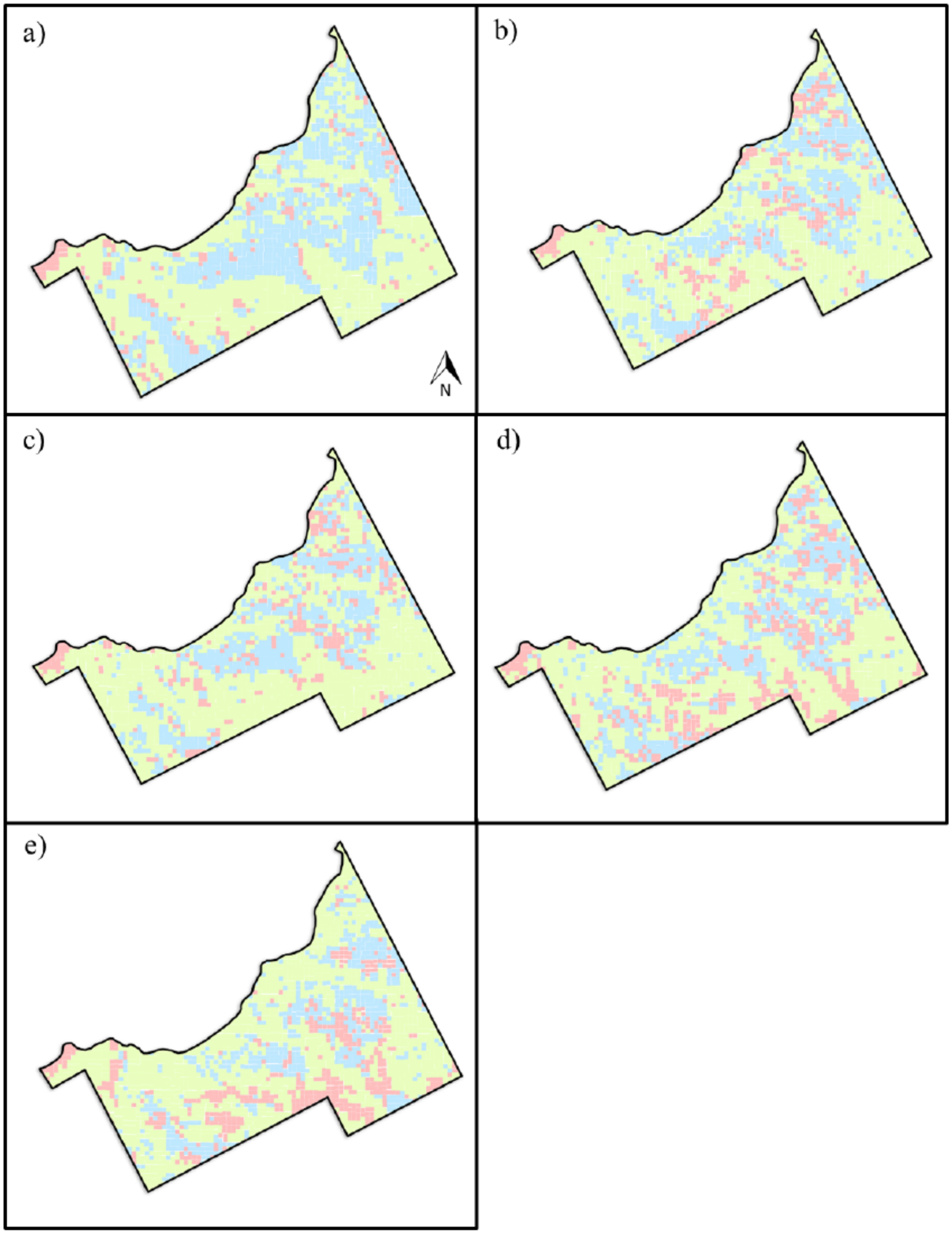

Figure 2.6. Compositional changes in Salmonier property for a) 1969, b) 1978, c) 1985, d) 1995 and e) 2009. Green=conifer, blue=birch and red=open. The amount of birch trees in the canopy has decreased by 35% and the amount of open canopied patches within the property has increased by 136%.

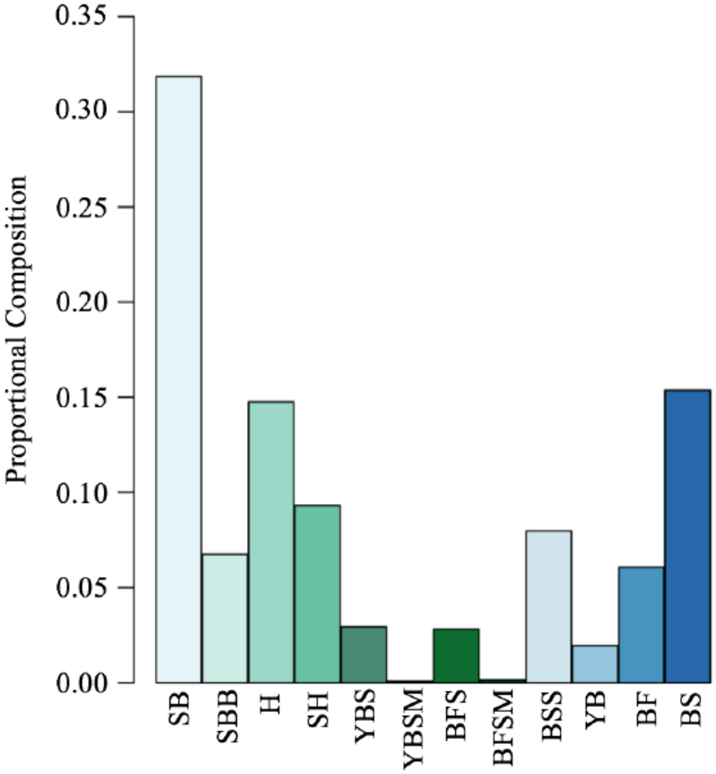

Figure 2.7. Stationary distribution for the baseline boreal forest regeneration model. The baseline model is a stationary Markov model without the transition probability weights for moose browsing pressure (M=1, no browsing) and gap specific regeneration. The stationary distribution shows the equilibrium distribution of the forest if moose were to be removed from the system. Stationary distributions are calculated through eigenvector analysis based on the transition matrix (Table 2.2). Good seedbed (SB), poor seedbed (SBB), herbaceous (H), shrubs (SH), birch saplings (YBS), browsed birch saplings (YBSM), balsam fir (BFS), browsed balsam fir saplings (BFSM), spruce saplings (BSS), birch trees (YB), balsam fir trees (BF) and spruce trees (BS).

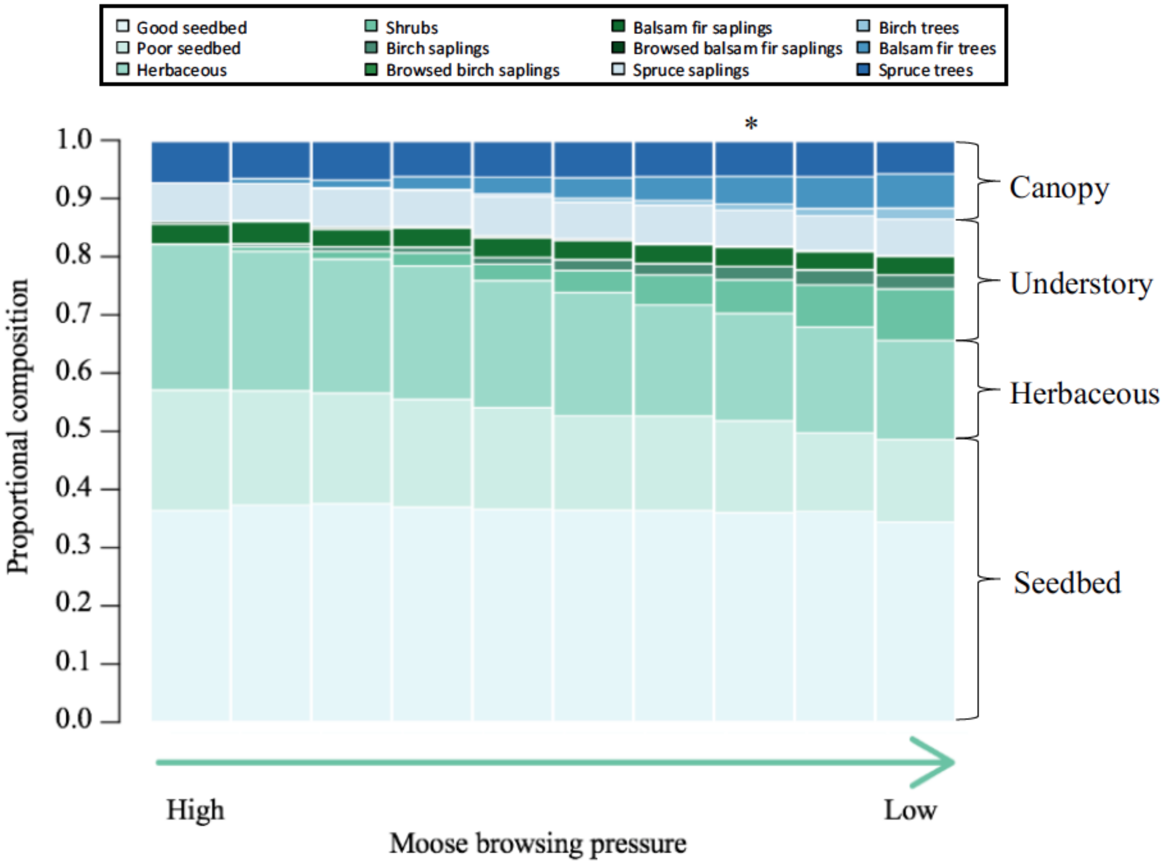

Figure 2.8. Proportional composition of vegetation layers in large boreal forest canopy gaps under an increasing moose browsing pressure (low=0.9, high=0.001). Browsing pressure ranges between 0.001 (high) to 0.9 (low) and we simulated increments of 0.1 from 0.9 to 0.1 and by 0.099 for 0.1 to 0.001. Regardless of moose browsing pressure the forest fails to regenerate, resulting in a persistent open canopied system. At a low level of browsing pressure (M=0.7) birch begins to emerge in the canopy (birch proportional cover >0.005) indicated by an asterisk (*). Active restoration protocols are required to close the gap and increase birch and balsam fir recruitment to the canopy. The proportional composition calculations are based on the mean of 500 simulations for each browsing pressure at the 100th time (year) step.

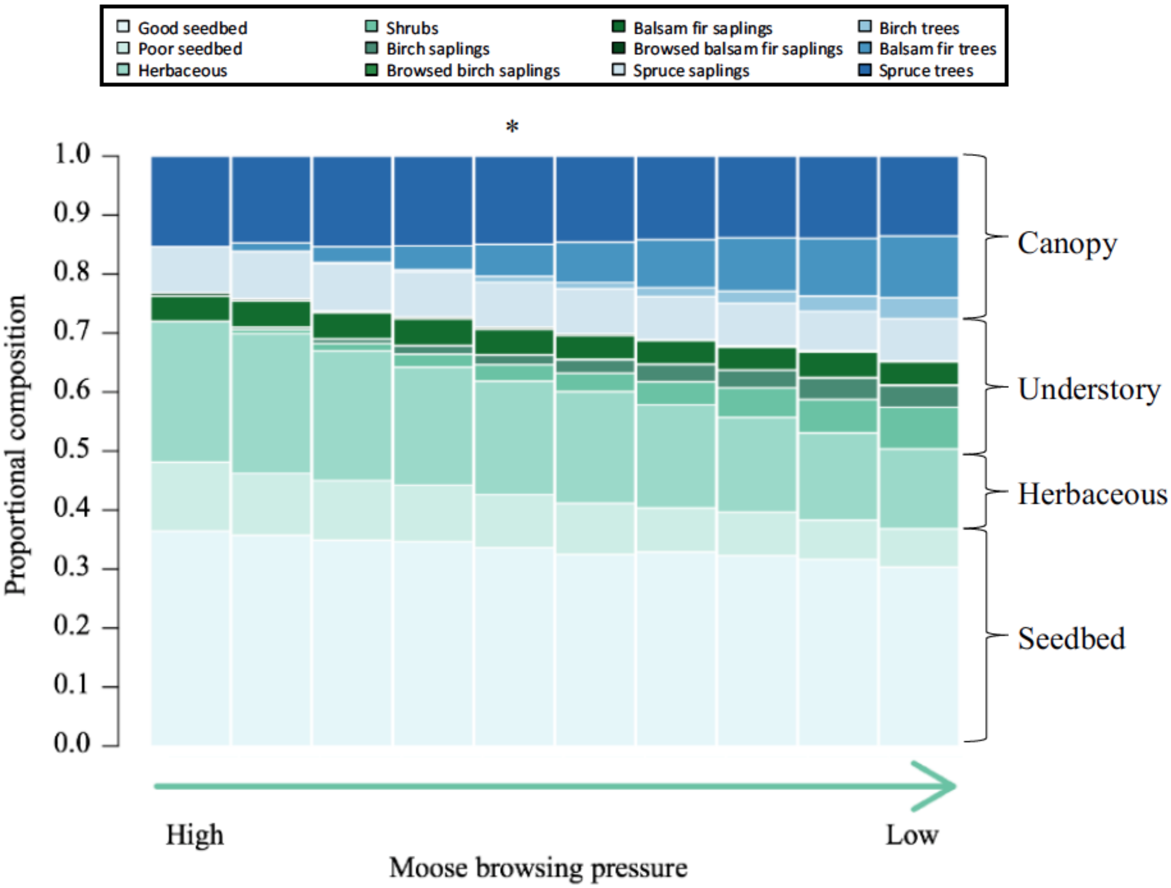

Figure 2.9. Proportional composition of vegetation layers in small boreal forest canopy gaps (<5 ha) under an increasing moose browsing pressure. Browsing pressure ranges between 0.001 (high) to 0.9 (low) and we simulated increments of 0.1 from 0.9 to 0.1 and by 0.099 for 0.1 to 0.001. Reducing browsing pressure from a high (M=0.001) to low level of browsing (M=0.8, M=0.9) closes the canopy and successfully recruits balsam fir into the canopy. If browsing pressure is reduced to the lowest value of browse (M=0.9) 11.1% of the canopy will be birch, otherwise the percent of birch in the canopy is less than 10%, with birch failing to recruit at medium and high levels of browse. At a medium level of browsing pressure (M=0.4) birch begins to emerge in the canopy (birch proportional cover >0.005) indicated by an asterisk (*). There is double the amount of canopy proportional cover, representing the level of canopy closure, in this small canopy gap compared to the large canopy gap (Figure 2.8). The proportional composition calculations are based on the mean of 500 simulations for each browsing pressure at the 100th time (year) step.

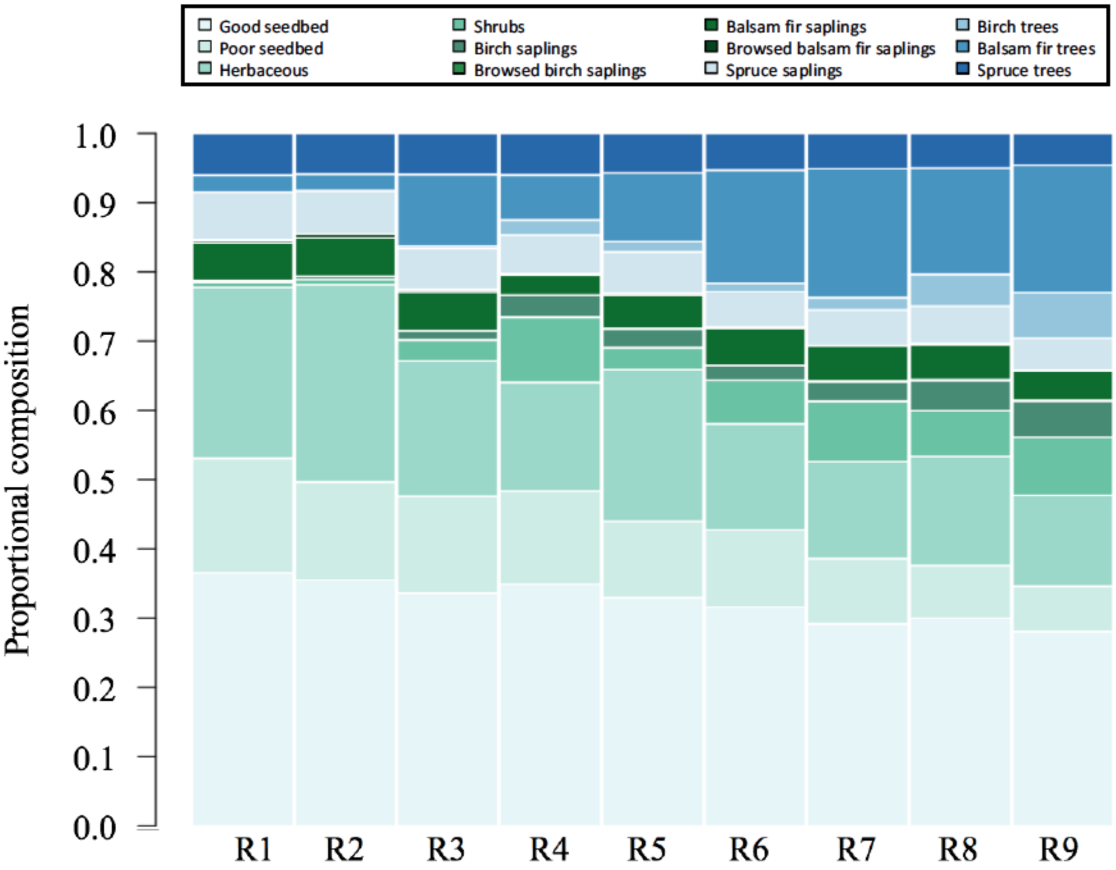

Figure 2.10. Proportional composition of the boreal forest under nine active restoration scenarios in large canopy gaps. Restoration scenarios are labeled R1 through R9, in ascending order of effectiveness for reaching restoration targets; R1, planting balsam fir seedlings under high moose browsing pressure (M=0.001); R2, planting birch and balsam fir seedlings under high moose browsing pressure (M=0.001); R3, planting balsam fir seedlings under medium moose browsing pressure (M=0.45); R4, placing an exclosure with no planting (M=1); R5, planting birch and balsam fir seedlings under medium moose browsing pressure (M=0.45); R6, planting balsam fir seedlings under low moose browsing intensity (M=0.8); R7, planting balsam fir seedlings in an exclosure (M=1); R8, planting birch and balsam fir seedlings under low moose browsing intensity (M=0.8); R9, planting birch and balsam fir seedlings in an exclosure (M=1). The most effective restoration scenario based on restoration targets is R9. This scenario has the largest canopy recruitment of birch, largest canopy closure, second largest balsam fir recruitment and the most balanced ratio of herbs, shrubs and saplings within the understory. The proportional composition calculations are based on the mean of 500 simulations for each restoration strategy at the 200th time (year) step.

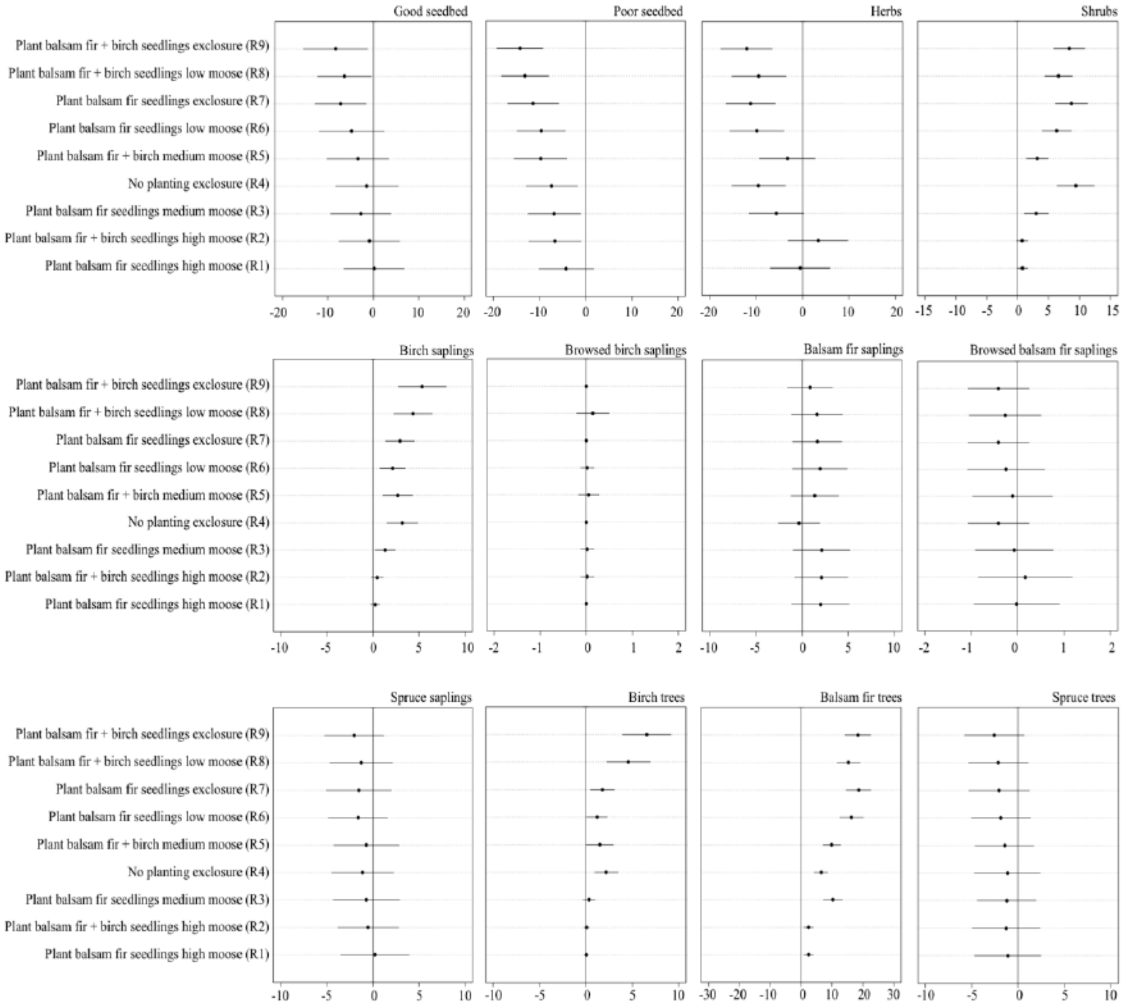

Figure 2.11. Mean change (+/- SD) in proportional percent cover for each vegetation layer between R0 (severe moose browsing pressure (M=0.001) with no simulated restoration) and all nine restoration scenarios in large canopy gaps (R1 to R9, see Table 2.3). Positive values indicate an increase and negative values indicate a decrease in proportional percent cover. Restoration targets aim to increase mean proportional percent cover of shrubs (SH), birch saplings (YBS), balsam fir saplings (BFS), birch trees (YB) and balsam fir trees (YB). The largest increases in mean proportional percent cover for each of the vegetation layers of interest based on restoration targets indicates the most effective restoration protocol for that individual vegetation layer. For instance, the most effective restoration scenario for shrubs is R4 while the most effective restoration protocol for birch is R9. See Table 2.3 for restoration scenario details. The change in proportional percent cover was calculated using the proportional cover for each of the 500 simulations for each restoration strategy at the 200th time (year) step.

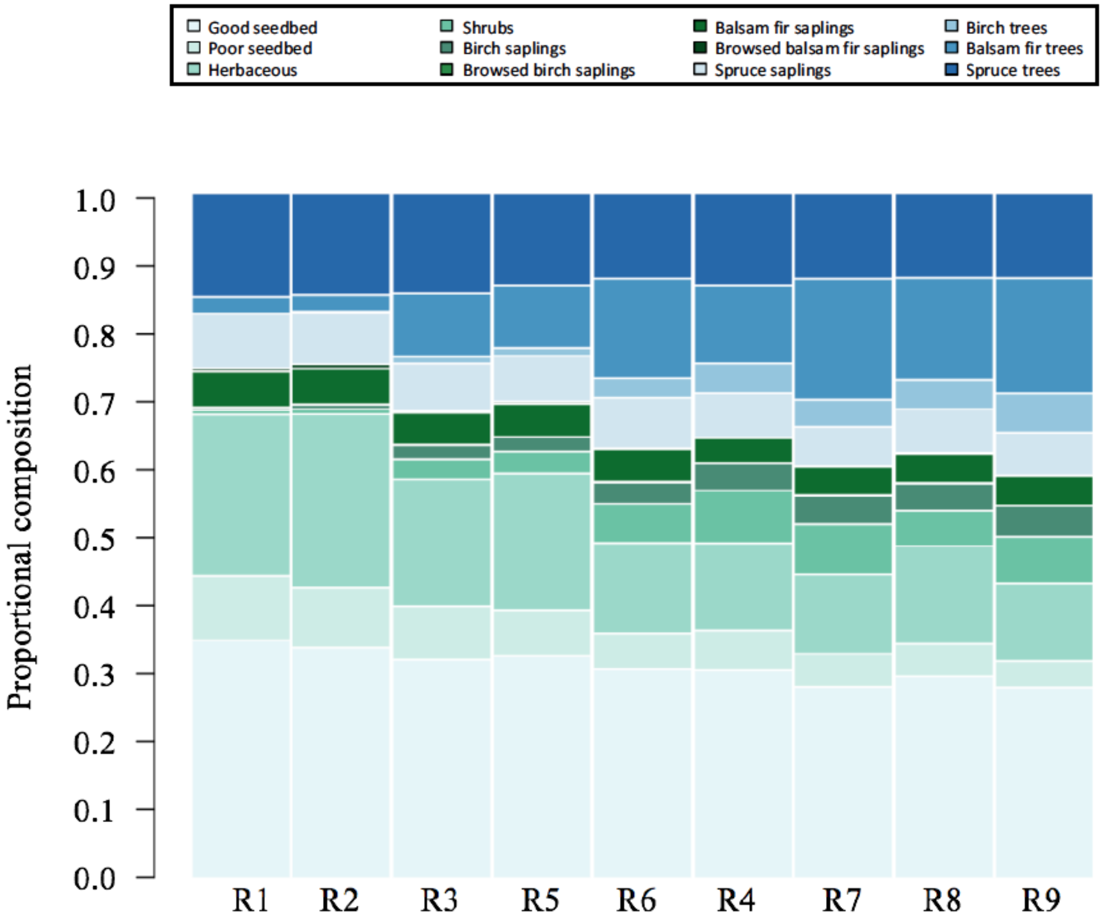

Figure 2.12. Proportional composition of the boreal forest under nine restoration scenarios in small canopy gaps. Restoration scenarios are labeled R1 through R9, in ascending order of effectiveness for reaching restoration targets; R1, planting balsam fir seedlings under high moose browsing pressure (M=0.001); R2, planting birch and balsam fir seedlings under high moose browsing pressure (M=0.001); R3, planting balsam fir seedlings under medium moose browsing pressure (M=0.45); R5, planting birch and balsam fir seedlings under medium moose browsing pressure (M=0.45); R4, placing an exclosure with no planting (M=1); R6, planting balsam fir seedlings under low moose browsing intensity (M=0.8); R7, planting balsam fir seedlings in an exclosure (M=1); R8, planting birch and balsam fir seedlings under low moose browsing intensity (M=0.8); R9, planting birch and balsam fir seedlings in an exclosure (M=1). The proportional composition calculations are based on the mean of 500 simulations for each restoration strategy at the 200th time (year) step

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CHAPTER 3: SUMMARY AND CONCLUSION

Degraded forests are failing to naturally regenerate on a global scale in part due to hyper-abundant herbivores which severely overbrowse and graze forest vegetation (Persson et al., 2000; Wade et al., 2003; Barrette et al., 2017; Betts et al., 2017). With increasing pressure on forested ecosystems from global change drivers the need for effective forest restoration is crucial to restore and preserve ecosystem health and function (Kurz et al., 2008; Moritz et al., 2012; de Groot et al., 2013). On the Island of Newfoundland moose selectively browse palatable species including balsam fir, yellow, and white birch and a variety of shrubs resulting in the loss of the advanced regeneration of fir saplings and the development of alternative stable states in severely browsed forest patches (i.e., spruce moose savanna) (McLaren et al., 2004; Gosse et al., 2011). Once these alternative stable states have been entered intervention is required to restore the ecosystem (Charron and Hermanutz, 2017).

Several studies have reported varying degrees of restoration success for the same restoration protocols used within unique forest ecosystems (Madsen and Löf, 2005; Cole et al., 2011; Gosse et al., 2011; Palma and Laurance, 2015). With the variability in restoration success dependent on local forest conditions experimental studies are heavily relied on to determine which restoration protocols to use within unique degraded landscapes (Palma and Laurance, 2015). Experimental studies are often short term and do not capture the full effect of restoration protocols on forest composition, potentially leading to a lack of diversity or failed restoration if environmental variability is not taken into account. In my thesis, I used available data to develop a model to aid in restoration planning. My specific objectives were to develop a transition model that can i) identify current regeneration trends within the Newfoundland balsam fir dominant boreal forest, ii) simultaneously examine the effects of moose on seedbed, herbaceous, shrub and canopy vegetation abundance and iii) evaluate the effectiveness of a suite of protocols to restore both the understory and canopy diversity and re-establish balsam fir in the canopy. My major contributions include:

1. The development of a model parameterized with aggregate data for simulating boreal forest dynamics on the island of Newfoundland. This model captured the dynamics of both forest understory and canopy, a key aspect often overlooked in regeneration and restoration research
2. The evaluation of a suite of restoration scenarios for my study system. Specific model predictions regarding effective restoration protocols are:
    a. Current regeneration trends of my study system indicate that birch may continue to decline unless actively restored via planting
    b. Planting of more than one foundation species may be required in severely degraded landscapes
    c. Biodiversity may not increase following foundation species restoration for species susceptible to herbivory
    d. Exclosures with multiple species seedling planting may be the most effective protocol for restoring shrubs, balsam fir and birch

Findings by Charron and Hermanutz (2017) as well as Humber and Hermanutz (2011) support my model predictions where seedling planting is believed to be the most effective protocol for restoring foundation species. Furthermore, my results showed ecosystem resilience indicated by the persistence of good quality seedbed regardless of moose browsing pressure and canopy gap size similar to findings from Charron and Hermanutz (2016) and Ellis and Leroux (2017).

The restoration of degraded forests is crucial for various reasons including, increasing forest resilience to climate change, carbon sequestration, protection of species at risk and for societal interests (Gauthier et al., 2015; Trumbore et al., 2015; Schmitz et al., 2018; Watson et al., 2018). Hyper-abundance of moose has cascading impacts on various species (Suominen et al., 2008; Rae et al., 2014). For example, the decline in understory vegetation and increase in non-native vegetation reduces ground nesting material and decreases in arthropod abundance, which then causes reduced abundance of ground nesting and insectivorous birds (Rae et al., 2014). The decline of birch within the forest can reduce the available microhabitats, which can lead to declines in lichen diversity (Boudreault et al., 2002; McLaren et al., 2004). Further, shifting towards homogenous forest stands increases forest susceptibility to large disturbances exacerbating the degradation of the system (Trumbore et al., 2015). As such, the development of effective restoration scenarios is of particular interest to agencies such as Parks Canada and Nature Conservancy Canada (NCC) who are working to restore native forests after moose disturbance.

A model based approach to restoration planning can aid in the development of restoration protocols and assist in identifying areas requiring restoration. The use of aggregate data in the parameterization of simulation models allows for a broader range of forest dynamics to be captured in regeneration and restoration modelling. I have shown that using this approach to data collection and model parameterization in conjunction with easily modified Markov models can be used to test restoration effectiveness for herbivore disturbed forests. My modelling approach can be used in other herbivore disturbed forests such as Anticosti Island with hyper-abundant deer (e.g., Côté et al., 2014) or severely moose disturbed Fennoscandian (e.g., Kolstad et al., 2018) or Nova Scotian (MacSween et al., 2019) forests. Additionally, my modelling approach can be adapted to simulate other disturbances to predict how restoration protocols will fair under various disturbance regimes. However, it is important to note that models are imperfect simplifications of a system and must be confronted with data and model predictions must be monitored (Otto and Day, 2011). Models are useful tools to support experimental studies and experimental studies support model development, with both approaches complementing each other and strengthening scientific findings. Consequently, the predictions made here should be tested via data collection and long-term monitoring.

Short term, quantities land managers and researchers could measure include balsam fir and birch seedling survival, mortality, browsing level and growth (Charron and Hermanutz, 2017). Additionally, the seedbed can be surveyed to ensure the poor seedbed in large gaps is transitioning back to good quality seedbed (e.g., feathermoss). The herbaceous and shrub layer should be measured to monitor shifts from sun loving to shade tolerant species, indicating a return to a forest composition more representative of a closed canopy naturally regenerating system (Gosse et al., 2011). Long term, sapling survival, seed production, canopy recruitment and canopy mortality of both balsam fir and birch should be monitored. Specifically, forests with several birch saplings above 2 m would be a good indication that restoration efforts are succeeding. Also, shrub composition should be measured to determine whether species previously suppressed and locally extirpated from severely browsed plots are returning to the understory (SER, 2004). Other important factors indicating restoration success would be the natural self-replacement of balsam fir and birch (i.e., seed rain, germination, seedling survival), forest composition similar to the surrounding intact forest (i.e., balsam fir dominance or mixed wood) and resilience to future disturbance (i.e., gap expansion versus closure) (SER, 2004). This long-term monitoring would not only aid in the evaluation of restoration success, but can also help parameterize future models to increase predictive capacity and reducing the number of model assumptions.

For future studies, I suggest the use of drone and aerial survey data for the parameterization of both understory and canopy transition probabilities. The biggest hurdles for the use of drones includes licensing the pilot and the initial cost of the drone, however, the flight process and image processing is fairly straightforward, with user friendly drone processing software that produces excellent data that captures understory and canopy dynamics in forest gaps. Aerial survey data such as LiDAR and aerial photography (Suárez et al., 2005), can be acquired online for free or from the government relatively cheaply. As aerial survey data technology is enhanced, the opportunity for quality data sources that capture larger ranges of forest dynamics increases, opening up the door for enhanced modelling. Calculating transition probabilities using strictly micro data sources simplifies the model and reduces ambiguity (Lee et al., 1970; Appendix J). I also suggest future studies use models to simulate restoration under various climate change predictions to ensure restoration scenarios still meets goals under changing environmental conditions (Liénard and Strigul, 2016). For instance, increased temperatures can affect several aspects of forest regeneration dynamics such as altering germination success, change vegetation growth patterns, reducing forest resilience to wind events, change fire frequency and increasing canopy mortality through increased insect outbreaks. Any number of these effects can be incorporated into models to determine whether restoration will still be effective with increasing temperatures to support restoration planning. Determining how restoration protocols fair in the face of climate change and increasing disturbance rates is an emerging concern for policy makers and restoration biologists (Palma and Laurance, 2015; Trumbore et al., 2015).

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APPENDIX A: YELLOW BIRCH AND BALSAM FIR PROFILES AND REGENERATION TRAJECTORIES

In this appendix, I provide background information on yellow birch and balsam fir regeneration trajectories in canopy gaps in the presence and absence of hyper-abundant moose. Note that gap size classification is highly variable and dependent on the study conducted. As such, for my thesis I followed gap size classifications from Charron and Hermanutz (2016) where small gaps are <5 ha and large gaps are >5 ha. For this appendix I discuss vegetation dynamics in minute (minute; <200 m^2 (Runkle, 1985; McCarthy, 2001)), small (200 m^2 to <5 ha (Charron and Hermanutz, 2016)) and large (>5 ha (Charron and Hermanutz, 2016)) canopy gaps. Minute gap sizes were not simulated as these gaps often regenerate regardless of the level of disturbance either through natural regeneration or canopy expansion. For my thesis, these gap sizes are of interest purely for the discussion of vegetation dynamics and may not be directly applicable to specific restoration scenarios.

Yellow Birch

Yellow birch is considered a mid-successional species but is usually present in the canopy through all successional stages (Boulanger et al., 2017). The abundance of yellow birch in the canopy remains relatively constant throughout each successional stage, however the abundance is slightly higher during early and mid-succession before shade tolerant species become abundant (Chen and Taylor, 2012). Within the canopy, yellow birch will either be sub-dominant or rare, with individual trees or small patches interspersed throughout the canopy.

Yellow birch reproduction can occur on a variety of microclimates but successful seeding, germination and seedling growth is dependent on soil drainage, soil type and light availability (Archambault et al., 1998). Yellow birch reproduces via seed banks that can remain viable for up to two years. Seed survival depends on the heat and soil moisture as hot dry climates cause the seeds to desiccate. Germination requires a moderate amount of light, moist seedbeds and moderately to well drained soils (Archambault et al., 1998). Germination is most successful on decaying woody debris, wet, thin layers of leaf litter, and organic or mineral soil (Lorenzetti et al., 2008). Seedling rooting ability is limited and they require thin seedbed for successful rooting. Once successfully rooted they require a moderate amount of sunlight for proper growth (Lorenzetti et al., 2008).

Yellow birch seedlings and saplings grow quickly in both shade and sunlight, usually having growth rates that exceed shade tolerant species (Beaudet and Messier, 1998). However, this continual rapid growth has trade-offs, a majority of the resources are allocated towards increasing sapling height, resulting in less strengthening of the roots and stems. This leads to higher sapling mortality rates than other slower growing species in shaded areas (Beaudet and Messier, 1998).

The ideal conditions for yellow birch growth is in a medium sized canopy gap (200 m^2 to <5 ha) after moderate levels of seedbed disturbance (Kern et al., 2012). Medium sized gaps allow for an increased amount of sunlight while maintaining the soil moisture (Kern et al., 2012). The moderate level of seedbed disturbance exposes mineral soil and produces decaying woody debris, ideal for germination and seedling growth (Houle and Payette, 1990). The disturbance also disrupts the shade tolerant advanced regeneration allowing for reduced competition for resources. Yellow birch is only moderately tolerant to competition, therefore reducing the advanced regeneration greatly increases the chance of the yellow birch reaching the canopy (Houle and Payette, 1990). Furthermore, after the initial 5 years of growth yellow birch becomes less shade tolerant, requiring higher levels of sunlight for growth and requiring more space for proper crown development (Jarvis, 1957).

Both very small and large canopy gaps produce unfavourable conditions for yellow birch regeneration (Lorenzetti et al., 2006; Kern et al., 2012). Very small gap sizes prevent the proper growth of saplings due to an increased level of competition with shade tolerant species and the reduced level light availability (Kern et al., 2012). In large gaps, the seedbed loses moisture, the heat can desiccate the yellow birch seeds and competition from shade intolerant species is high (Lorenzetti et al., 2006). In these gaps, yellow birch regeneration is more likely to occur along the perimeter of the gap where the soil moisture is higher and the competition is reduced (Prévost and Charette, 2015).

When moose are abundant, yellow birch often fails to regenerate because it is preferentially browsed on due to its palatable nature (Dodds, 1960; Bergerud and Manuel, 1968). Both seedlings and saplings are detrimentally impacted by moose browsing and trampling (Bergerud and Manuel, 1968). Seedlings are routinely uprooted by browsing due to shallow rooting systems on moist soils. Saplings are repeatedly browsed on suppressing growth. They can only withstand approximately 5 browsing years before dying from overbrowsing (Bergerud and Manuel, 1968). On rare occasions, yellow birch can avoid browsing if it established in an area moose cannot reach such as an area blocked by downed trees or an area surrounded with unpalatable species or thistle where the seedlings may go unnoticed (Kern et al., 2012). However, once the seedlings mature into saplings the costs of a sheltered location outweigh the benefits. These locations often have reduced light availability for sapling growth, have increased competition or reduced space which supresses crown growth (Jarvis, 1957). Therefore, when moose are overabundant yellow birch fails to regenerate and fails to replace the aging yellow birch canopy trees (McLaren et al., 2004). If this trend continues, yellow birch may be lost from the canopy completely, resulting in the loss of a key species for lichen diversity in the boreal forest (McLaren et al., 2004; McMullin and Wiersma, 2017; Wiersma et al., 2019).

Balsam Fir

Balsam fir is a late successional shade tolerant species which is found in both dry and wet climates (Kenkel et al., 1997). After a major disturbance disrupts the seedbed and advanced regeneration, balsam fir will emerge in the canopy after the early successional shade intolerant species begin to die off through senescence and small-scale disturbance (Gauthier et al., 2010). Balsam fir is most common in moist and wet climates, where dominance is at its peak on moist moderately well drained soils (McLaren and Janke, 1996). Balsam fir canopy dominance varies by location and stand type where dominant balsam fir canopies are most common in Newfoundland, Ontario and Quebec (Bakuzis, 1965). In other provinces balsam fir is less common, either occurring in mixed stands as a sub dominant or rare species (Bakuzis, 1965).

Balsam fir reproduction and growth can occur in a variety of climates with varying substrates, light availability and moisture levels (Duchesneau and Morin, 1999). Balsam fir produces seeds each year, with mast years providing a majority of seeds every few years depending on resource availability (Duchesneau and Morin, 1999). Seed viability is relatively low as seeds die within a year of being shed, seed predation is high and seeds can be smothered by leaf litter or thick layers of moss (McLaren and Janke, 1996; Morin and Laprise, 1997). As such, balsam fir does not form a persistent seedbank, rather it relies on a seedling bank for regeneration. Given adequate moisture, balsam fir seeds can germinate on almost any substrate, however, studies have found sphagnum and feather moss are the most successful seedbed for germination and seedling survival due to its ability to retain moisture (Duchesneau and Morin, 1999). Germination success is also dependent on light availability where the optimal conditions for germination occur between 40-79% canopy closure (McLaren and Janke, 1996). Less than 40% canopy closure results in a reduced germination success and over 80% causes increased risk of over winter mortality in seedlings. Seedling recruitment is most successful on moist moderately well drained soils but can occur at lower rates in dry and extremely wet environments (McLaren and Janke, 1996). In these environments balsam fir tends to be outcompeted by species that thrive in dry and wet nutrient poor locations such as black spruce (Kenkel, 1997).

The balsam fir seedlings and saplings form a layer of advanced regeneration in the understory that is able to rapidly grow to fill canopy openings after disturbance (Messier et al., 1999). Seedlings continue to grow in the understory in extremely slow increments, allocating resources to root growth and small incremental height and diameter growth.

Seedling banks can persist for up to thirty years in the shaded understory (Frank, 1990). Both seedlings and saplings are difficult to age due its ability to reallocate resources to lateral growth instead of vertical growth in low light conditions (Messier et al., 1999). This results in several missing rings in the trunk, however saplings between the age of 50-100 have been found in understories ready to rapidly grow to fill the canopy after disturbance. The saplings are well suited for both crowded and open understories as they have the ability to shed lower branches (Messier et al., 1999). This layer of advanced regeneration is what gives balsam fir a competitive advantage when regenerating in gaps within balsam fir dominant boreal forests stands (Gosse et al., 2011).

There is a positive relationship between balsam fir abundance and small and medium scale disturbance as it releases the layer of advanced regeneration allowing balsam fir to fill the canopy gaps (McCarthy, 2001). Once there is a canopy opening the seedlings and saplings rapidly grow to fill the gap. Gap size has little impact on the ability of balsam fir to fill the canopy opening as long as the advanced regeneration remains intact (Salmon et al., 2016). Due to the advanced regeneration and rapid growth after disturbance, balsam fir has a competitive advantage over less shade tolerant species. The layer of advanced regeneration limits the amount of light that can reach the seeds and seedlings of other species preventing their growth (Gosse et al., 2011). If the seedling layer is disrupted, more light is available for the shade intolerant species and balsam fir loses its competitive advantage resulting in moderately shade tolerant and shade intolerant species filling the gap (McLaren et al., 2009; Chen and Taylor, 2012).

Balsam fir is a moderately palatable species, however due to its accessibility it is one of the main browsing sources for moose during the winter and early spring (Dodds, 1960; Persson et al., 2005). Seedlings are browsed when snow cover is limited, resulting in the uprooting of exposed seedlings (Bergerud and Manuel, 1968). Saplings are browsed when snow cover increases, where any new growth protruding through the snow provides easy access for moose browsing. Large, open canopied areas are browsed on first. Once snow cover gets too high the moose move to the closed canopied areas (Bergerud and Manuel, 1968). Saplings survive for several years under severe browsing pressure and once the pressure is removed they can rapidly grow to fill small and medium canopy gaps (Charron and Hermanutz, 2016). If advanced regeneration is disrupted and severely suppressed by moose in large canopy openings, balsam fir fails to naturally regenerate. This could potentially lead to altered successional trajectories and the continuation of an opened canopied system (Charron and Hermanutz, 2016).

Regeneration

Minute canopy gaps

Minute canopy gaps (<200 m^2) are predominantly caused by the death of a couple canopy trees or micro-scale disturbances such as a small insect outbreak or mild wind throw (Runkle, 1981; McCarthy, 2001). In minute gaps the light availability is minimal resulting in limited changes to understory vegetation. However, minute canopy openings maintain understory diversity and nutrient recycling through decaying wood and the development of pit mounds (McLaren and Janke, 1996). Small disturbances are an important factor in maintaining a heterogeneous, uneven aged boreal forest stand which increases biodiversity and increases stand resilience to large scale disturbances (Grandpré et al., 2000; Taylor et al., 2017).

In balsam fir dominant forests, with no moose overbrowsing, minute canopy gaps will almost always be filled by balsam fir trees (McCarthy, 2001). The advanced regeneration within the understory will rapidly grow once the light availability increases. The advanced regeneration will prevent other canopy species from regenerating within the gap by preventing light from reaching the seeds and seedlings (McCarthy, 2001). In gaps with less than 25% canopy cover the light availability will be the main factor impacting which saplings are recruited into the canopy (Duchesneau et al., 2001). In rare cases, where the advanced regeneration layer has been disrupted, yellow birch or other deciduous trees may fill the canopy opening depending on the suitability of the site (McCarthy and Weetman, 2007).

In the presence of moose overbrowsing the extra small canopy gap regeneration trajectories may be altered (Figure A. 1). The gap can either be filled by balsam fir, unpalatable species or the canopy gap can be closed by crown growth of the surrounding canopy trees if the gap is small enough (Pretzsch et al., 2015; Taylor et al., 2017). The altered regeneration trajectory is dependent on the vegetation prior to disturbance, abiotic factors such as soil moisture and light availability and the level of moose overbrowsing (Tubbs, 1969; McLaren and Janke, 1996; Taylor and Chen, 2011). Regardless of moose overbrowsing, the original seedbed properties remain relatively intact as the reduced light availability prevents the seedbed from drying out. If other species have failed to fill the canopy gap, this allows for the reestablishment of balsam fir advanced regeneration after browsing pressure is reduced (McLaren and Janke, 1996; Taylor and Chen, 2011). Therefore, these sites are generally of low concern as they almost always regenerate without active restoration (Charron and Hermanutz, 2016).

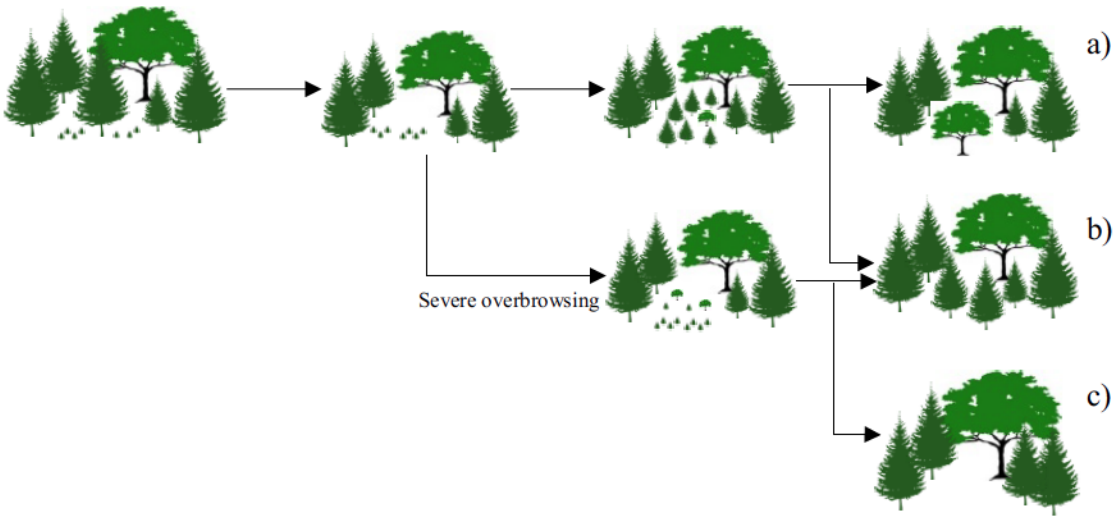

Figure A. 1. Regeneration trajectories in a minute canopy gap in the absence and presence of moose overbrowsing. Three different trajectories are pictured, a) yellow birch fills the gap b) balsam fir fills the gap and c) canopy tree crown growth fills the gap. Each scenario has a different probability of occurring where some states cannot be reached after severe overbrowsing.

Small gap

Small sized canopy gaps are primarily caused by spruce budworm defoliation and severe wind throw events (Arsenault et al., 2016). Both black spruce and balsam fir are the primary species impacted by wind throw and insect outbreaks (McLaren and Janke, 1996; Taylor and Chen, 2011). The shallow rooting and rapid growth by balsam fir makes it more susceptible to wind throw then yellow birch (Achim et al., 2005). After insect disturbance canopy trees die approximately ten years after defoliation (Taylor et al., 2017). Therefore, stands are more susceptible to large wind throw events ten years after moderate to severe insect disturbance as the standing dead wood is easily disturbed

(Arsenault et al., 2016). During insect outbreaks the larvae rarely reach small saplings and seedlings, as spruce budworm targets trees older trees (70+ years), leaving the balsam fir advanced regeneration intact (Taylor et al., 2017). Therefore, balsam fir can readily fill the canopy openings after wind throw and insect disturbance. However, with small sized gaps a few moderately shade tolerant species are able to reach the canopy if abiotic conditions are suitable.

The advanced regeneration of balsam fir inhibits the growth of most yellow birch seedlings but the yellow birch is well adapted to growth in small sized gaps and a couple yellow birch will reach the canopy provided that the soil moisture and light availability is adequate (Houle and Payette, 1990; Salmon et al., 2016). Yellow birch is most successful at reaching the canopy in small sized gaps due to the increased light availability, reduced competition levels and increased room for crown development. Yellow birch regeneration success is greater when the disturbance has resulted in the patches of disrupted advanced regeneration and disturbed seedbed (Salmon et al., 2016). Wind throw events provide optimal conditions for yellow birch regeneration as wind throw can cause the development of pit mounds, caused by tree uprooting, which exposes mineral soils (McLaren and Janke, 1996). Furthermore, the downed tree can disturb some of the advanced regeneration providing several sites with limited competition with balsam fir seedlings and saplings (Ulanova, 2000). Shade intolerant species cannot capitalize on small gap sizes as readily as yellow birch due to their inability to rapidly grow without direct sunlight (Kern et al., 2012). Therefore, yellow birch moderate shade tolerance gives it a competitive advantage against pioneer species in these gaps (Beaudet and Messier, 1998).

Other moderately shade tolerant species and the occasional shade intolerant species may also reach the canopy after moderate disturbance (Taylor and Chen, 2011). The likelihood of these species reaching the canopy is dependent on soil nutrients, moisture levels, aspect and the level of balsam fir advanced regeneration disturbance (Kneeshaw and Bergeron, 1998; Tremblay et al., 2007). Therefore, small sized gaps promote biodiversity and are crucial for the perpetuation of less dominant hardwood species in the balsam fir dominant boreal forest (McCarthy and Weetman, 2006).

If the small sized canopy gap forms in unfavourable sites such as dry, nutrient poor or extremely wet sites, the canopy will likely be more sporadic and dominated by black spruce and balsam fir (Kenkel, 1997). Balsam fir can regenerate on these sites to a lesser extent, however they are usually outcompeted by black spruce due to the unfavourable growing conditions (Duchesneau and Morin, 1999). Yellow birch and hardwoods cannot regenerate in these locations as they require moderate levels of moisture (Archambault et al., 1998). The canopy will be more open as black spruce form generally grow in less dense patches (Kenkel, 1997).

In the presence of moose browsing small sized canopy gaps can have several regeneration trajectories (Figure A. 2). The two main trajectories include the canopy being filled by balsam fir or the canopy remaining open and dominated by unpalatable shrubs and herbaceous species (Bradner et al., 1990; Kneeshaw and Bergeron, 1998). If the disturbance was on an unfavourable site, such as a wetland, a third trajectory is possible where black spruce will likely become dominant (Kenkel, 1997). The first and most common trajectory can occur if balsam fir saplings were above 2 m prior to gap formation. Alternatively, if the seedling bank is fully stocked it is likely that balsam fir will be able to regenerate once the browsing pressure is reduced (Tremblay et al., 2007). If the advanced regeneration remains suppressed for an extended period of time and seedlings are uprooted, the potential for regeneration is reduced (Bergerud and Manuel, 1968). The longer the gap remains open and the seedbed is exposed to light, the increased likely hood that seedbed quality will diminish and herbaceous species will become dominant in the understory resulting in an open canopied system (Mallik, 2013).

Although it is likely that balsam fir will be able to regenerate in these locations given reduced browsing pressure, yellow birch and other palatable hardwood species will be unable to reach the canopy due to preferential browsing (Brandner et al., 1990; Thomas and Curran, 1993; Zhu et al., 2010). Therefore, moose browsing in small sized gaps can reduce overall stand diversity by suppressing hardwood regeneration resulting in the loss of crucial boreal forest species (Zhu et al., 2010).

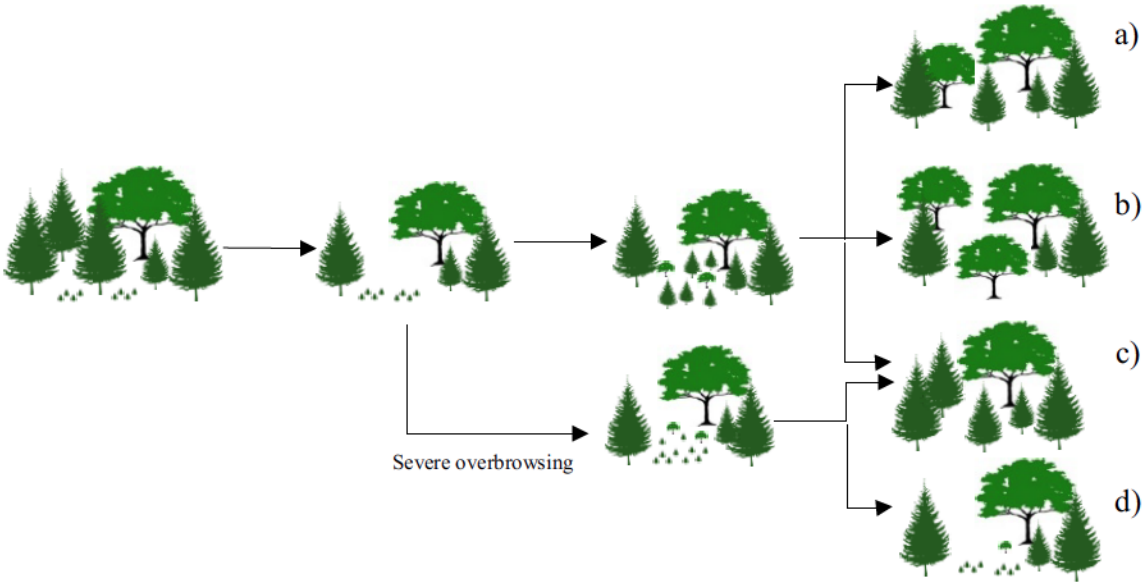

Figure A. 2. Regeneration trajectories in the small sized gap in the absence and presence of moose overbrowsing. Four different trajectories are possible, a) balsam fir and yellow birch fill the gap b) only yellow birch fills the gap c) only balsam fir fills the gap and d) no regeneration within the gap. Each scenario has a different probability of occurring where some states cannot be reached after severe overbrowsing.

Large gap

Large canopy gaps can occur from severe natural and anthropogenic disturbance such as fire, insect outbreaks, hurricane winds and forestry (Chen and Taylor, 2012). Fire is uncommon in the Avalon Peninsula, however if it did occur balsam fir advanced regeneration would be wiped out and pioneer species would dominate the canopy (Chen and Taylor, 2012; Arsenault et al., 2016). If a severe insect outbreak or hurricane winds cause a large gap most of the advanced regeneration should remain intact and balsam fir will fill the canopy. In larger gaps, other shade intolerant and moderately shade tolerant species will also be able to reach the canopy (Ulanova, 2000). In large gaps competition increases which results in shade intolerant species regenerating near the middle of the gap with the highest light availability (Messier et al., 1999). Moderately shade tolerant species, such as yellow birch, will regenerate along the perimeters where competition is reduced and the seedbed remains moist (Prevost and Charette, 2015). Balsam fir will still remain a dominant species but the canopy will be mixed wood instead of purely balsam fir stand (Ulanova, 2000).

Alternatively, large canopy gaps can be formed by the continued disturbance in small sized gaps after failure to regenerate resulting in gap expansion (Mitchell, 2013; Barrette et al., 2017). One way gap expansion occurs is when an area has been severely suppressed after an initial disturbance and a funnel effect occurs where wind throw becomes more severe along the gap perimeters (Mitchell, 2013). Otherwise, a gap can expand when a slow acting disturbance, such as an insect outbreak, causes the mortality of canopy trees over several years resulting in different parts of the stand succumbing to secondary disturbance at different time intervals (Kneeshaw and Bergeron, 1998). The continued suppression of balsam fir advanced regeneration results in an alternate regeneration trajectory where the canopy remains open (Gosse et al., 2011).

When moose are hyper abundant in large canopy gaps, alternative regeneration trajectories can occur where the canopy fails to regenerate and the canopy remains open with black spruce interspersed (Figure A. 3; Charron and Hermanutz, 2016). The seedbed ends up losing moisture and transitioning to a dry, nutrient poor seedbed dominated by ericaceous shrubs, grasses or invasive species (Mallik, 2003). Any balsam fir seedlings will eventually die due to the lack of moisture and exposure to full sunlight while being suppressed (Frank, 1990). Saplings have a better chance of survival after moose overbrowsing and some may reach the canopy if moose are removed. However, it will still be an open canopied system and will not regenerate without intervention due to the inability for balsam fir germination and seedling establishment on this unfavourable seedbed (Duchesneau and Morin, 1999; Charron and Hermanutz, 2017). In addition, the environment in large gaps is inhospitable for hardwoods, especially yellow birch, which cannot regenerate in this environment even after moose have been removed (Lorenzetti et al., 2008). Therefore, large canopy gaps alter forest compositions and if moose remain above carrying capacity more of the closed canopy forest may transition to a moose spruce savanna (McLaren et al., 2004; Gosse et al., 2011).

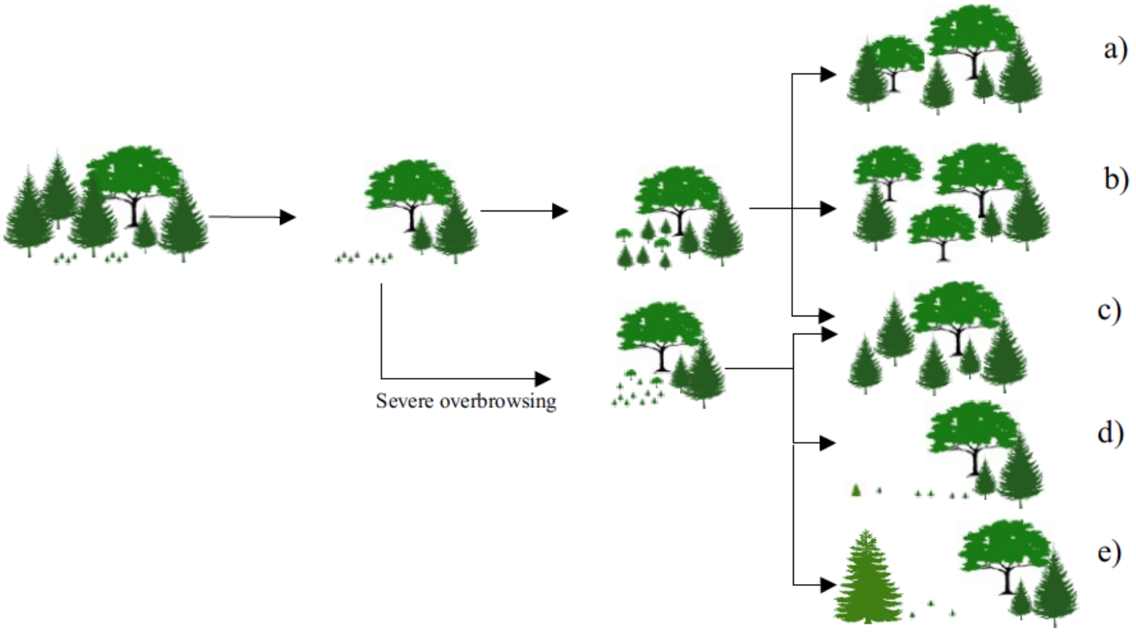

Figure A. 3. Regeneration trajectories in the large sized gap in the absence and presence of moose overbrowsing. Five different trajectories are depicted, a) balsam fir and yellow birch fill the gap b) only yellow birch fills the gap c) only balsam fir fills the gap and d) no regeneration within the gap, e) the formation of a spruce moose savanna. Each scenario has a different probability of occurring where some states cannot be reached after severe overbrowsing.

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APPENDIX B: MARKOV MODELS

In this appendix, I provide a brief overview of Markov models and a few of their variants.

The Markov chain is a discrete time stochastic model which uses transition probabilities to describe the transition from one state to another (Horn, 1975). Markov models can be easily modified to fit a variety of systems, are simple to interpret and are not data intensive (Yemshanov, 2002). The primary assumption of Markov models is the Markov property which means each transition is only dependent on the state the system was in in the previous time step (Usher, 1979). Essentially this means the initial state of the system has little influence on the final states of the system. Rather, it is the transition probabilities and the current state that influences the final state (Usher, 1979). In ecology, Markov models and their variants have been used to simulate animal movement (Franke et al., 2004; Patterson et al., 2009; Langrock et al., 2014), land use change (Muller and Middleton, 1994; Yang et al., 2014), succession in subtidal and intertidal communities (Wootton, 2001; Hill et al., 2004) and vegetation succession and dynamics (Horn 1975, Seabloom and Richards, 2003; Liénard and Strigul, 2016).

Markov models can be modified to fit the ecological systems and increase predictive power. Some variants on the traditional Markov model include hidden Markov models (HMMs), weighted Markov models and higher order Markov models. The hidden Markov model does not inherently violate any Markov assumptions, rather it is a Markov model within unobservable states (Tucker and Anand, 2005; Gong et al., 2017). For the HMM there is an underlying ‘hidden’ sequence, where each element in the hidden chain connects to observable states (Tucker and Anand, 2005; Gong et al., 2017). The weighted Markov chain is a modified time-inhomogeneous Markov model where the transition probabilities are altered in these models either by adding additional state matrices or by weighting certain transition probabilities (Liénard and Strigul, 2016). This allows environmental change, such as disturbance, nutrient cycling, altered browsing pressure and restoration, to be accounted for in the model. A larger amount of theoretical or empirical data is required to parametrize the model (Liénard and Strigul, 2016). The higher order Markov chain is modified to allow for the model to retain memory of the previous states and the future state of the system is dependent on the current and previous states to the nth order (Aaviksoo, 1995; Shamshad et al., 2005). Larger time series datasets are required to parametrize the model making them highly data intensive (Aaviksoo, 1995; Shamshad et al., 2005).

Studies have compared the predictive power of basic Markov models and modified Markov models, finding the basic model is sometimes better at predicting system dynamics (Logofet, 2000; Wootton, 2002). However, other studies have called for further study of modified Markov models to incorporate more biotic and abiotic factors to capture additional system dynamics and examine system response to perturbations (Balzter, 2000; Tucker and Anand, 2005). The predictive power of Markov models has been debated with some ecologists using exact numerical outputs while others use the observed model patterns, such as shifts in dominance or responses to perturbations, to draw conclusions about the system (Lippe et al., 1985; Balzter, 2000; Wootton, 2001; Hill et al., 2004). In my thesis, I focus on the qualitative patterns of forest composition (e.g., birch and balsam fir recruitment to the canopy, is the canopy closing, are shrubs present or absent) as opposed to qualitative patterns.

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APPENDIX C: SENSITIVITY ANALYSIS

In this appendix, I conduct a sensitivity analysis to assess the sensitivity of the transition matrix to perturbations.

METHODS

Sensitivity analysis is a technique used to assess model outputs robustness to uncertainty of input parameters and variables by varying model parameters and analyzing the changes in model output (Hamby, 1994). I used a modified local one-at-a-time (OAT) perturbation sensitivity analysis and a global scenario based perturbation sensitivity analysis to analyze the sensitivity of my model to variations in the transition probability matrix (Pianosi et al., 2016). The local perturbation approach analyzes the variation in model output after perturbing one input parameter. The global perturbation approach analyzes the variation in model output while varying across the entirety of the parameter inputs (Pianosi et al., 2016). A key aspect of the row wise Markov community model used in my analyses is that the rows sum to 1 within the matrix (Wootton, 2001). Therefore, I had to modify the approaches while ensuring the rows summed to 1.

Local OAT Perturbation Sensitivity Analysis – I conducted a modified local perturbation sensitivity analysis on the transition probabilities to determine the overall sensitivity of the model to my assumptions pertaining to ecological transitions. Specifically, I grouped ecologically similar transition probabilities (Table C. 1) and individually varied each group of transition probabilities. First, I grouped transition probabilities with similar life histories and ecological function. I grouped browsed balsam fir saplings with the unbrowsed balsam fir saplings and the browsed birch saplings with the unbrowsed birch saplings. I also grouped the good and poor seedbed due to their similar ecological function (Kenkel et al., 1997) (Table C. 1). After grouping similar transition probabilities, this resulted in a total of 26 transition probabilities undergoing local OAT sensitivity analysis (Table C. 1; Table C. 2).

Next, I used a modified Latin hypercube to randomly draw a number between a range of -15% and +15% (*X*) of the baseline transition probability (Eq. C. 1a, b, c; Haefner, 2005). To ensure the rows still summed to 1, I proportionally allocated the difference between the perturbed transition probability and the unperturbed transition probability to the remainder of the transition probabilities within the row (Eq. C. 2) (Wootton, 2001). By proportionally allocating the difference between the perturbed and unperturbed transition probability, it ensures the integrity of the matrix is maintained by ensuring large transition probabilities maintain their relative magnitude for each class. For example, if we vary $P_{YBSM,YBSM}$ by +15% (Eq. C. 1b) the row would be proportionally allocated according to Eq. C. 2b, and if $P_{YBSM,YBSM}$ by -15% (Eq. C. 1b) the row would be proportionally allocated according to Eq. C. 2b.

$$P_{YBSM,YBDSMALT} = P_{YBSM,YBSM} +/-(P_{YBSM,YBSM} * X) \quad \text{Eq. C. 1a}$$

$$P_{YBSM,YBDSMALT} = 0.1 + (0.1 * 0.15) \quad \text{Eq. C. 1b}$$

$$P_{YBSM,YBDSMALT} = 0.115$$

$$P_{YBSM,YBDSMALT} = 0.1 - (0.1 * 0.15) \quad \text{Eq. C. 1c}$$

$$P_{YBSM,YBDSMALT} = 0.085$$

$$1 = P_{YBSM,SB} + \left(\frac{P_{YBS,SB}}{P_{YBSM,SB}+P_{YBSM,YB}} * \left(P_{YBSM,YBSM} - P_{YBSM,YBSMALT}\right)\right) + P_{YBSM,YBSMALT} + P_{YBSM,YB} + \left(\frac{P_{YBSM,YB}}{P_{YBSM,SB}+P_{YBSM,YB}} * \left(P_{YBSM,YBSM} - P_{YBSM,YBSMALT}\right)\right)$$

Eq. C. 2a

$$1 = 0.7 + \left(\frac{0.7}{0.7+0.2} * (0.1 - 0.115)\right) + 0.115 + 0.2 + \left(\frac{0.2}{0.7+0.2} * (0.1 - 0.115)\right)$$ Eq. C. 2b

$$1 = 0.7 + \left(\frac{0.7}{0.7+0.2} * (0.1 - 0.085)\right) + 0.085 + 0.2 + \left(\frac{0.2}{0.7+0.2} * (0.1 - 0.085)\right)$$ Eq. C. 2c

I sampled from four strata [-15% to -7.5%, -7.5% to 0, 0 to 7.5%, 7.5% to 15%] and drew 10 numbers randomly from each strata for a total sample size of 40 per 20 grouped transition probabilities (Table C. 1). For each randomly drawn transition probability, 500 simulations of the full model dynamics were run for 100 time steps. The mean percent cover (+ standard deviation) was calculated from the 500 simulations for the 100th time step per random draw.

I determined the sensitivity of each transition probability by calculating the change in mean proportional cover and performing a rank analysis. For the rank analysis, I used the steady state distributions to determine the dominance of each vegetation layer for each of the four strata in the modified models. I then compared the dominance of the vegetation layers for the modified models to the *baseline model* to determine the sensitivity of the transitions. I deemed the transition probability sensitive if two or more vegetation layers switched in dominance. I used the dominance of the vegetation layers as it represents the major qualitative trends from the model output which is the focus of my thesis (Lippe et al., 1985; Baltzer, 2000; Wootton, 2001; Hill et al., 2004; Appendix B). If the rank analysis revealed a sensitive transition probability, indicated by switched dominance between two or more vegetation layers, I performed an eigen analysis and calculated the gap value using the second eigenvalue (Liénard and Strigul, 2016). I calculated the eigenvalue for each sensitive transition probabilities for +15% and -15% of the baseline transition probabilities. I considered transition probabilities only mildly sensitive if they were identified as sensitive with the rank analysis but the gap value was the same as the gap value for the *baseline model*. I considered them severely sensitive if they were identified as sensitive with the rank analysis and they had a different gap value than the *baseline model* (Liénard and Strigul, 2016). For the severely sensitive transition probabilities, I extended the range in which the transition probabilities were varied to -20% and 20% of the baseline transition probability. Figures for this additional analysis are provided with the corresponding changes to other transition probabilities within the row. For any grouped transition probabilities that were sensitive I ungrouped and reanalyzed them. This was to determine whether the sensitivity was a result of the grouping or the transition probabilities being analyzed. In addition, I calculated the percent change between the modified (X_m) and baseline (X_{un}) models (Eq. C. 3). I used this calculation to further examine the transition probabilities identified as sensitive to take a closer look at the states with altered ranking.

$$Percent\ Change = \left(\frac{X_m - X_{un}}{X_{un}}\right) * 100 \qquad \text{Eq. C. 3}$$

Global Scenario Perturbation Sensitivity Analysis – In addition to the local sensitivity analysis, I conducted a global sensitivity analysis (Pianosi et al., 2016), where I varied several transition probabilities simultaneously by increasing several transition probabilities by +15% of the baseline transition probability (Table C. 3 column 2) and decreasing other transition probabilities through proportional allocation (Table C. 3 column 3). I tested ten ecologically meaningful scenarios using global sensitivity analysis (see Table C. 3). Each of the scenarios were specifically designed to test the methods used to calculate the transition probabilities and mimic ecological processes. I assessed the results of the analysis through the change in mean proportional cover and rank analysis as outlined above. I performed an additional rank analysis by grouping the vegetation layers into the four forest layers: forest floor (good seedbed and poor seedbed), herbaceous (herbs), understory (shrubs, birch saplings, balsam fir saplings and spruce saplings) and canopy (birch, balsam fir and spruce trees). The additional rank analysis allowed for a broader look at the sensitivity of each of the scenarios by examining the overall changes in forest composition. Changes in the forest layer dominance would indicate a severely sensitive scenario as it suggests large changes in forest composition and dynamics. Depending on the compositional changes within these severely sensitive scenarios the sensitivity could indicate restoration conclusions may be inaccurate. I further examined the compositional changes and conducted an eigen analysis for each scenario to determine whether restoration conclusions would still be sound.

RESULTS

Local OAT Perturbation Sensitivity Analysis – Of the twenty-six transition probabilities tested, seven were identified as sensitive (Table C. 4). Out of the seven transition probabilities identified as sensitive using the rank analysis, only three were identified as severely sensitive using the eigen analysis ($p_{BF,BF}$, $p_{BF,BF}$ and $p_{BS,SB}$; Table C. 5). The mildly sensitive transition probabilities ($p_{SB,H}$, $p_{SB,BFS}$, $p_{H,SB}$, and $p_{H,H}$) did not substantially alter model output as the overall composition of the forest remained qualitatively similar. In each of these cases there was only a switch in vegetation dominance between two different vegetation layers of similar percent covers. Therefore, the ratio between forest floor, herbaceous, understory and canopy layers remained comparable. The severely sensitive transition probabilities substantially altered the model output, changing the dominance between several vegetation layers and modifying the overall composition of the forest (Figure C. 1; Figure C. 2).

Global Scenario Perturbation Sensitivity Analysis – Out of the ten scenarios tested, five were identified as sensitive using rank analysis (Table C. 6; Figure C. 3; Figure C. 4). None of the sensitive scenarios that were identified via rank analysis were identified as severely sensitive by the eigen analysis. However, one scenario that was not identified as sensitive by the rank analysis was identified as sensitive by the eigen analysis (scenario

8). Of the sensitive scenarios three of them (scenario 1, scenario 2 and scenario 7) changed the overall composition of the forest (Figure C. 5).

In each of the sensitive scenarios large increases in vegetation abundance occurred in spruce saplings, spruce trees or herbaceous plants (Figure C. 4; Figure C. 5). In scenario 1, scenario 2 and scenario 3, large decreases in vegetation abundance occurred in birch trees. In scenario 4 and scenario 7, small decreases in shrub abundance occurred. In scenario 9 and scenario 10 canopy cover was reduced while seedbed cover was increased (Table C. 7). All of the scenarios tested had the same pattern as the *baseline model*, with spruce being the most dominant tree in both the understory and canopy. None of the scenarios result in a substantial increase in birch or balsam fir trees.

DISCUSSION

The local and global sensitivity analysis revealed some sensitivity within the model. Within the local analysis, three transitions ($p_{BF,BF}$, $p_{BF,BF}$ and $p_{BS,SB}$) of twenty-six tested were deemed severely sensitive, changing the overall forest composition. The remaining sensitive transition probabilities ($p_{SB,H}$, $p_{SB,BFS}$, $p_{H,SB}$, and $p_{H,H}$) were not sensitive enough to vary the overall forest composition. Furthermore, the rank analysis revealed the switches in dominance occurred only between vegetation layers that were similar in percent cover prior to model alterations. For example, transition $p_{SB,YBS}$ had a switch in dominance between balsam fir saplings and birch saplings, where birch saplings were dominant in the *baseline model* and balsam fir saplings dominant in the modified model. Prior to alteration birch saplings percent cover was 2.9% and balsam fir saplings was 2.8%. In the modified model birch saplings percent cover was 2.9% and balsam fir saplings was 3.2%. These changes to percent cover are very minor and therefore would not impact model conclusions. For all of the severely sensitive transition probabilities, spruce trees still remain dominant within the canopy indicating a lack of balsam fir regeneration. As such, the sensitivity identified does not change restoration recommendations as both birch and balsam fir trees still fail to meet targets based on historic forest compositions (Meades, 1987; Meades, 1989). Therefore, the sensitivity identified through local analysis would not impact the conclusions made based on model output or the forest restoration scenarios suggested.

The global analysis revealed five of the ten scenarios were sensitive based on the rank analysis, none of which were severely sensitive based on the eigen analysis. The eigen analysis identified one additional sensitive scenario that had the same dominance patterns as the *baseline model*. The additional scenario that was identified as sensitive through the eigen analysis (Scenario 8) had a forest composition with reduced shrub and sapling cover compared to the *baseline model*. This would indicate a heightened need for restoration as compared to the *baseline model* in order to restore understory diversity and abundance. Out of all the sensitive scenarios only three of them (scenario 1, scenario 2 and scenario 7) altered the overall composition of the forest (Figure C. 5). Both scenario 7 and scenario 2 had increased canopy cover, however, both birch and balsam fir fail to sufficiently recruit. Scenario 1 had a reduced canopy cover indicating an increased failure in canopy recruitment.

In each of the 10 scenarios tested, all of them, regardless of the sensitivity, remained spruce sapling and spruce tree dominant. Furthermore, they all lacked sufficient birch and balsam fir abundance in the canopy. Therefore, for each of the scenarios restoration protocols would still be required to restore birch in the canopy and correct the lack of balsam fir dominance. In conclusion, the sensitivity identified by both the local and global analysis is not substantial enough to impact the restoration recommendations made within Chapter 2.

Table C. 1. Transition probabilities undergoing local sensitivity analysis and the rationale behind grouping several transitions. For notation see Table C. 2.

Transition Probabilities	**Grouping Rationale**
$p_{SB,SB}$, $p_{SBB,SB}$	Good seedbed and poor seedbed comprise the forest floor and have similar ecological function. Both facilitate nutrient transport and are important for vegetation growth.[1]
$p_{SB,SBB}$, $p_{SBB,SBB}$	Good seedbed and poor seedbed comprise the forest floor and have similar ecological function. Both facilitate nutrient transport and are important for vegetation growth.
$p_{SB,H}$	Not grouped
$p_{SB,SH}$	Not grouped
$p_{SB,YBS}$	Not grouped
$p_{SB,BFS}$	Not grouped
$p_{SB,BSS}$	Not grouped
$p_{H,SB}$	Not grouped
$p_{H,H}$	Not grouped
$p_{SH,SB}$	Not grouped
$p_{SH,SH}$	Not grouped
$p_{YBS,SB}$, $p_{YBSM,SB}$	Unbrowsed and browsed birch saplings have the same life histories and function within the ecosystem. They both transition to seedbed when they die.
$p_{YBS,YBS}$, $p_{YBS,YBSM}$, $p_{YBSM,YBSM}$	Unbrowsed and browsed birch saplings have the same life histories and function within the ecosystem. They both persist and thrive in the same environment.
$p_{YBS,YB}$, $p_{YBSM,YB}$	Unbrowsed and browsed birch saplings have the same life histories and function within the ecosystem. They both transition to birch trees provided there are sufficient resources and sapling growth is not suppressed.
$p_{BFS,SB}$, $p_{BFSM,SB}$	Unbrowsed and browsed balsam fir saplings have the same life histories and function within the ecosystem. They both transition to seedbed when they die.
$p_{BFS,BFS}$, $p_{BFS,BFSM}$, $p_{BFSM,BFSM}$	Unbrowsed and browsed balsam fir saplings have the same life histories and function within the ecosystem. They both persist and thrive in the same environment.
$p_{BFS,BF}$, $p_{BFSM,BF}$	Unbrowsed and browsed balsam fir saplings have the same life histories and function within the ecosystem. They both transition to balsam fir trees provided there are sufficient resources and sapling growth is not suppressed.

(continued)

Transition Probabilities	**Grouping Rationale**
$p_{BSS,SB}$	Not grouped
$p_{BSS,BSS}$	Not grouped
$p_{BSS,BS}$	Not grouped
$p_{YB,SB}$	Not grouped
$p_{YB,YB}$	Not grouped
$p_{BF,SB}$	Not grouped
$p_{BF,BF}$	Not grouped
$p_{BS,SB}$	Not grouped
$p_{BS,BS}$	Not grouped

[1] Tubbs, C. H. (1969). The influence of light, moisture, and seedbed on yellow birch regeneration. *Research Paper NC-27. St. Paul, MN: U.S. Dept. of Agriculture, Forest Service, North Central Forest Experiment Station*, *27*. Retrieved from https://www.fs.usda.gov/treesearch/pubs/10548 and McLaren, B. E., & Janke, R. A. (1996). Seedbed and canopy cover effects on balsam fir seedling establishment in Isle Royale National Park. *Canadian Journal of Forest Research*, *26*(5), 782–793. doi:10.1139/x26-088

Table C. 2. Transition probability notation for the 12x12 matrix. Notation is $p_{i,j}$which is a transition from *i* to *j* (e.g., $p_{SB,H}$ is the transition from seedbed to herbs).

Vegetation Layer	Notation
Good Seedbed-Good Seedbed	$p_{SB,SB}$
Good Seedbed-Poor Seedbed	$p_{SB,SBB}$
Good Seedbed-Herb	$p_{SB,H}$
Good Seedbed-Shrub	$p_{SB,SH}$
Good Seedbed-Yellow Birch Saplings	$p_{SB,YBS}$
Good Seedbed-Balsam Fir Saplings	$p_{SB,BFS}$
Good Seedbed-Spruce Saplings	$p_{SB,BSS}$
Poor Seedbed-Good Seedbed	$p_{SBB,SB}$
Poor Seedbed-Poor Seedbed	$p_{SBB,SBB}$
Herb-Good Seedbed	$p_{H,SB}$
Herb-Herb	$p_{H,H}$
Shrub-Good Seedbed	$p_{SH,SB}$
Shrub-Shrub	$p_{SH,SH}$
Birch Saplings-Good Seedbed	$p_{YBS,SB}$
Birch Saplings-Birch Saplings	$p_{YBS,YBS}$
Birch Saplings-Browsed Birch Saplings	$p_{YBS,YBSM}$
Birch Saplings-Birch Tree	$p_{YBS,YB}$
Browsed Birch Saplings-Good Seedbed	$p_{YBSM,SB}$
Browsed Birch Saplings-Browsed Birch Saplings	$p_{YBSM,YBSM}$
Browsed Birch Saplings-Birch Tree	$p_{YBSM,YB}$
Balsam Fir Saplings-Good Seedbed	$p_{BFS,SB}$
Balsam Fir Saplings-Balsam Fir Saplings	$p_{BFS,BFS}$
Balsam Fir Saplings-Browsed Balsam Fir Saplings	$p_{BFS,BFSM}$
Balsam Fir Saplings-Balsam Fir Tree	$p_{BFS,BF}$
Browsed Balsam Fir Saplings-Good Seedbed	$p_{BFSM,SB}$
Browsed Balsam Fir Saplings- Browsed Balsam Fir Saplings	$p_{BFSM,BFSM}$
Browsed Balsam Fir Saplings- Balsam Fir Tree	$p_{BFSM,BF}$
Spruce Saplings-Good Seedbed	$p_{BSS,SB}$
Spruce Saplings-Spruce Saplings	$p_{BSS,BSS}$
Spruce Saplings-Spruce Tree	$p_{BSS,BS}$
Birch Tree-Good Seedbed	$p_{YB,SB}$
Birch Tree-Birch Tree	$p_{YB,YB}$
Balsam Fir Tree-Good Seedbed	$p_{BF,SB}$
Balsam Fir Tree-Balsam Fir Tree	$p_{BF,BF}$
Spruce Tree-Good Seedbed	$p_{BS,SB}$
Spruce Tree-Spruce Tree	$p_{BS,BS}$

Table C. 3. Global analysis scenarios with corresponding ecological and analytic purposes for each scenario. Transitions were increased by 15% and decreased through proportional allocation.

Scenario	Increased	Decreased	Ecological Purpose	Analytic Purpose
Scenario 1	$p_{SB,SB}$, $p_{SB,SBB}$, $p_{SH,SB}$, $p_{YBS,SB}$, $p_{YBSM,SB}$, $p_{BFS,SB}$, $p_{BFSM,SB}$, $p_{BSS,SB}$	$p_{SB,SH}$, $p_{SB,YBS}$, $p_{SB,BFS}$, $p_{SB,BSS}$, $p_{SH,SH}$, $p_{YBS,YBS}$, $p_{YBS,YBSM}$, $p_{YBS,YB}$, $p_{YBSM,YBSM}$, $p_{YBSM,YB}$, $p_{BFS,BFS}$, $p_{BFS,BFSM}$, $p_{BFS,BF}$, $p_{BFSM,BFSM}$, $p_{BFSM,BF}$, $p_{BSS,BSS}$, $p_{BSS,BS}$	Simulating increased dominance of seedbed over understory vegetation	Testing sensitivity of node 1 favouring seedbed
Scenario 2	$p_{SB,SH}$, $p_{SB,YBS}$, $p_{SB,BFS}$, $p_{SB,BSS}$, $p_{SH,SH}$, $p_{YBS,YBS}$, $p_{YBS,YBSM}$, $p_{YBSM,YBSM}$ $p_{BFS,BFS}$, $p_{BFS,BFSM}$, $p_{BFSM,BFSM}$, $p_{BSS,BSS}$	$p_{SB,SB}$, $p_{SB,SBB}$, $p_{SH,SB}$, $p_{YBS,SB}$, $p_{YBSM,SB}$, $p_{BFS,SB}$, $p_{BFSM,SB}$, $p_{BSS,SB}$	Simulating increased dominance of understory vegetation over seedbed	Testing sensitivity of node 1 favouring shrubs and saplings

(continued)

Scenario	Increased	Decreased	Ecological Purpose	Analytic Purpose
Scenario 3	$p_{SB,SH}$, $p_{SH,SH}$, $p_{YBS,SB}$, $p_{YBSM,SB}$, $p_{BFS,SB}$, $p_{BFSM,SB}$, $p_{BSS,SB}$	$p_{SB,YBS}$, $p_{SB,BFS}$, $p_{SB,BSS}$, $p_{SH,SB}$, $p_{YBS,YBS}$, $p_{YBS,YBSM}$, $p_{YBS,YB}$, $p_{YBSM,YBSM}$, $p_{YBSM,YB}$, $p_{BFS,BFS}$, $p_{BFS,BFSM}$, $p_{BFS,BF}$, $p_{BFSM,BFSM}$, $p_{BFSM,BF}$, $p_{BSS,BSS}$, $p_{BSS,BS}$	Simulating increased dominance of shrubs over saplings	Testing sensitivity of node 3 favouring shrubs
Scenario 4	$p_{SB,YBS}$, $p_{SB,BFS}$, $p_{SB,BSS}$, $p_{SH,SB}$, $p_{YBS,YBS}$, $p_{YBS,YBSM}$, $p_{YBSM,YBSM}$, $p_{BFS,BFS}$, $p_{BFS,BFSM}$, $p_{BFSM,BFSM}$, $p_{BSS,BSS}$	$p_{SB,SH}$, $p_{SH,SH}$, $p_{YBS,SB}$, $p_{YBSM,SB}$, $p_{BFS,SB}$, $p_{BFSM,SB}$, $p_{BSS,SB}$	Simulating increased dominance of shrubs over saplings	Testing sensitivity of node 3 favouring saplings
Scenario 5	$p_{SB,BFS}$	$p_{SB,BSS}$	Simulating dominance of balsam fir saplings over spruce	Testing sensitivity of field data transitions for balsam fir and spruce seedling growth
Scenario 6	$p_{YBS,YB}$, $p_{YBSM,YB}$, $p_{BFS,BF}$, $p_{BFSM,BF}$, $p_{BSS,BS}$	$p_{YBS,SB}$, $p_{YBSM,SB}$, $p_{BFS,SB}$, $p_{BFSM,SB}$, $p_{BSS,SB}$	Simulating increased sapling growth	Aerial photo transition probabilities

(continued)

Scenario	Increased	Decreased	Ecological Purpose	Analytic Purpose
Scenario 7	$p_{SB,YBS}$, $p_{SB,BFS}$, $p_{SB,BSS}$, $p_{YBS,YB}$, $p_{YBSM,YB}$, $p_{BFS,BF}$, $p_{BFSM,BF}$, $p_{BSS,BS}$	$p_{SB,SB}$, $p_{SB,SBB}$, $p_{SB,H}$, $p_{SB,SH}$, $p_{YBS,SB}$, $p_{YBSM,SB}$, $p_{BFS,SB}$, $p_{BFSM,SB}$, $p_{BSS,SB}$	Simulate increased seedling and sapling growth	Testing sensitivity of aerial photo transition probabilities of sapling to tree growth combined with field data transitions of seedbed to saplings
Scenario 8	$p_{YBS,YB}$, $p_{YBSM,YB}$, $p_{BFS,BF}$, $p_{BFSM,BF}$, $p_{BSS,BS}$, $p_{YB,SB}$, $p_{BF,SB}$, $p_{BS,SB}$	$p_{YBS,SB}$, $p_{YBS,YBS}$, $p_{YBS,YBSM}$, $p_{YBSM,SB}$, $p_{YBSM,YBSM}$, $p_{BFS,SB}$, $p_{BFS,BFS}$, $p_{BFS,BFSM}$, $p_{BFSM,SB}$, $p_{BFSM,BFSM}$, $p_{BSS,SB}$, $p_{BSS,BSS}$	Simulate higher canopy turnover rates	Testing sensitivity of aerial photo transition probabilities of tree death and sapling growth
Scenario 9	$p_{YB,SB}$, $p_{BF,SB}$, $p_{BS,SB}$	$p_{YB,YB}$, $p_{BF,BF}$, $p_{BS,BS}$	Simulate higher canopy death rates	Testing sensitivity of aerial photo transition probabilities of tree death
Scenario 10	$p_{BFS,BF}$, $p_{BFSM,BF}$, $p_{BSS,SB}$	$p_{BFS,SB}$, $p_{BFSM,SB}$, $p_{BSS,BS}$	Simulate balsam fir dominance during canopy recruitment	Testing sensitivity of the balsam fir spruce split from aerial photo transition probabilities

Table C. 4. Local OAT perturbation rank analysis results for strata 1 (-15 to -7.5%), strata 2 (-7.5 to 0%), strata 3 (0 to 7.5%) and strata 4 (7.5 to 15%). Transition probabilities that are sensitive switch in dominance between two or more vegetation layers (Yes[x]) and transition probabilities that are not sensitive have the same vegetation dominance order as the *baseline model* (No). For transition notation see Table C. 2.

Transition	Strata 1	Strata 2	Strata 3	Strata 4
$p_{SB,SB}$, $p_{SBB,SB}$	No	No	No	No
$p_{SB,SBB}$, $p_{SBB,SBB}$	No	No	No	No
$p_{SB,H}$	No	No	No	Yes[a]
$p_{SB,SH}$	No	No	No	No
$p_{SB,YBS}$	No	No	No	No
$p_{SB,BFS}$	No	No	No	Yes[b]
$p_{SB,BSS}$	No	No	No	No
$p_{H,SB}$	Yes[a]	No	No	No
$p_{H,H}$	No	No	No	Yes[a]
$p_{SH,SB}$	No	No	No	No
$p_{SH,SH}$	No	No	No	No
$p_{YBS,SB}$, $p_{YBSM,SB}$	No	No	No	No
$p_{YBS,YBS}$, $p_{YBS,YBSM}$, $p_{YBSM,YBSM}$	No	No	No	No
$p_{YBS,YB}$, $p_{YBSM,YB}$	No	No	No	No
$p_{BFS,SB}$, $p_{BFSM,SB}$	No	No	No	No
$p_{BFS,BFS}$, $p_{BFS,BFSM}$, $p_{BFSM,BFSM}$	No	No	No	No
$p_{BFS,BF}$, $p_{BFSM,BF}$	No	No	No	No
$p_{BSS,SB}$	No	No	No	No
$p_{BSS,BSS}$	No	No	No	No
$p_{BSS,BS}$	No	No	No	No
$p_{YB,SB}$	No	No	No	No
$p_{YB,YB}$	No	No	No	No
$p_{BF,SB}$	No	No	No	No
$p_{BF,BF}$	No	No	No	Yes[c]
$p_{BS,SB}$	No	No	No	Yes[a]
$p_{BS,BS}$	Yes[a]	No	No	No

[a] H more dominant than BS

[b] BFS more dominant than YBS

[c] BF more dominant than BSS, H

Table C. 5. Sensitive transition probabilities from the local OAT perturbation sensitivity analysis identified using the rank analysis and their corresponding gap values. The table shows the gap values calculated using the eigen values for +15% and -15% of the baseline transition probability. Bolded gap values differ from the gap values calculated for the *baseline model* and thus indicate a severely sensitive transition probability.

	Gap Value	
Transition	**-15%**	**+15%**
$p_{SB,H}$	0.227	0.227
$p_{SB,BFS}$	0.227	0.227
$p_{H,SB}$	0.227	0.227
$p_{H,H}$	0.227	0.227
$p_{BF,BF}$	**0.267**	**0.123**
$p_{BS,SB}$	**0.214**	**0.232**
$p_{BS,BS}$	**0.238**	**0.150**

Table C. 6. Rank analysis for global scenario perturbation sensitivity analysis for the vegetation layers (good seedbed, poor seedbed, herbs, shrubs, birch saplings, browsed birch saplings, balsam fir saplings, browsed balsam fir saplings, spruce saplings, birch trees, balsam fir trees and spruce trees) and forest layers (forest floor, herbaceous, understory, canopy). Rank analysis on vegetation layers gives a more detailed look at the changes in model output for each of the scenarios being tested. Rank analysis on forest layers gives a broader look at the changes in the overall forest composition for each scenario. For details on transitions altered for each scenario and the purpose of the analysis see Table C. 3.

Global Analysis	**Vegetation Layers**	**Forest Layers**
Scenario 1	Yes[a]	Yes[b]
Scenario 2	No	Yes[c]
Scenario 3	Yes[d]	No
Scenario 4	Yes[e]	No
Scenario 5	No	No
Scenario 6	No	No
Scenario 7	Yes[f]	Yes[c]
Scenario 8	No	No
Scenario 9	No	No
Scenario 10	No	No

[a] SH more dominant than BSS
[b] The overall composition of the forest is altered with herbaceous layer more dominant than saplings
[c] The overall composition of the forest is altered with the canopy more dominant than the seedbed
[d] H more dominant than BS
[e] BSS and BF more dominant than SH
[f] BSS more dominant than SH

Table C. 7. Sensitive scenarios from the global perturbation sensitivity analysis identified using the rank analysis and with their corresponding gap values. The table shows the gap values calculated using the eigenvalues for +15% of the baseline transition probabilities outlined in Table C. 3. Bolded gap values differ from the gap values calculated for the *baseline model* and thus indicate a severely sensitive transition probability.

Global Analysis	**Gap Value**
Scenario 1	0.227
Scenario 2	0.227
Scenario 3	0.227
Scenario 4	0.227
Scenario 5	0.227
Scenario 6	0.227
Scenario 7	0.227
Scenario 8	**0.261**
Scenario 9	0.227
Scenario 10	0.227

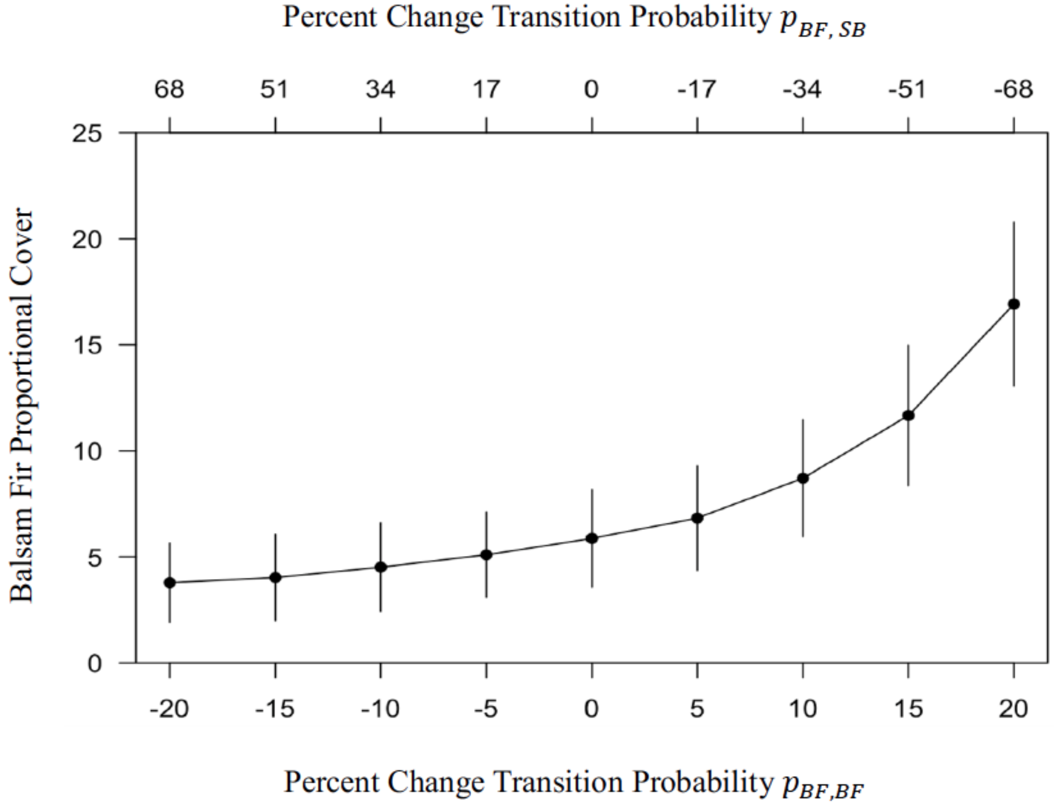

Figure C. 1. The mean proportional percent cover (+/- SD) of balsam fir trees based on the percent change to the balsam fir tree transition probabilities ($p_{BF,SB}$, $p_{BF,BF}$). The sensitivity of the balsam fir to balsam fir transition probability ($p_{BF,BF}$) to variations of -20 to 20% of the baseline transition probability (by 5% increments). The upper axis depicts the rescaled balsam fir to seedbed transition probabilities ($p_{BF,SB}$) after allocating the change between the perturbed and baseline balsam fir to balsam fir ($p_{BF,BF}$) transition probability. As evident in the figure a small variation of 5% to the balsam fir to balsam fir transition results in 17% variation in the balsam fir to seedbed transition probability. A total of 500 simulations were run for each 5% increase between -20 to 20% for 100 time steps. The mean was calculated from the 500 simulations with the 100th time (year) step.

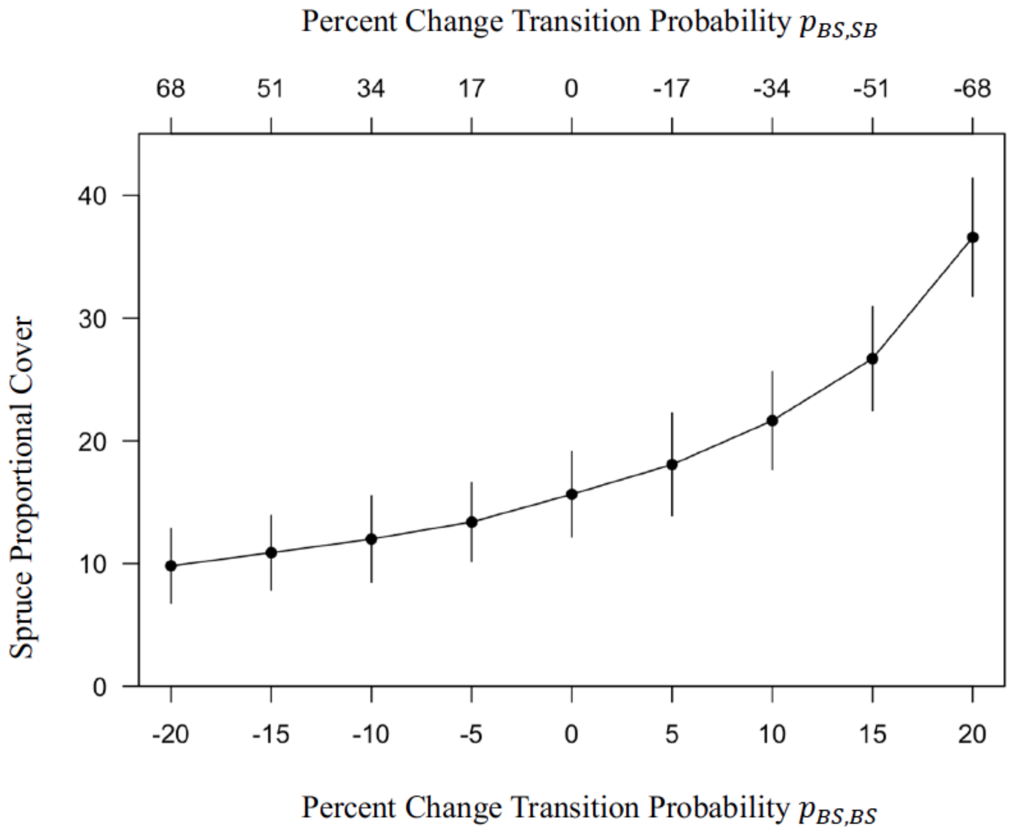

Figure C. 2. The mean proportional percent cover (+SD) of spruce trees based on the percent change to the spruce tree transition probabilities ($p_{BS,SB}$, $p_{BS,BS}$). The figure depicts the sensitivity of the spruce to spruce transition probability ($p_{BS,BS}$) to variations of -20 to 20% of the baseline transition probability (by 5% increments). The upper axis depicts the rescaled spruce to seedbed transition probabilities ($p_{BS,SB}$) after allocating the change between the perturbed and baseline spruce to spruce ($p_{BS,BS}$) transition probability. As evident in the figure a small variation of 5% to the spruce to spruce transition results in 17% variation in the spruce to seedbed transition probability. A total of 500 simulations were run for each 5% increase between -20 to 20% for 100 time steps. The mean was calculated from the 500 simulations with the 100th time (year) step.

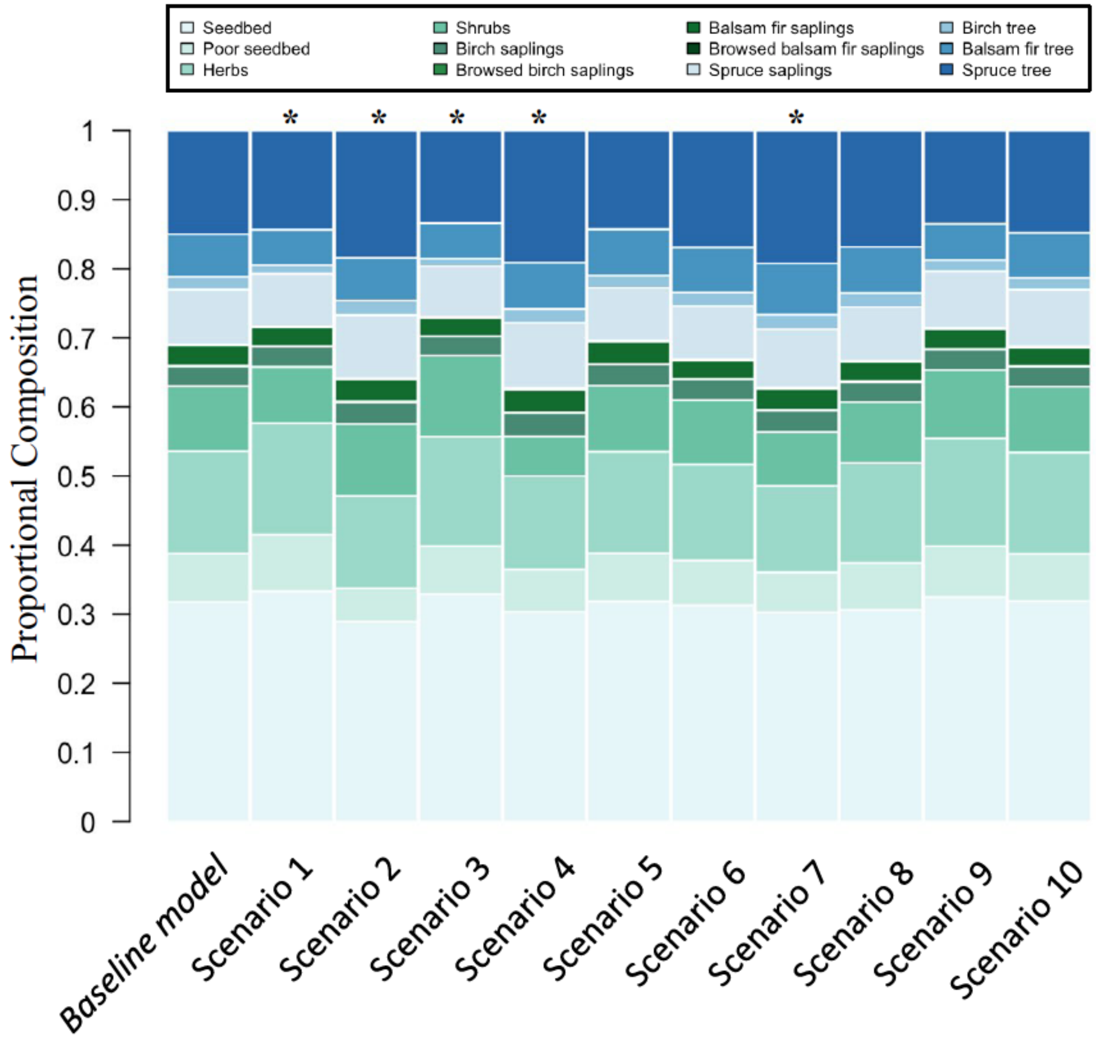

Figure C. 3. Mean proportional composition of vegetation for each of the global analysis scenarios (* indicates a change in layer dominance). For scenario information see Table C. 3. The proportional composition calculations are based on the mean of 500 of simulations for each scenario at the 100th time (year) step.

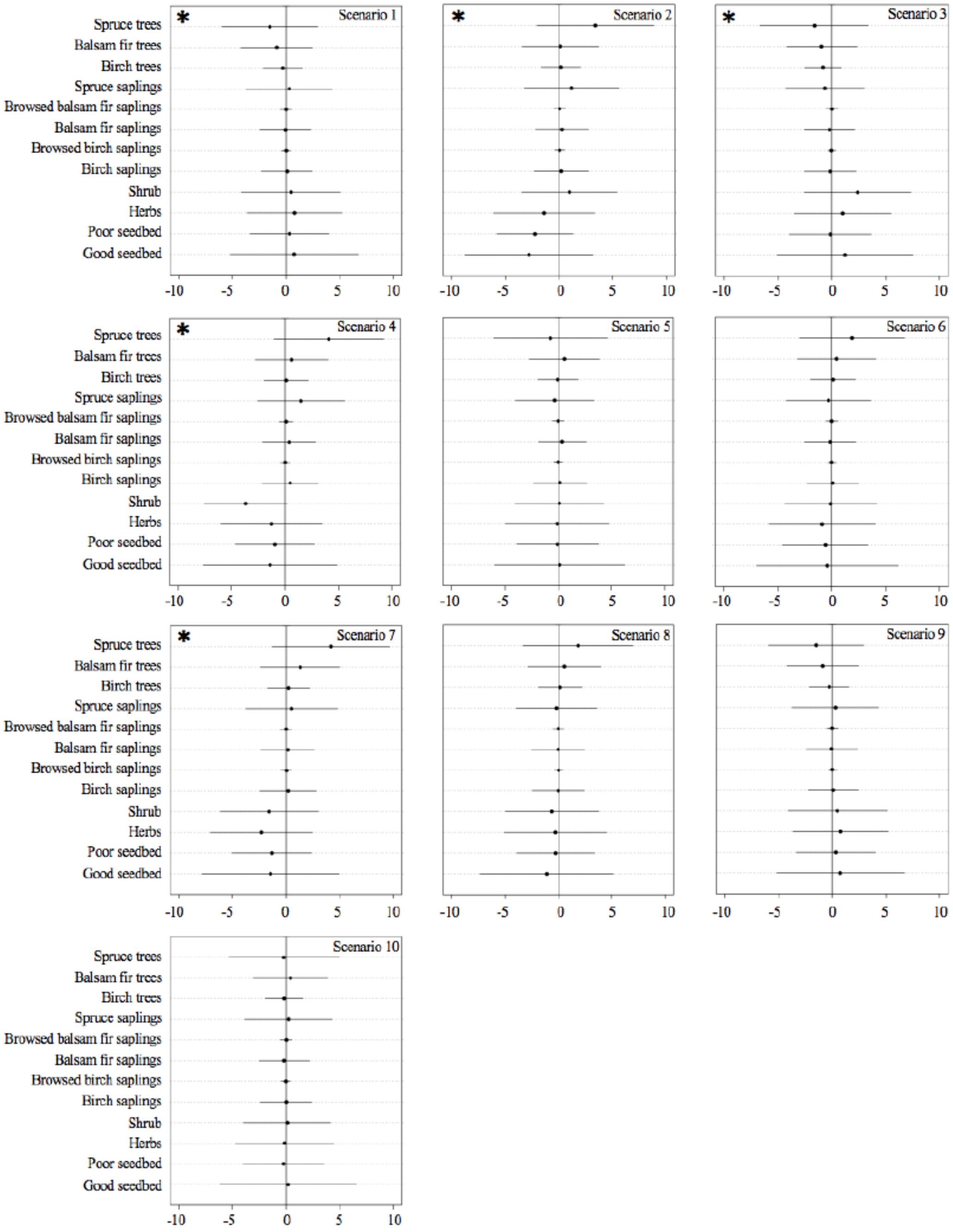

Figure C. 4. Change in mean proportional composition (+SD) of vegetation between altered transition probabilities (+15% of the baseline transition probability) and the calculated transition probabilities for each scenario of the global analysis (* indicates a change in layer dominance). See Table C. 3 for scenario details. The change in proportional percent cover was calculated using the proportional cover for each of the 500 simulations for each scenario at the 100th time (year) step.

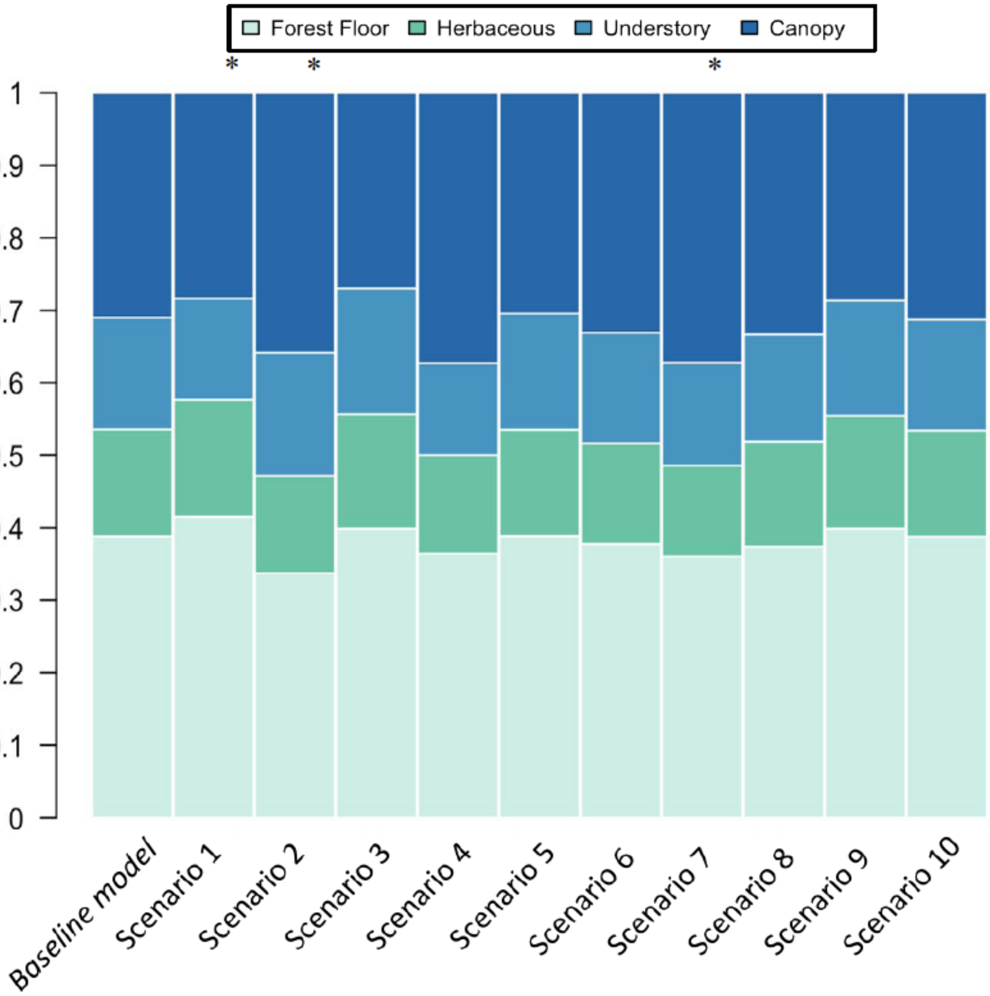

Figure C. 5. Mean proportional composition of forest layers for each of global analysis scenarios (* indicates a change in layer dominance). The proportional composition calculations are based on the mean of 500 simulations for each scenario at the 100th time (year) step. For scenario information see Table C. 3.

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APPENDIX D: MOOSE MODEL

In this appendix, I briefly present the results from the moose model regeneration trajectories under a gradient of moose browsing pressure and simulated restoration.

The moose model was not modified to reflect regeneration within specific sized canopy gaps. Therefore, this model has not been modified using RPK value. Rather, this model reflects the average forest regeneration after disturbance. I ran each of the restoration scenarios on the non-gap specific moose model to determine whether restoration conclusions remained the same when the model was not modified to reflect gap dynamics. Based on the results, the forest is shifting to a spruce dominant forest and birch is being lost from the canopy. The most effective restoration protocols are planting birch and balsam fir seedlings in low simulated browsing pressure and within a moose exclosure. Results support gap specific restoration findings with the same top effective restoration scenarios identified.

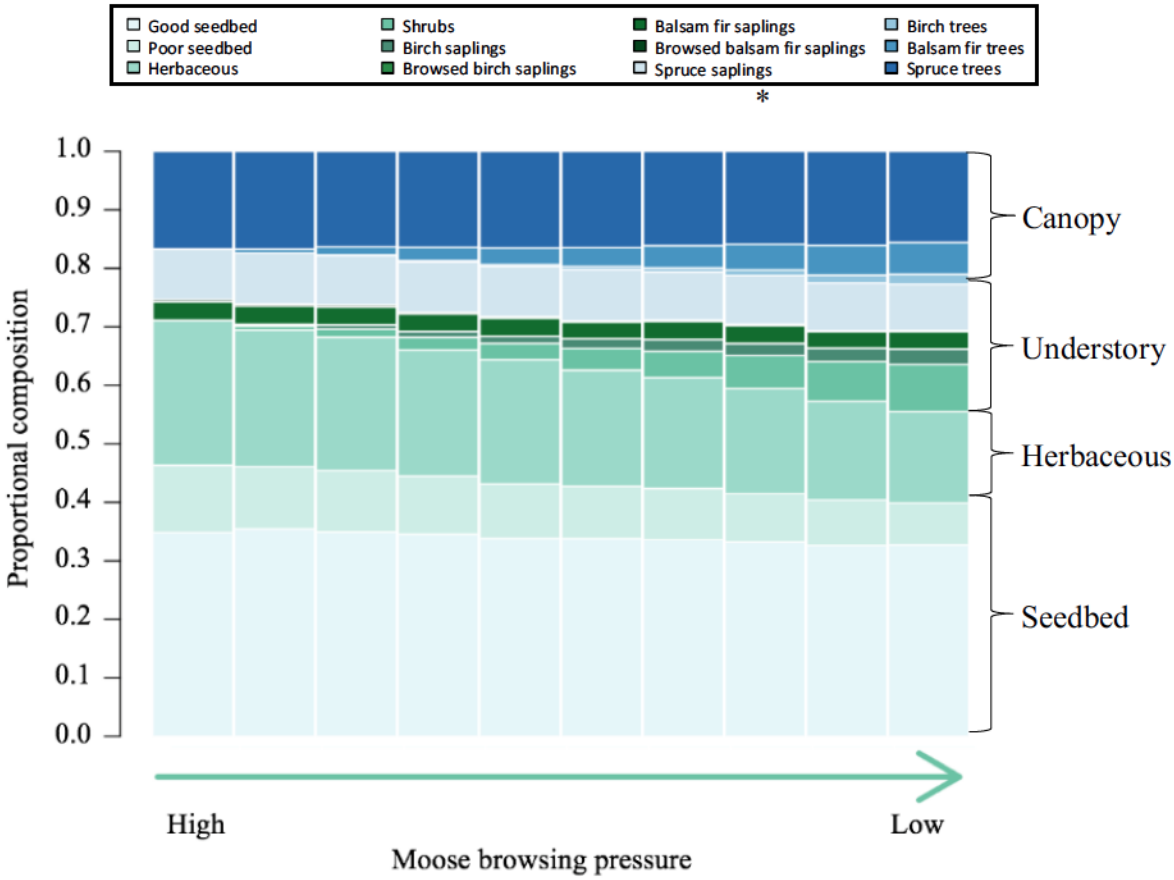

Figure D. 1. Proportional composition of vegetation layers under an increasing moose browsing pressure (low=0.9, high=0.001). Browsing pressure ranges between 0.001 (high) to 0.9 (low) and we simulated increments of 0.1 from 0.9 to 0.1 and by 0.099 for 0.1 to 0.001. Regardless of moose browsing pressure the forest fails to fully regenerate, resulting in a patchy spruce dominant system. Furthermore, even with reduced browsing pressure birch fails to sufficiently regenerate resulting in reduced canopy diversity. At a low level of browsing pressure (M=0.7) birch begins to emerge in the canopy (birch proportional cover >0.005) indicated by an asterisk (*). Active restoration protocols are required to completely close the gap and increase birch and balsam fir recruitment to the canopy. The proportional composition calculations are based on the mean of 500 simulations for each moose browsing pressure at the 100th time step.

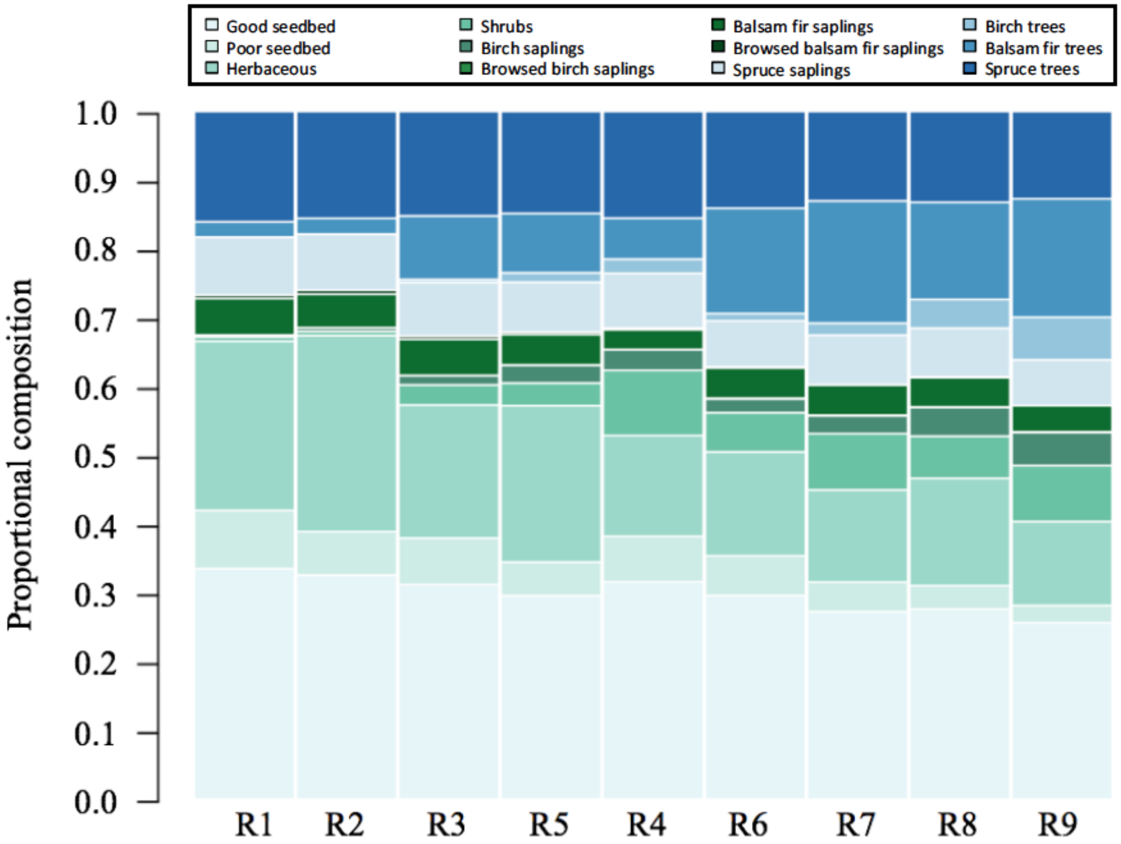

Figure D. 2. Proportional composition of the boreal forest under nine restoration scenarios. Restoration scenarios are labeled R1 through R9, in ascending order of effectiveness for reaching restoration targets in large canopy gaps; R1, planting balsam fir seedlings under high moose browsing pressure (M=0.001); R2, planting birch and balsam fir seedlings under high moose browsing pressure (M=0.001); R3, planting balsam fir seedlings under medium moose browsing pressure (M=0.45); R5, planting birch and balsam fir seedlings under medium moose browsing pressure (M=0.45); R4, placing an exclosure with no planting (M=1); R6, planting balsam fir seedlings under low moose browsing intensity (M=0.8); R7, planting balsam fir seedlings in an exclosure (M=1); R8, planting birch and balsam fir seedlings under low moose browsing intensity (M=0.8); R9, planting birch and balsam fir seedlings in an exclosure (M=1). The proportional composition calculations are based on the mean of 500 simulations for each restoration strategy at the 200th time (year) step.

APPENDIX E: RESTORATION PARAMETER

In this appendix, I discuss the effect of varying restoration parameter (R_{PK}) on the model output and conclusions.

I varied the restoration parameter (R_{PK}) to determine whether the value effected the restoration conclusions. The R_{PK} value is used to simulate seedling planting. As such, as the parameter is reduced, the effectiveness of simulated seedling planting is decreased. Therefore, too small of an R_{PK} value would show no effect of active restoration through seedling planting which is why I tested the R_{PK} value between 1.25 and 2 in large canopy gaps and 1.08 and 1.3 in small canopy gaps. An important condition of Markov models is that the probabilities are between $0 \leq p_{ij} \leq 1$ and each row in a right stochastic Markov model (from-to) must sum to 1 (Horn 1975; Wootton, 2001). The transition probabilities were weighted by R_{PK} through multiplication. In large canopy gaps, the R_{PL} value could not be increased much higher than 2 or the $0 \leq p_{ij} \leq 1$ condition would not be met. Similarly, in small canopy gaps the R_{PS} value could not be increased much higher than 1.3. I ran each of the 9 restoration scenarios (R1 to R9) in large canopy gaps with an R_{PL} value of 2 (presented in the main thesis), 1.75, 1.5 and 1.25 and in small canopy gaps with an R_{PS} value of 1.3 (presented in the main thesis), 1.25, 1.16 and 1.08.

In large canopy gaps the main conclusions of the model remain consistent regardless of the tested R_{PL} value (Figure E. 1). The three most effective restoration protocols being the planting of balsam fir seedlings in an exclosure (R7), the planting of balsam fir and birch seedlings under low simulated moose browsing pressure (R8) and the planting of balsam fir and birch seedlings within an exclosure (R9) (Figure E. 1). The most notable difference between the four simulated restoration parameters (R_{PL}) is that the exclosure with no planting restoration scenario (R4) becomes more effective than planting balsam fir and birch seedlings under medium moose simulated browsing pressure (R5).

In small canopy gaps the main trends remain the same for R_{PS} values of 1.16 and 1.25 where the three most effective restoration protocols are still R7, R8 and R9 (Figure E. 2). In the small canopy gaps the exclosure with no planting restoration scenario (R4) becomes more effective than planting balsam fir and birch seedlings under medium moose simulated browsing pressure (R5) and planting balsam fir seedlings under low moose browsing intensity (R6) when R_{PS}= 1.16 and 1.25. When R_{PS}=1.08 the effectiveness of planting is nearly diminished, with the three exclosure treatments (R4, R7 and R9) becoming the most effective restoration protocols. This suggests an R_{PS} value of 1.08 is too low to simulate the benefits of planting.

In conclusion, the major trends remained consistent for all simulated R_{PK} values in both large and small canopy gaps except for the lowest R_{PS} value in small canopy gaps (R_{PS}=1.08). The sensitive R_{PS} value in small canopy gaps (R_{PS}=1.08) approaches 1 resulting in a lack of accurate seedling planting simulation. Based on the results, restoration conclusions remain the same. The most effective restoration strategies require both balsam fir and birch seedling planting, either under low simulated moose browsing pressure or within exclosures.

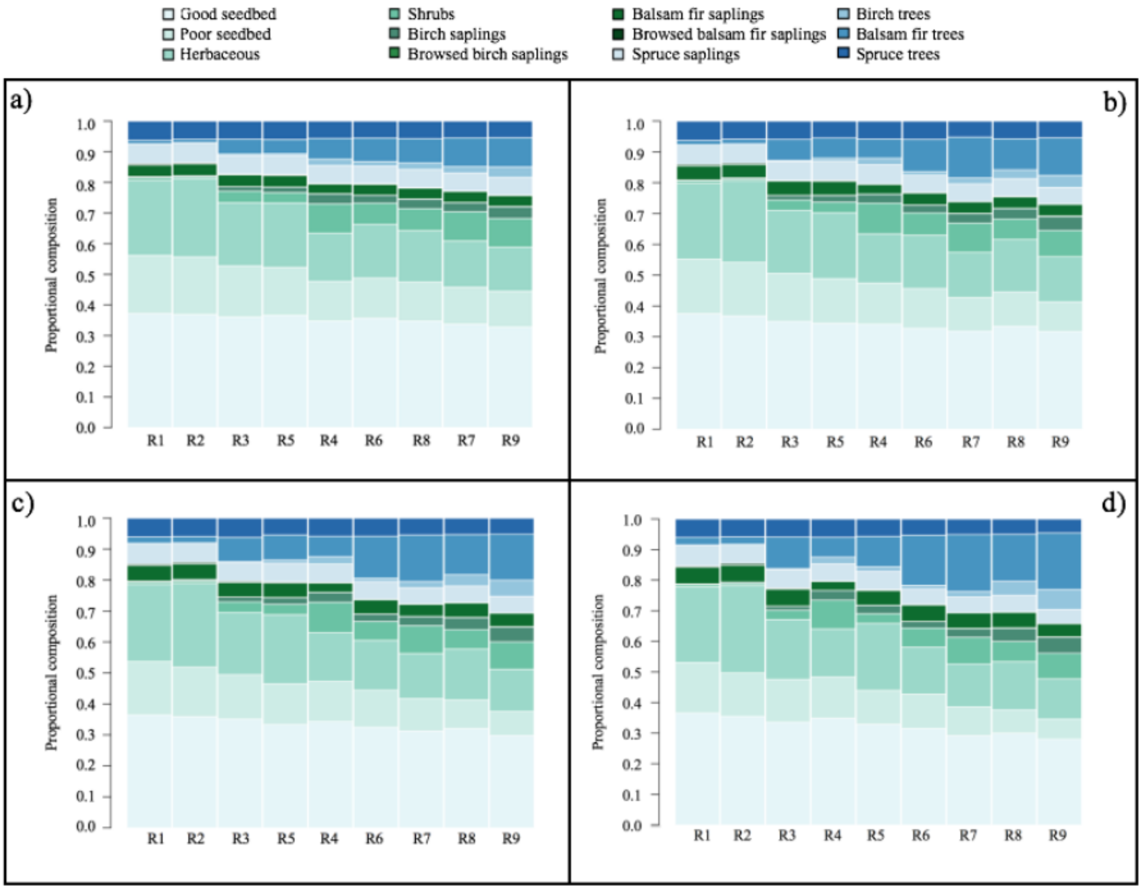

Figure E. 1. Proportional composition of the boreal forest under nine active restoration scenarios in large canopy gaps with varying R_{PL} parameter values, a) $R_{PL} = 1.25$, b) $R_{PL} = 1.5$, c) $R_{PL} = 1.75$ and d) $R_{PL} = 2$. The R_{PK} parameter was altered to determine how restoration protocols varied after altering the R_{PK} parameter. Restoration scenarios are labeled R1 through R9, in ascending order of effectiveness for reaching restoration targets in large canopy gaps when $R_{PL} = 2$: R1, planting balsam fir seedlings under high moose browsing pressure (M=0.001); R2, planting birch and balsam fir seedlings under high moose browsing pressure (M=0.001); R3, planting balsam fir seedlings under medium moose browsing pressure (M=0.45); R4, placing an exclosure with no planting (M=1); R5, planting birch and balsam fir seedlings under medium moose browsing pressure (M=0.45); R6, planting balsam fir seedlings under low moose browsing intensity (M=0.8); R7, planting balsam fir seedlings in an exclosure (M=1); R8, planting birch and balsam fir seedlings under low moose browsing intensity (M=0.8); R9, planting birch and balsam fir seedlings in an exclosure (M=1). The broad trends remain the same with all R_{PL} values except the effectiveness of the exclosure only restoration protocol (R4) becomes more effective then planting birch and balsam fir seedlings under medium moose browsing pressure (R5) for R_{PL} =1.25, 1.5 and 1.75. The three most effective restoration scenarios are the same regardless of R_{PL} parameter value. The proportional composition calculations are based on the mean of 100 simulations for each restoration strategy at the 200th time (year) step.

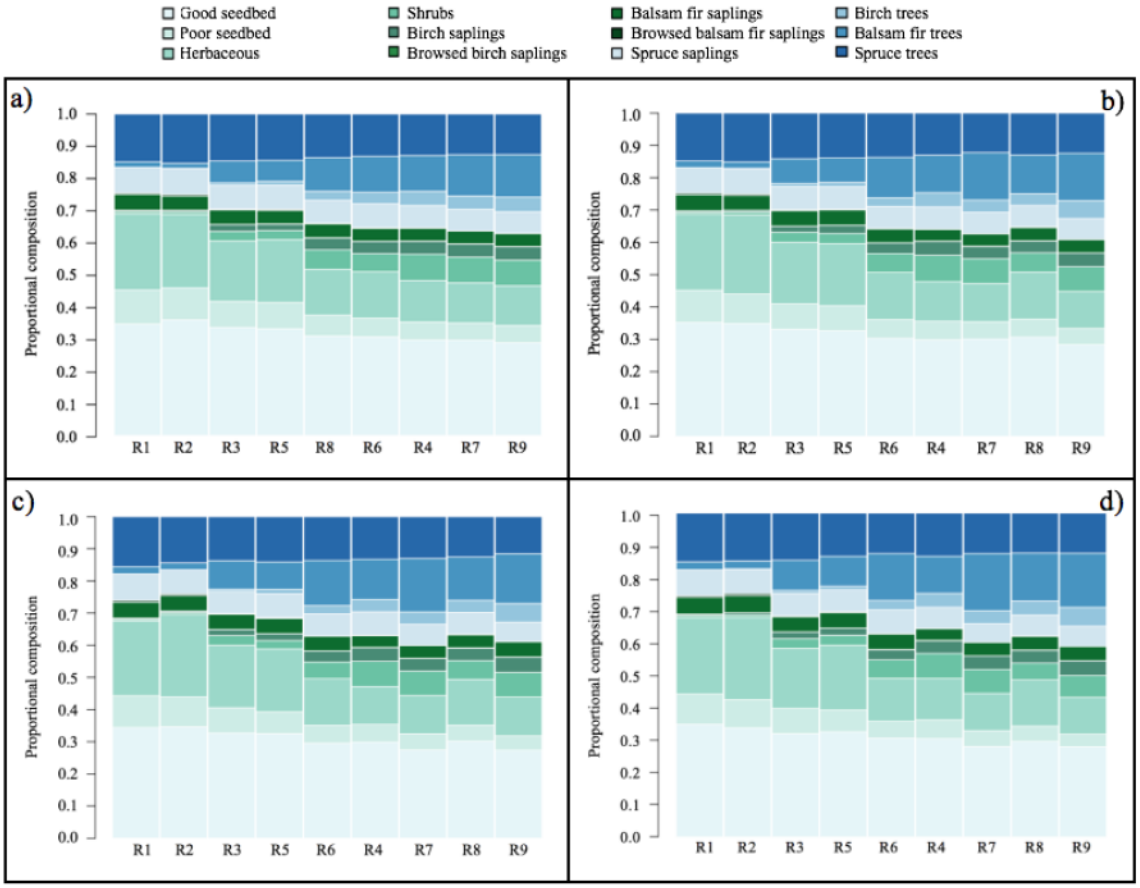

Figure E. 2. Proportional composition of the boreal forest under nine active restoration scenarios in small canopy gaps with varying R_{PS} parameter values, a) $R_{PS} = 1.08$, b) $R_{PS} = 1.16$, c) $R_{PS} = 1.25$ and d) $R_{PS} = 1.33$. The R_{PK} parameter was altered to determine how restoration protocols varied after altering the R_{PK} parameter. Restoration scenarios are labeled R1 through R9, in ascending order of effectiveness for reaching restoration targets in large canopy gaps when $R_{PL} = 2$: R1, planting balsam fir seedlings under high moose browsing pressure (M=0.001); R2, planting birch and balsam fir seedlings under high moose browsing pressure (M=0.001); R3, planting balsam fir seedlings under medium moose browsing pressure (M=0.45); R4, placing an exclosure with no planting (M=1); R5, planting birch and balsam fir seedlings under medium moose browsing pressure (M=0.45); R6, planting balsam fir seedlings under low moose browsing intensity (M=0.8); R7, planting balsam fir seedlings in an exclosure (M=1); R8, planting birch and balsam fir seedlings under low moose browsing intensity (M=0.8); R9, planting birch and balsam fir seedlings in an exclosure (M=1). The broad trends remain the same with R_{PS} values below 1.16 except the effectiveness of the exclosure only restoration protocol (R4) becomes more effective then R5 and R6. When R_{PS}=1.08 the effectiveness of simulated seedling planting is nearly diminished and R4 becomes more effective than R8, with R7 and R9 being the two most effective protocols. The proportional composition calculations are based on the mean of 100 simulations for each restoration strategy at the 200th time (year) step.

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APPENDIX F: DETAILED FIELD METHODS

In this appendix, I provide details on the field data collection for the Salmonier property. Field data protocol is based on TNNP sampling protocols.

Data were collected in August 2016 by Nichola Ellis, a former graduate student from the Leroux lab and a hired contractor for NCC. She sampled 20 predetermined sites to examine the impacts of moose throughout the Salmonier property based on sampling protocols used in TNNP. At each of the sites she developed a temporary 400 m^2 circular plot which was then separated into triangular sections using 9.14 m tape measures. Each triangular section faced a different cardinal direction. Each plot had five 1 m^2 subplots, one located at the center of the 400 m^2 circular plot and one in each of the cardinal directions.

Each plot was assessed by measuring the slope, aspect and soil pH. One soil sample was obtained per plot using a 10 cm deep core. The pH was determined using a slurry which was made using a 1:1 ratio of soil to distilled water. In addition to the abiotic factors, dominant canopy tree species and stand type was determined to aid in site classification.

Within each plot all the canopy trees greater than 2 m in height were identified and measured. Each tree was grouped into a height category (2 m-5 m, 5 m-10 m, 10 m-15 m and >15 m) and had its diameter at breast height (DBH) measured using DBH tape. The average canopy closure was determined by taking a picture within each sub plot facing a cardinal direction using a camera at eye level. Using the four photos, the percentage of the image shaded by the canopy was used to estimate canopy closure for each plot. The dominant tree species was determined and had the average, minimum and maximum DBH measured.

Within each sub plot the seedbed and shrub layers were classified. The seedbed was classified as either moss, woody debris, rock, water or leafy debris in 5% intervals for a total of 100% cover in each sub plot. All shrub layer species were identified and measured to the nearest 5% for abundant species and 1% for rare species. The total shrub layer ranged from 0 to > 100% as the shrub species often overlap. For each species in the shrub layer the maximum, minimum and average height and DBH was measured.

The yellow birch and balsam fir sapling abundance was determined by counting and measuring saplings (<2 m in height) within the 15 cm transect along both sides of the tape measures that separated the plot into cardinal directions. While walking along the tape measure balsam fir and yellow birch saplings, trees under 2 m tall, were counted and had the height and DBH measured. The saplings were grouped into height categories (0-49.4 cm, 50-99.9 cm, 100-149.99 cm and 150-199 cm). After a total of five saplings of the same species within the same height category were counted the distance from that point to the middle of the plot was measured to aid in a sapling density analysis. In addition, each sapling was examined for moose browse. Browse intensity was rated on a 0-4 scale, where 0 was no browse and 4 indicated all terminal leaders and a majority of branches had been browsed.

To examine whether the plots were representative of the Salmonier property I conducted several analyses and used the data to pinpoint areas requiring additional sampling. For the spatial analysis NCC provided several shape files including the property border, a referenced 2008 aerial photo, and site wide habitat classification. I downloaded a digital elevation model (DEM) from Geogratis, in addition to some topographical features surrounding the property. I used ArcGIS to combine the DEM, Nichola's plots and the property border and analyzed the distribution of plots along the elevation gradient. Using the NCC shapefiles I was able to extract habitat data from the attribute table and used this to create a new shapefile. Based on the file I determined the percent of the property within each habitat type and compared the number of plots within each habitat type. Lastly, I analyzed the proportion of plots with low, medium and high canopy openness values. By combining the results of the DEM, habitat stand classification and canopy openness analysis I identified five suitable locations for new plots and the minimum number of new plots required to complete a disturbance and habitat gradient for the site.

I collected data from the five new plots I identified via ArcGIS in the summer of 2018. I used the same field sampling methods as the methods outlined above, except I also collected data on spruce saplings (abundance, DBH, height). In addition, I surveyed all 20 plots that data were collected from in 2016 and counted spruce saplings in each of the plots along 30 ft transects that separate the circular plot into four triangular subsections. This additional data were used to help classify the understory data which was used to inform TNNP site selection and transition probabilities (Figure 2.5).

APPENDIX G. DETAILED DRONE IMAGERY METHODS

In this appendix, I outline the drone flight planning and processing methods for drone imaging. A third of the Salmonier property was captured with drone imagery to aid in model parameterization and help locate priority sites for active restoration for NCC.

Drone flight planning

Recent aerial imagery was unavailable for NCC's Salmonier property, with the last available aerial imagery from 2009 (Figure 2.4c). To determine recent canopy transitions and identify any new large canopy gaps a phantom 4 pro drone was flown over the Salmonier NCC property. A FC6310_8.8_5472x3648 (RGB) camera model was used with a front lap of 80, side lap of 70 and 180 degree camera angle. The coordinate system used for image geolocations was WGS 84 (EGM 96 Geoid).

To accommodate drone flight restrictions and regulations, several separate flights were conducted. A total of 10 flights were piloted over two days, capturing approximately one third of the Salmonier NCC property. The locations of the flights were informed by field data collected in 2016 and 2018 to ensure degraded non-regenerating landscapes were captured in order to help NCC prioritize restoration planning based on habitat degradation and species composition. The other two thirds of the property were not flown due to time limitations and unsuitable flight conditions. The flights ranged from 30 m^2 to 100 m^2 depending on drone visibility from the ground during the flight. Small gaps with large birch required shorter flights to keep the drone within view of the pilot whereas large gaps dominated by conifer species allowed for larger flights due to increased visibility. Each adjacent flight had an overlap of 25 m to ensure proper flight stitching during processing.

Within each mission 2-4 ground control points (GCP's) were used. GCP locations were determined prior to flight by identifying gaps and elevation changes within each of the predetermined flight paths. The GCP's were made from light weight floor tile covered with duct tape in a checkered pattern. Each GCP was double sided with a slightly different design and colouring to aid in identification during flight processing. A GARMIN GPSmap 62st was used to determine GCP coordinates and elevation.

Drone image processing

Drone images were processed using Pix4D mapper. I created several projects by possessing the drone images using different settings to determine which techniques produced the best results. The projects processed with GCP's, regardless of the processing settings used, produced inaccurate results with significant image distortion. The GCP coordinates were less accurate than the geolocation tags within the images causing the vertical and horizontal shifts.

The most accurate results were produced by processing each flight separately during the initial processing stage. The flights were then merged using four manual tie points between each overlapping flight. The project was then re-optimized and any uncalibrated cameras were either manually calibrated or disabled. After successful merging, the project was taken through the point cloud and mesh processing. The only settings altered were key point image scale from full to ½ image size, point cloud densification image scale from ½ to ¼ image size and raster DSM method from inverse distance weighting to triangulation. All other settings were left at default setting. Mosaic editing was only used for distorted images along the perimeter where image overlap was insufficient. It was not used for any other areas as it increased image sharpness at the expense of location accuracy.

The drone imagery from the merged project was imported into ArcGIS where geolocation accuracy was compared to the 2009 aerial photo. The drone imagery aligned with the 2009 aerial photo and did not require any georeferencing. The 15 m x 15 m fishnet was applied to the drone image and every grid cell within the Salmonier property was identified as either open, balsam fir, spruce or birch.

APPENDIX H: DECISION TREE

In this appendix, I describe the decision tree used to estimate the transition probabilities for the seedbed, herbaceous and understory vegetation using TNNP field data. I outline an example of how I used the decision tree to estimate transition probabilities for one of the subplots within TNNP by converting the macro data (e.g., percent cover data) into micro data (e.g., aerial imagery, tagged trees). I transformed the macro data into micro data to incorporate all 12 vegetation layers and follow Markov model restrictions (See Appendix B).

The TNNP data were collected from each of the plots in 1998, 2004, 2010 and 2016. The data collected were macro percent cover data for each species within the seedbed, herbaceous layer and understory layer. To transform data from macro to micro data I developed a decision tree (Lee et al., 1970). There are several other methods to transform macro data to micro data including Bayesian statistics, restricted least squares and linear programming. All of these methods require assumptions to be made about the data to transform it (Lee et al., 1970). Given the limited data available for my study, I opted not to determine forest transitions via statistical methods. Instead, I developed a decision tree and I based the thresholds for each decision node based on vegetation dominance. Prior to development of thresholds I examined the TNNP field data and determined the mean, median, mode and standard deviation of all percent covers to determine the distribution. Based on these calculations I was able to tell that herbs and seedbed formed more continuous patches whereas saplings and shrubs (understory vegetation) formed smaller scattered patches. As such, the thresholds were adjusted to account for this disparity in cover types. Given that this decision tree and subsequent transition probabilities are influenced by the particular thresholds, I conducted a local and global sensitivity analysis (See Appendix C). The goal of this sensitivity analysis was to assess the robustness of my simulations to the specific transition probabilities and indirectly on the decision tree.

I used the decision tree to estimate transition probabilities by applying the tree to each of the twenty-five subplots (five subplots per plot) for each year data were collected (1998, 2004, 2010, 2016). I first used the tree to transform all macro percent cover data within each subplot to micro point source data by assigning the subplot as good seedbed, poor seedbed, herbaceous, shrubs, birch saplings, balsam fir saplings or spruce saplings. Once each subplot was classified as one of the seven states I used the equation (Eq. 2.2), to calculate the transition probabilities between each year. I made three assumptions to estimate transition probabilities using this method including:

a) Transitions from different understory and herbaceous states must first pass through the seedbed states. This is because a balsam fir sapling would not spontaneously turn into a spruce sapling, rather, the balsam fir saplings would die and spruce saplings would germinate within the seedbed (McLaren and Janke, 1996; Kenkel, 1997; Duchesneau and Morin, 1999). Therefore, transitions from balsam fir saplings to spruce saplings is actually considered two transitions, balsam fir saplings to seedbed and seedbed to spruce saplings. This allows seedbed processes to be simulated within the model and mortality to more accurately be depicted.

b) Good seedbed is the only state that turns into poor seedbed. As such, transitions from saplings, such as balsam fir saplings, cannot transition to an automatically poor seedbed. This is because the decline in seedbed quality is not instantaneous, rather good quality seedbed dries out or herbaceous and deciduous leaf litter builds up causing a more gradual shift from good seedbed to poor seedbed (McLaren and Janke, 1996; Kenkel, 1997; Duchesneau and Morin, 1999).
c) Poor seedbed cannot transition to balsam fir or birch saplings as I based the category on both balsam fir and birch germination success within poor seedbed (McLaren and Janke, 1996; Kenkel, 1997; Duchesneau and Morin, 1999). As such, any transitions from poor seedbed to balsam fir saplings would be considered two transitions, poor seedbed to good seedbed to balsam fir saplings. This was to simulate the actual effect of shifting to a poor seedbed on balsam fir germination success. If the transition could happen the same as the good quality seedbed the poor seedbed would not be representative of ecological processes.

These assumptions were made to simulate ecological processes as six years passed between each data collection period and what is observed in these discrete data is not the only processes occurring.

Example

To calculate the transition probabilities for the Bread Cove plot I start by transforming the macro data into micro data using the decision tree I developed (See Figure H. 2 for a worked example using the decision tree to classify the subplots). Next, I develop a count matrix of all the transitions that occur, following my three outlined assumptions when required (Table H. 2). Next, I used the equation H. 1 to determine the transition probabilities based on the count matrix (Table H. 3). For instance, the calculation for herbaceous self-replacement (H to H) is,

$$p_{H,H} = \frac{N_{H,H}}{\sum_j N_{H,j}} \tag{Eq. 2.2a}$$

$$p_{H,H} = \frac{N_{H,H}}{N_{H,SB}+N_{H,H}} \tag{Eq. 2.2b}$$

$$p_{H,H} = \frac{4}{2+4} \tag{Eq. 2.2c}$$

$$p_{H,H} = 0.67 \tag{Eq. 2.2c}$$

for a final herbaceous self-replacement transition probability of 0.67.

Table H. 1. Bread Cove subplot classifications estimated using the decision tree (Figure H. 1) for each of the years data were collected.

Subplot	1998	2004	2010	2016
A	Good seedbed	Herb	Good seedbed	Herb
B	Herb	Herb	Poor seedbed	Good Seedbed
C	Herb	Herb	Herb	Herb
D	Spruce saplings	Spruce saplings	Spruce saplings	Spruce saplings
E	Balsam fir saplings	Balsam fir saplings	Poor seedbed	Balsam fir saplings

Table H. 2. Count matrix of transitions observed from the Bread Cove plot based on observed sequences and ecological assumptions. Self-replacement transition counts are bolded for reference.

	To:						
From:	SB	SBB	H	SH	YBS	BFS	BSS
SB	**0**	2	2	0	0	1	0
SBB	2	**0**	0	0	0	0	0
H	2	0	**4**	0	0	0	0
SH	0	0	0	**0**	0	0	0
YBS	0	0	0	0	**0**	0	0
BFS	1	0	0	0	0	**1**	0
BSS	0	0	0	0	0	0	**4**

Table H. 3. Transition probability matrix for the Bread Cove plot calculated using Eq. H. 1 with the count matrix data (Table H. 3). Self-replacement transition probabilities are bolded for reference.

	To:						
From:	SB	SBB	H	SH	YBS	BFS	BSS
SB	**0**	0.4	0.4	0	0	0.2	0
SBB	1	**0**	0	0	0	0	0
H	0.33	0	**0.67**	0	0	0	0
SH	0	0	0	**0**	0	0	0
YBS	0	0	0	0	**0**	0	0
BFS	0.5	0	0	0	0	**0.5**	0
BSS	0	0	0	0	0	0	**1**

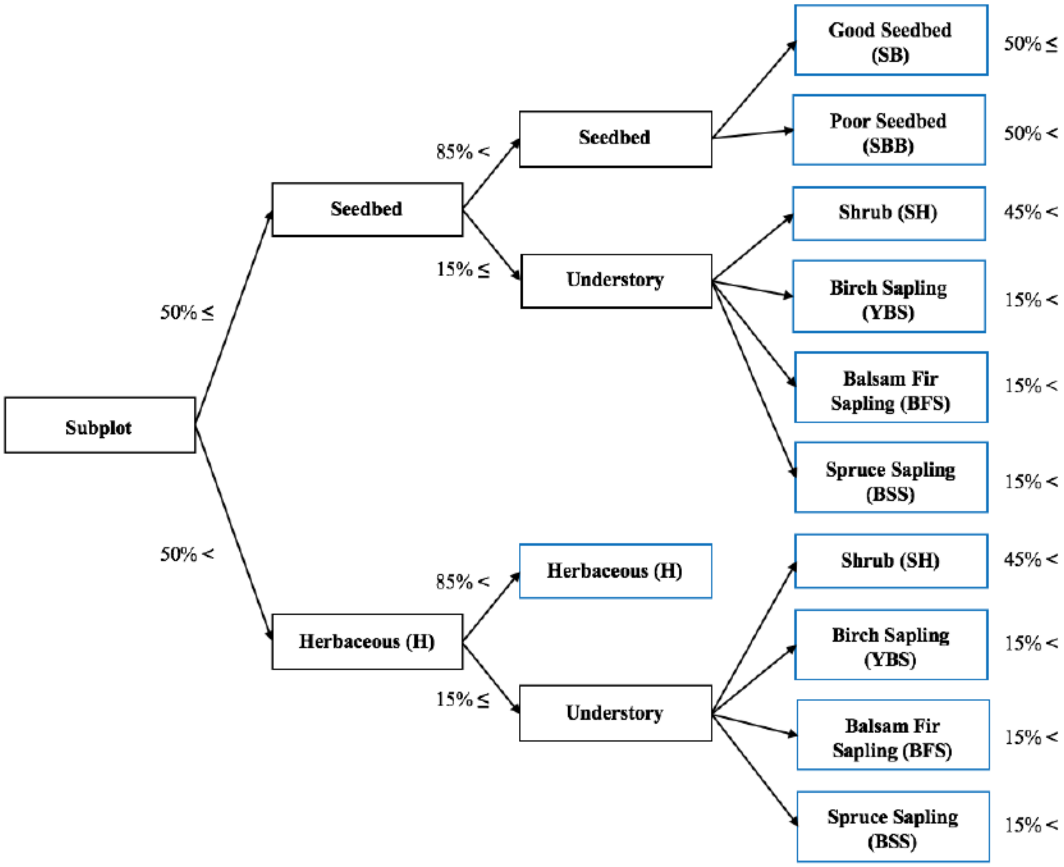

Figure H. 1. Decision tree I developed based on TNNP data analysis to develop transition probabilities.

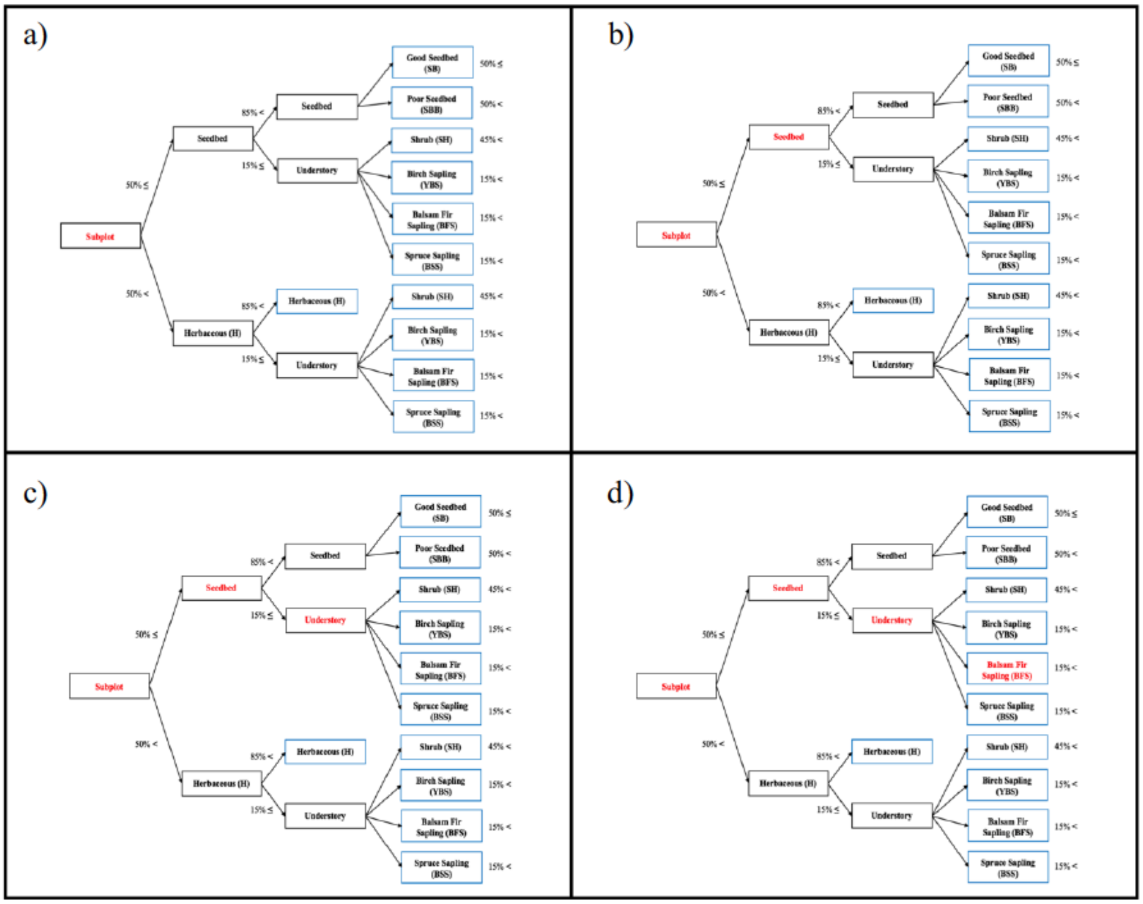

Figure H. 2. Example walkthrough of the decision tree for Bread Cove subplot E 2016. Starting composition of the subplot was SB=23%, SBB=20%, H=42%, SH=0, YBS=4.3%, BFS=10.1%, BSS=0. For the first node (A) comparing SB and H, SB makes up 50.5% of the forest composition ($50.5\% = \frac{43\%}{43\%+42\%}$) as such we follow the seedbed branch. The second node (B) comparing SB and understory, understory makes up 26% of the forest composition ($26\% = \frac{15\%}{43\%+15\%}$) as such we follow the understory branch. For the final node (C), BFS=70% of the forest composition ($70\% = \frac{10.1\%}{10.1\%+4.3\%}$) as such the entire subplot is classified as balsam fir saplings (D).

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APPENDIX I: ADDITIONAL RESULTS

In this appendix, I provide additional results for the regeneration and restoration simulations. I give more detail on the results of ineffective restoration scenarios in large and small canopy gaps that are not discussed in the main chapter of my thesis.

Baseline dynamics

The *baseline model* was used as the foundation of the all gap models and restoration simulations. The *baseline model* was built using the calculated transition probabilities (Table 2.2) and reflects the current regeneration trajectories within the balsam fir dominant boreal forest without simulated moose browsing pressure or gap specific dynamics.

The calculated transition probabilities show a high level of self-replacement and low mortality for balsam fir trees and spruce trees as compared to birch tree self-replacement (Table 2.2). The highest self-replacement values for the understory are for herbs and spruce saplings, indicating a high-level herb and spruce persistence within the system. Shrubs have a higher level of mortality than self-replacement, indicating they do not survive in the understory for long durations. Birch saplings have the highest mortality rate, aside from poor seedbed, indicating unfavorable conditions for birch sapling survival. As such, birch have a higher mortality rate and lower canopy recruitment rate than both spruce and balsam fir indicating that they would be the least likely to fill any canopy gaps.

Restoration Scenarios

Large gap – The two least effective restoration scenarios were restoration scenario 1 (R1), planting of balsam fir seedlings under high moose browsing pressure (M=0.1) and restoration scenario 2 (R2), planting of balsam fir and birch seedlings under high simulated moose browsing pressure (M=0.1) (Figure 2.10). Both scenarios fail to close the canopy gap and recruit birch to the canopy. The understory is devoid of shrubs and birch saplings for both scenarios indicating a severe lack of understory diversity. The two scenarios were nearly identical in sapling and canopy composition; however, the seedbed was better quality under scenario R2 as the herbaceous layer increased in percent cover from 25% to 29% (Figure 2.11).

Restoration scenario 3 (R3), planting balsam fir seedlings after reducing moose browsing pressure to a medium level (M=0.45), and restoration scenario 5 (R5), planting balsam fir and birch seedlings after simulating a reduction of moose browsing pressure to a medium level (M=0.45) also failed to recruit enough balsam fir trees to the canopy, failing to generate full canopy closure (Figure 2.10). While both of these scenarios increase balsam fir recruitment, with 10% balsam fir percent cover within both scenarios, birch still fails to recruit to the canopy with no birch recruitment under scenario R3 and only 2% birch in R5. Both of these scenarios have increased diversity within the understory with the emergence of birch saplings and shrubs, with 2% more birch saplings in R5 (Figure 2.11).

Restoration scenario 4 (R4), with the establishment of an exclosure and no planting of either birch or balsam fir saplings, is the most effective scenario for restoring shrubs in the understory. Under this scenario shrubs represent 9% of the forest composition (Figure 2.11. Understory diversity is increased under this scenario, with both birch and balsam fir saplings present. Some birch successfully recruits to the canopy; however, this scenario does not effectively close the canopy gap, with only 14% of the forest canopy trees, and has a 2% decrease in balsam fir percent cover compared to scenario R3 (Figure 2.11).

Restoration scenario 6 (R6), planting balsam fir seedlings after reducing moose browsing pressure to a low level of browsing (M=0.8) and restoration scenario 8 (R8), planting balsam fir and birch seedlings under low levels of browsing are both effective at restoring understory diversity (M=0.8) (Figure 2.10). The canopy in mostly closed, with the canopy representing 23% and 25% respectively. Scenario R6 fails to recruit birch trees into the canopy while scenario R8 recruits the second largest amount of birch to the canopy, 5% (Figure 2.11). Therefore, planting of birch seedlings is essential for birch restoration.

Small gap – Similar to the *large gap model*, restoration scenario 1 and 2 were ineffective restoration protocols (Figure 2.12). In both restoration scenarios, there was no birch recruitment to the canopy and no birch or shrub growth in the understory. Balsam fir recruitment was minimal with balsam fir representing only 12% (R1) and 13% (R2) of the canopy. The canopy was semi closed and heavily dominated by spruce. Restoration protocol R3 and R5 were also ineffective, lacking birch and shrub growth. However, balsam fir recruitment was substantially higher with 37% and 35% balsam fir, an increase of approximately 300%. Furthermore, the canopy was predominantly closed with some diversity introduced to the understory with approximately 3% of the proportional composition shrubs.

Birch was 68% higher under restoration scenario R9 compared to the passive restoration scenario of simulated decreased moose browsing pressure (M=0.9). For all other restoration protocols, birch had less than 26% increase in proportional cover compared to the passive restoration scenario (M=0.9). Balsam fir proportional cover increased by 35% for restoration scenario R7 and 30% for restoration scenario R9 compared to the passive restoration scenario (M=0.9). Shrubs had a negligible decrease in proportional cover for restoration scenario R9 and R8 compared to the passive restoration (M=0.9).

Out of all the restoration scenarios three meet all targets; R7, R8 and R9 (Table 2.6; Table 2.7). The two scenarios with seedling planting within an exclosure (R7, R9) are the most effective for balsam fir canopy recruitment, canopy closure and shrub abundance. The scenarios with birch seedling planting under low moose browsing pressure (R8) or within an exclosure (R9) are the most effective for birch sapling regeneration and birch recruitment to the canopy. Poor seedbed, good seedbed, herbs and spruce saplings are at the lowest percent covers under the restoration scenario with an exclosure and the planting of both birch and balsam fir seedlings (R9), leading to a more balanced and diverse understory.