Understanding the effects of combined disturbances on eastern boreal forests using empirical and mathematical approaches

By

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A thesis submitted to the school of Graduate Studies
in partial fulfillment of the requirements for the
degree of **Master of Science**

Department of Biology
Memorial University of Newfoundland and Labrador
January 2025

St. John's, Newfoundland

Abstract

Throughout eastern boreal forests, multiple anthropogenic and natural disturbances have influenced the forests' ability to regenerate, with consequences for carbon storage, biodiversity and other ecosystem services. We examined responses of the boreal forest to the combination of gap forming disturbances (e.g., insect defoliation, forest fires) and moose herbivory through empirical (Chapter 2) and mathematical (Chapter 3) approaches. From our statistical models fit to field and remote sensed data, we found areas more likely to be gaps have lower carbon storage and are characterized by forests with shorter vegetation and higher seasonality in vegetation greenness. Furthermore, we provided evidence that moose may have impeded the recovery of up to 13 megatons of carbon storage across our study area, 20-30 years after disturbances. Our mathematical model of an eastern boreal forest provides additional evidence moose herbivory can impede regeneration of boreal forests. However, aspects of plant growth can interact with moose herbivory to ultimately determine whether a gap regenerates to boreal forest or transitions to grassland. Our integration of statistical and mathematical approaches provides novel insights that may inform where forest gaps exist, why regeneration is important, and what needs to be done to restore mature boreal forest regeneration.

Dedication

I would like to dedicate this thesis to my moms, Bethany and Dee-Anne. They have always shown me where hard work and compassion can get you.

Acknowledgements

I would like to acknowledge that I conducted this research on the ancestral lands of the Mi’kmaq and Beothuk, and I study forests that are a part of the ancestral lands of the Mi’kmaq, Wolastoqiyik, Abenaki, Penobscot, Passamaquoddy, Beothuk, and Innu Peoples. Where possible, I strive to conduct inclusive and equitable science, because it is an integral step in order for scientists from colonial institutions to engage with reconciliation.

The support and mentorship of my supervisor Dr. Shawn Leroux has made my thesis possible, and has made me a better writer, critical thinker, and overall better scientist. This thesis was made more thorough and well-rounded by the advice of my committee members, Dr. Yolanda Wiersma and Dr. Amy Hurford.

A huge thanks goes out to all the people I had the pleasure of working with over the past two years. Lilly MacDaniel was an amazing field technician who was incredibly hard working, and along with Jeremy Hussey, Zach Wallot-Beale, Lauren Gover, and Elizabeth Forbs made the field season so enjoyable. On top of that, Lilly MacDaniel and Niels van Miltenberg made the lab processing super smooth. My lab mates in EEL continue to push me be a better scientist and I thank them for all their recommendations.

Finally, thanks to my support system. Cameron, and my moms, Bethany and Dee-Anne have helped me in more ways than I can put in this acknowledgments section. Thanks for all of your love and support.

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Chapter 1: General Introduction

The boreal forest is the largest biome on Earth, forming a near continuously forested belt between 50° and 70° N (Hagner 1999). It contains 30% of the world's forested area (International Boreal Forest Research Association 2022) and is dominated by cold-tolerant tree species, mostly conifers with interspersed broadleaf trees. This large stock of above ground vegetation, in addition to the slow decomposition of organic matter in the soil, contributes to the potential for the boreal forest to act as a large carbon sink (Pan et al. 2011; Kurz et al. 2013). The large stock of aboveground vegetation is relied upon by many countries within the boreal forest for economic productivity in the form of timber and associated industries (Brandt et al. 2013; Kayes and Mallik 2020), as well as for sustenance (Stroink and Nelson 2012; Robidoux and Mason 2017; Hossain et al. 2018; Settee and Shukla 2020; Robidoux et al. 2021). Beyond carbon storage and direct harvest, humans also benefit from the range of ecosystem services provided by the boreal forest, such as oxygen production, water filtration, disease regulation, and cultural significance (Brandt et al. 2013). For thousands of years, Indigenous peoples have cultivated relationships of reciprocity with the boreal forest, and continue to be at the forefront of conservation (Indigenous Leadership Initiative 2021), protecting the more than 90 000 species of the boreal forest (Kayes and Mallik 2020). Thus, adding to our understanding of the dynamics of the boreal forest has wide reaching implications for how humans currently interact with and benefit from the boreal forest.

Throughout boreal forests there exists a mosaic of different aged stands created by the cycle of forest clearing disturbances then successional pathways that lead back to a mature forest. Disturbances —such as insect defoliation, forest fires, wind and logging—create gaps in the canopy by killing or removing adult trees (Payette 1992; Engelmark 1999; Reich et al.

2001; Charron and Hermanutz 2016; Boucher et al. 2017; Leroux et al. 2021). Within the newly formed gaps there is an abundance of light and a lack of competition which allows fast growing, early successional species to colonize (Hart and Chen 2006; Franklin and Harper 2016; Bartels et al. 2016). These initial species are subsequently outcompeted by slower growing tree species and eventually the area can regenerate into a mature boreal forest (Archambault et al. 1998; Bartels et al. 2016). At any given point, stands across the landscape may be at different stages in this successional pathway, creating a heterogenous landscape that meets a broad range of habitat needs and ecosystem functions (Pickett et al. 1985; Engelmark 1999; McCarthy and Weetman 2006; Bergeron and Fenton 2012; Rodríguez and Kouki 2017).

1.1. Disturbances in the boreal forest

Unfortunately, the ecosystem services, carbon storage, biodiversity, and natural resources of eastern North American boreal forests (Canadian National Vegetation Classification: Macrogroup M495; Chapman et al. 2020) are at risk because anthropogenic influence has increased the occurrence and severity of disturbances (Fleming and Candau 1998; Connor et al. 2000; Dymond et al. 2010; Leroux et al. 2020). This increased pressure from disturbances is partly a consequence of climate-change and forest management, which has altered the distribution and intensity of key disturbances such as defoliating insects, forest fires, and ungulate herbivory. Spruce budworm outbreaks are now more widespread and severe (Blais 1983; Navarro et al. 2018; Morin et al. 2021), forest fire regimes in North America are exceeding long-term historical rates while being suppressed as frequent, low disturbance events (Gillett et al. 2004; Macias Fauria and Johnson 2008; Nuttle et al. 2013; Kelly et al. 2013), the extent of area affected by windthrow has increased because of more frequent extreme weather events (Emanuel 2005; Webster et al. 2005; Quine and Gardiner

2007; Mitchell 2013), and moose populations in eastern balsam fir forests have become some of the densest in the world (Nosko et al. 2020). It is now understood that these alterations to disturbances can have negative, and sometimes interacting effects on forest ecosystems. For example, they can decrease the amount of carbon stored by boreal forests (Bergeron and Leduc 1998; Dymond et al. 2010; Leroux et al. 2020), alter the identity and diversity of species present (de Grandpre and Bergeron 1997; Connor et al. 2000; Suominen et al. 2008; Mathisen and Skarpe 2011; Norvez et al. 2013; Rae et al. 2014), influence the susceptibility to further disturbances (Blais 1983; James et al. 2011; Boucher et al. 2017; Bysouth et al. 2024), and reduce availability of natural resources and ecosystem services (Thom and Seidl 2016; Pohjanmies et al. 2017; Triviño et al. 2023).

1.1.1. Defoliating insects

The two most predominant defoliating insects in boreal forests of eastern North America are spruce budworm (*Choristoneura fumiferana* Clem.; SBW) and hemlock looper (*Lambdina fiscellaria*; Arsenault et al. 2016; Béland et al. 2022). They are both native to North America, and responsible for vast areas of coniferous tree defoliation and mortality across boreal forests (Natural Resources Canada 2013, 2016). Defoliation occurs when larval stages of either moth feed on coniferous trees, with preference for balsam fir. SBW larvae consume buds and annual shoots during the spring (Miller 1975), and hemlock looper larvae consume the old and young needles later in the season (Natural Resources Canada 2016). Eventually, repeated exposure to high levels of herbivory by high densities of these insects can cause tree mortality (Forest Protection,). High densities of SBW and hemlock looper occur cyclically, and outbreaks causing mass defoliation have been occurring in about 30 years cycles for SBW (Blais 1983; Bouchard et al. 2018), and 7-18 year cycles for hemlock looper (Otvos et al. 1979). The defoliated areas form gaps in the canopy, usually precipitating stand regeneration, and an overall heterogenous age structure within a landscape (Bouchard et al. 2005; Gauthier 2009; MacLean 2016).

Although under historical contexts insect disturbances are important for a healthy ecosystem, they are becoming increasingly widespread and severe (Blais 1983; Navarro et al. 2018; Morin et al. 2021). This is often attributed to forest management practices that increase fir and spruce prevalence, such as fire suppression, monocultures, and pesticides (Blais 1983; Morin et al. 2021). Increased rates of insect disturbances can reduce carbon storage by increasing heterotrophic respiration and decreasing photosynthesis (Dymond et al. 2010; Leroux et al. 2021a). It can also promote different species assemblages, change the age structure of forests and, thus, alter available habitat (Venier and Holmes 2010). Insect disturbances also cause substantial loss of harvestable wood throughout managed boreal forests (Sterner and Davidson 1980; MacLean et al. 2002). One way of reducing the impacts of insect disturbances, is to limit the occurrence of outbreaks. A common strategy, the early intervention strategy (EIS), sprays pesticide on emerging populations to prevent populations from reaching epidemic levels which can cause mass defoliation and tree mortality (Natural Resources Canada 2023a).

1.1.2. Forest fires

Forest fires have and are believed to have always burned throughout the boreal forest, playing an important role in boreal forest dynamics. Fires occurred in natural cycles and were applied by Indigenous people to maintain a variety of ecosystem functions (Christianson et al. 2022). Historically, an area of boreal forest would burn on average once every 100 years (Payette 1992), but this could depend on interacting effects of climatic conditions, species composition, legacy effects of past disturbances, and fuel buildup (Macias Fauria and Johnson 2008; James et al. 2011; Gralewicz et al. 2012; Kelly et al. 2013). These factors can also influence the severity and size of forest fires, leading to variation in remaining biomass and different sized gaps in the canopy (Payette 1992; James et al. 2011; Parisien et al. 2011). The creation of gaps, and subsequent successional stages of vegetation, can lead to a patchy landscape with diverse habitats and ecosystem services. Fires can also be important for the reproduction of some species of tree (Alfaro-Sánchez et al. 2022), and thus may influence the continuation of habitat for other species reliant on such trees.

During the past few centuries, humans have induced changes to fire regimes in the boreal forest, directly through the management of forests and indirectly through climate change (Gillett et al. 2004; Lynch et al. 2004; Macias Fauria and Johnson 2008; Johnstone et al. 2010; James et al. 2011; Kasischke and Stocks 2012; Kelly et al. 2013; Hagmann et al. 2021). Fire suppression and forestry practices have increased the abundance of fuel and more highly flammable coniferous species (James et al. 2011; Hagmann et al. 2021). Furthermore, climatic changes have influenced temperature and precipitation patterns which can govern fire regimes (Lynch et al. 2004; Johnstone et al. 2010; Kelly et al. 2013). Consequently, the average area burned in North America has almost tripled since the mid 1900s (Kasischke and Stocks 2012). This increase in fire regime has caused the boreal forest to release more carbon to the atmosphere through combustion than it absorbs (Zhao et al. 2021). In addition, the increased area burned destroys potential timber resources and removes available habitat for boreal forest species (Natural Resources Canada 2023b). The effect on available habitat by altered fires regimes can then be exacerbated because changes in fire return intervals may hinder the regeneration of species such as black spruce (Lesieur et al. 2002; Johnstone et al. 2010; Baltzer et al. 2021). Unfortunately, these negative implications are expected to escalate as anthropogenic influence further warms the climate (Flannigan et al. 2005; Gralewicz et al. 2012). To mitigate the impacts of a changing climate, management of forests could implement forestry practices that promote a more historically comparable fire regime, such as prescribed burning (Weber and Taylor 1992; Bergeron et al. 2002).

1.1.3. Windthrow

Powerful wind can form gaps throughout forest canopies in what is referred to as "windthrow" (Mitchell 2013). Windthrow occurs at many scales, from events that disturb several stands of trees, to events that affect only small clusters or single trees (Ulanova 2000). While all windthrow depends on the occurrence of high wind speeds, the severity of events can be mediated by biotic and abiotic factors such as stand age, aspect, and past disturbances (Bouchard et al. 2005; Mitchell 2013; Girard et al. 2014). The trees that do get blown down then form important habitat throughout the length of their decomposition, create microtopography and add organic material to the soil (Kuuluvainen and Juntunen 1998; Ulanova 2000; Quine and Gardiner 2007; Mitchell 2013). Soil is also affected by the uprooting of trees during windthrow, as a form of bioturbation (Ulanova 2000; Mitchell 2013). Following windthrow events, gaps created in the canopy reduce competition for resources such as light and nutrients. This reduced competition combined with added bioturbation and microtopography creates optimal microsites for seedling establishment, and subsequent forest regeneration (Mitchell 2013). The pattern of windthrow then regeneration, along with variation is stand susceptibility to wind events, creates a mosaic of stand ages, kinds of habitat, and ecosystem services (Nowacki and Kramer 1998).

Changes to the extent and severity of windthrow under anthropogenic influence are not as clear as for other disturbances. This is partly because of uncertainty in the effects climate change will have on extreme wind events throughout the boreal forest. An increase in severe storms in the North Atlantic ocean has been observed over the last decade (Webster et al. 2005), and is predicted to continue to increase (Colle et al. 2015), potentially increasing windthrow. However, the number of storms in general is expected to decrease (Long et al. 2009; Colle et al. 2015), with similar overall wind speeds predicted (Saad et al. 2017). However, wind speed is just one factor influencing susceptibility to windthrow. The susceptibility of eastern boreal forests to windthrow may increase as soil remains thawed for longer periods of the year because of warming climate (Saad et al. 2017). Although, a warming climate may also alter tree growth patterns, vulnerability to infections, species compositions, etc. It is, therefore, difficult to know how a changing climate might alter windthrow. One way humans have altered forest susceptibility to windthrow is through the creation of gaps (Damschen et al. 2014). Because open areas can increase wind speed at the downwind edge (Zeng et al. 2009; Damschen et al. 2014), wind can be a large cause of gap expansion. With increased expanses of boreal forest being logged (Natural Resources Canada 2023b), burned (Kasischke and Stocks 2012), and defoliated (Blais 1983; Navarro et al. 2018; Morin et al. 2021), gap expansion by wind may be expected to increase.

1.1.4. Logging

Almost two thirds of the boreal forest in Canada is managed by humans, supplying 40% of Canada’s wood supply (Bogdanski 2008; Canada 2013). In the Canadian boreal forest, logging is focused on the harvest of spruce, poplar, pine, and fir, and is done almost entirely through clear cutting (Natural Resources Canada 2023b). This extraction of timber and the industries associated with forestry directly and indirectly employ almost 500 000 people across Canada, and timber resources for building and export, contributed approximately $33 billion to the Canadian Gros Domestic Product in 2022 (Natural Resources Canada 2023b). Additional benefits of forestry can include the long-term storage of carbon in certain wood products, while promoting fast accrual of carbon in young replanted trees after harvest (Smyth et al. 2014; Bysouth et al. 2024). Furthermore, similar to natural disturbances, gaps created in the canopy by logging can precipitate stand regeneration and, thus, promote a more diverse habitat and ecosystem services (Reich et al. 2001). However, current prevalent forestry methods, such as clear cutting, logging old growth forests, and replanting via monocultures instead create even aged stands of single species, more prone to disease and with increased susceptibility to further disturbances and with fewer large intact older forests which are important habitat for boreal species' communities (Blais 1983; Burton et al. 2006; St-Laurent et al. 2009; James et al. 2011; Venier et al. 2014; Boucher et al. 2017; Mackey et al. 2024; Bysouth et al. 2024). The increased prevalence of disturbances caused by logging can also cause a net release of carbon to the atmosphere within the boreal forest (James et al. 2011; Bysouth et al. 2024). As a result, the sustainable management of boreal forests has become a matter of consequence for both boreal forest health and our continued reliance on its services (Berkes and Davidson-Hunt 2006; Burton et al. 2006; Carlson et al. 2015).

1.1.5. Moose

Moose (*Alces alces*) are one of the largest mammals in North America. Their native range stretches across the mainland of North America (Hundertmark et al. 2003), and they have been introduced to the island of Newfoundland (Government of Newfoundland 2015). Across their range, moose can be considered ecosystem engineers because of the cascading impacts of their herbivory, trampling, and excretion (Bryant and Ruess 2006). Through preferential browsing of new growth of deciduous trees and balsam fir, and the large extent and severity of their trampling and excretion, moose can influence species composition, plant stoichiometry, nutrient cycling, and soil physical structure and elemental cycling (Pastor et al. 2006; Ellis and Leroux 2017; Kolstad et al. 2018; Swain et al. 2023). On top of their important ecological influence, they provide cultural significance and food security to people across the boreal forest (McLaren 2011; Government of Newfoundland 2015; Hossain et al. 2018; Ross and Mason 2020; Priadka et al. 2022; Shafiee et al. 2024).

Over the past century moose populations have increased substantially across much of the eastern North American boreal forests because of their introduction to new habitat and/or the extirpation or reduction in predator populations (primarily wolves; McInnes et al. 1992; McLaren et al. 2004; Smith 2007). Abundant, or hyperabundant, populations of moose have allowed for continued managed harvest by both Indigenous and non-Indigenous hunters throughout much of eastern North America (Timmermann and Rodgers 2017). However, extremely high moose densities also have known negative consequences for the ecosystem, such as limiting the regeneration of boreal tree species, decreasing plant species diversity, altering litterfall and soil characteristics, reducing soil fertility, reducing carbon storage, and influencing bird communities and gastropod diversity (Pastor et al. 1993, 2006; Connor et al. 2000; McLaren et al. 2004; Suominen et al. 2008; Mathisen and Skarpe 2011; Ellis and Leroux 2017; Kolstad et al. 2019; De Vriendt et al. 2021; Moran et al. In Review).

1.1.6. Combined effect of moose and forest clearing disturbances

Evidence suggests that high densities of moose can slow or even halt the regeneration of boreal forests after forest clearing disturbances, such as insect defoliation, forest fires, windthrow, or logging (Pastor et al. 1988; Brandner et al. 1990; McInnes et al. 1992; Moen et al. 1998; Pastor et al. 2006, p. 200; Smith 2007; Hidding et al. 2013; Rotter and Rebertus 2015; Parks Canada Agency 2018; Leroux et al. 2021a). When moose are at high densities the fact that they preferentially browse new growth of species that would eventually come to dominate stands of mature boreal forest (e.g., balsam fir, birch; Belovsky 1978; Thompson and Vukelich 1981; Cumming 1987; Hjeljord et al. 1990; Schwartz 1992; Figure 3.1), allows fast-growing, early succession species characteristic of grasslands or shrublands to persist for longer than anticipated (e.g., kalmia; Mallik 2003; Royo and Carson 2006; De Vriendt et al. 2021). The growth of new trees is further hindered by the poor seedbed often created by shrubland and grassland species (Mallik 2003; Gosse et al. 2011; Charron and Hermanutz 2016), while moose prevent trees from reaching a mature enough state to add to the seed bank (Gosse et al. 2011; Charron and Hermanutz 2016). In extreme cases, moose can hinder the regeneration of boreal forest tree species to such an extent that the forest continues indefinitely as a grassland or shrubland (Brandner et al. 1990; Smith et al. 2010; Hidding et al. 2013; Rotter and Rebertus 2015; Parks Canada Agency 2018; Leroux et al. 2021a). This can be seen in areas of Isle Royale, US (Brandner et al. 1990; McInnes et al. 1992; Rotter and Rebertus 2015), Cape Breton, CA (Smith et al. 2010; Parks Canada Agency 2018), and Newfoundland, CA (Charron and Hermanutz 2016; Leroux et al. 2021a).

Delayed or halted succession after forest clearing disturbances as a result of high moose herbivory can then have many impacts on the remainder of the ecosystem. The changes in succession have implications for biodiversity; significantly lowering plant (Connor et al. 2000) and spider diversities (Suominen et al. 2008), and altering songbird assemblages (Rae et al. 2014). Areas with high moose herbivory following insect defoliation and forest fires had significantly less carbon than mature boreal forests, 25 years after the disturbances (Petersen et al. 2023; Moran et al. In Review). The effect of gap forming disturbances alone (decreased photosynthesis and increased combustion or heterotrophic respiration) can create an intial decrease in carbon uptake or even cause a net release of carbon into the atmosphere (Kurz et al. 2008; Dymond et al. 2010; Liu et al. 2019; Quirion et al. 2021). The subsequent delayed or halted regeneration of aboveground biomass resulting from moose herbivory may then limit the capacity of forest stands to be a carbon sink (Ellis and Leroux 2017; Kolstad et al. 2018; Petersen et al. 2023; Swain et al. 2023). However, the effects of combined disturbance aboveground may not cascade below ground to affect soil properties (Swain et al. 2023). Furthermore, the delay in succession results in longer cut intervals for logging and reduce wood quality (Edenius et al. 2002). Consequently, many have promoted the mitigation of such impacts through a decrease in moose populations via hunting (McLaren and Mercer 2005; Gosse et al. 2011; Rae et al. 2014; Government of Newfoundland 2015).

1.1.7. Management of disturbances in the boreal forest

Disturbances throughout eastern North American boreal forests are managed for many reasons, often in order to maintain the ecosystem services outlined in the first paragraph. Therefore, depending on the goal, management actions may vary. Gap forming disturbances may be limited (e.g., via early intervention strategy for spruce budworm, or fire reduction strategies) to protect timber volume for harvest, maintain carbon stocks in large mature trees, or protect the habitat of species reliant on mature forests (Kurz et al. 2013; MacLean et al. 2019). However, forest management could also prioritize gap forming disturbances to promote landscape heterogeneity and biodiversity, ecological integrity, decrease albedo, encourage carbon sequestration during the pulse of new growth after disturbances, or protect habitat of species reliant on disturbed areas. Similarly, when contemplating the management of moose populations in eastern North American boreal forests, management must balance the impacts of moose hyperabundance, with food security of human populations. Consequently, when making decisions concerning management of disturbances, it is important to quantify the negative impacts of disturbances across the landscape so they may be considered against the benefits. Furthermore, we must take into consideration that some effects of gap forming disturbances across the landscape may result from their interaction with other disturbances, such as herbivory.

1.2. Thesis overview

In this thesis we use the combination of an empirical study and a mathematical model to examine how aspects of eastern North American boreal forests respond to combined disturbances. The specific aspects we study are the spatial responses of carbon storage to gap forming disturbances (i.e., insect defoliation, forest fires, windthrow, and logging), and forest regeneration after gap forming disturbances, all under the influence of hyperabundant moose densities.

My thesis is an example of how the integration of empirical and modeling approaches can shed light on ecological questions (Connolly et al. 2017; Laubmeier et al. 2020; Schlüter et al. 2023). For example, we used my empirical study (Chapter 2) to select realistic parameter estimates for my mathematical model (Chapter 3) which helped to ensure model assumptions reflect empirical patterns. Meanwhile, the use of a mathematical model in accompaniment to an empirical study helps broaden the range of scenarios examined, as empirical data are limited to the scenarios accessible during data collection. The mathematical model also allows us to examine the influence of specific biological processes that may shed light on the correlative relationships found in the empirical study. In all, by approaching this topic empirically and mathematically, we are able to compare and contrast results to provide more robust insights on how eastern North American boreal forest respond to combined disturbances.

In Chapter 2: “Predicting carbon storage across maritime boreal forests under combined disturbances”, we add to our understanding of how disturbances are impacting carbon across a boreal landscape. To accomplish this, we used a combination of data collected in field and by remote sensing to predict the spatial patterns in carbon stocks as well as where gaps have been created by disturbances across each study area. We hypothesized both carbon storage, and the probability an area is a mature forest or disturbed gap, would be related to similar remotely sensed variables describing vegetation. To further inform how disturbances are influencing carbon storage across the landscape, we assessed the relative impacts of disturbed gaps and subsequent moose herbivory on carbon stocks. We hypothesized gaps with subsequent browsing by moose would have a larger negative effect on carbon than gaps without moose herbivory, when compared to mature forests. The relative impact of combined disturbances compared to mature forests then allowed us to estimate the potential total impacts of these disturbances on carbon storage across the study areas. This work fills gaps in our understanding of factors influencing carbon storage, including gap forming disturbances, and can help us inform nature-based climate solutions.

In Chapter 3: “Modelling the mechanisms of regime shifts in eastern boreal forests”, we explored the relative impact of various drivers leading to alternate regimes in eastern North American boreal forests. Specifically, we examined the thresholds that govern whether the boreal forest regenerates or becomes a grassland following a forest clearing disturbance through the derivation of a mathematical model. Through simulations, we tested our hypotheses that the thresholds dividing possible end conditions of the system may be influenced by aspects of moose herbivory, growth of vegetation, and competition between forms of vegetation. These models may help resolve the drivers of regime shifts in this system, as well as variable experimental findings of the impact of moose on boreal forest regeneration. With an increased understanding of what governs successful boreal forest regeneration under moose herbivory, we can help inform the management of disturbances and moose populations.

The final chapter, chapter 4, explores ways the empirical work of chapter 2 and the mathematical model of chapter 3 can be integrated to better understand how eastern North American boreal forests respond to combined disturbances. We also outline how management can be informed by this integration.

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Chapter 2. Predicting carbon storage in maritime boreal forests under combined disturbances

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Key words: boreal forest, carbon, disturbances, herbivory, landscape, remote sensing

2.1. Abstract

Understanding how forest disturbances, such as fire and herbivory, affect carbon storage across the landscape can help inform forest management and disturbance mitigation. However, this is made difficult by uncertainties in carbon predictions and limited records of disturbance histories. Our objectives were to predict carbon stocks and predict where gaps have been formed by disturbances across the study areas, and to assess the relative effects of disturbances and subsequent moose herbivory on carbon stocks. We used field measurements of carbon stocks (e.g., live above-ground plant carbon stocks, organic soil carbon stocks) and disturbances (gap or mature forest) from a two-year field study on the island of Newfoundland, Canada, along with remotely sensed environmental variables (e.g., forest height, elevation), to predict spatial patterns in carbon stocks as well as predict where gaps formed by disturbances may exist across each study area. We found that the remotely sensed variables of forest height and productivity were the most informative predictor variables for both carbon stocks and whether an area was a disturbed gap. Our models predict less carbon in areas classified as gaps, and more carbon in areas classified as mature forest. Further, we observed that moose herbivory may impede the recovery of carbon stocks in gaps after disturbances, leading to a reduction in carbon storage of up to 13 megatonnes. Overall, we find there is potential to increase or maintain carbon storage in maritime boreal forests by limiting moose herbivory in areas regenerating following disturbance. This work adds to our understanding of drivers of forest carbon storage and can help inform nature-based climate solutions.

2.2. Introduction

As climate change poses an ever-growing threat across the globe, solutions are being sought to mitigate the increases in atmospheric carbon dioxide contributing to global warming. These can include advancing carbon capture technologies, reducing society's use of fossil fuels, and working to maintain current carbon storage and promote further sequestration through nature-based climate solutions. Nature-based climate solutions are well suited for implementation in the boreal forest, as this biome has already been identified as a major carbon sink. This includes large amounts of carbon in above ground biomass, as well as large stable stocks of below ground organic matter rich in carbon (Bradshaw et al. 2009; Sothe et al. 2022). However, anthropogenic influence (e.g., forest management, alteration to key disturbance regimes) can both positively or negatively impact the ability of boreal forest ecosystems to store carbon (Bradshaw et al. 2009; Kurz et al. 2013; Bysouth et al. 2024).

Under historic regimes, forest disturbances have been important drivers of forest renewal and maintenance of biodiversity (Pickett et al. 1985; Engelmark 1999b; McCarthy and Weetman 2006; Bergeron and Fenton 2012; Rodríguez and Kouki 2017). However, during the Anthropocene, boreal forests have come under increased pressure from disturbances (Dymond et al. 2010; Leroux et al. 2020). This has resulted from such factors as changing climate, forest management, and the introduction of new species. For example, warming temperatures facilitated the range expansion of mountain pine beetles across the northern Rocky Mountains into the taiga cordillera boreal ecozone (Carroll et al. 2006; Cullingham et al. 2011; de la Giroday et al. 2012). Additionally, widespread fire suppression in post-colonial North America has led to increased wildfire severity (Hagmann et al. 2021). Other human-influenced alterations to disturbance regimes include more widespread and severe spruce budworm outbreaks (Blais 1983; Navarro et al. 2018; Morin et al. 2021); increased forest fire activity in North America (Nuttle et al. 2013; Kelly et al. 2013; Hagmann et al. 2021); increased windthrow due to more frequent extreme weather events (Emanuel 2005; Webster et al. 2005; Quine and Gardiner 2007; Mitchell 2013); and the expansion of ungulate populations in North American forests (Rooney 2001; McLaren et al. 2004; Gosse et al. 2011). These changes in disturbance regimes can have interacting consequences, reducing the amount of carbon stored by boreal forests (Bergeron and Leduc 1998; Dymond et al. 2010; Leroux et al. 2020; Moran et al. In Review). However, the extent and spatial distribution of the effects of disturbances on carbon can be difficult to quantify because of inconsistences between carbon field measurements and carbon predictions made across broad regions (Bradshaw and Warkentin 2015; Ballantyne et al. 2021), as well as the lack of robust records of disturbance histories for many areas (Williams et al. 2016).

Disturbances affect carbon storage in the boreal forest by altering carbon stocks and fluxes. Insect defoliation, forest fires, wind blowdown and logging create gaps in the forest, reducing live biomass and, therefore, initially decreasing photosynthesis and carbon sequestration (Gross 1992; Houghton 1996; Malhi et al. 1999; Balshi et al. 2009; Dobor et al. 2018). Disturbances can also increase the rate at which carbon is released to the atmosphere, through combustion in the case of forest fires (Conard and A. Ivanova 1997; Balshi et al. 2007, 2009), and by increasing heterotrophic respiration in the soil in the case of insect defoliation and windthrow (Dobor et al. 2018; Liu et al. 2019). The net effect of decreased photosynthesis and increased combustion or heterotrophic respiration is a decrease in carbon uptake or even a net release of carbon into the atmosphere (Kurz et al. 2008; Dymond et al. 2010; Liu et al. 2019; Quirion et al. 2021). Logging may further decrease carbon storage by increasing susceptibility of the boreal forest to insect outbreaks, forest fires and windthrow (Blais 1983; Boucher et al. 2017; Bysouth et al. 2024).

Large herbivores, such as white-tailed deer (Hidding et al. 2013; Nuttle et al. 2013) and moose (Speed et al. 2013; De Vriendt et al. 2021; Petersen et al. 2023) can interact with gap forming disturbances to impact the regeneration of forests. In the boreal forest, when moose are present in gaps formed by disturbances, they can preferentially browse new growth of trees and shrubs to such an extent that it impedes forest regeneration, limiting biomass and carbon storage (Schmitz et al. 2014; Leroux et al. 2020, 2021b; Petersen et al. 2023). Areas affected by a gap forming disturbance and subsequent moose herbivory have significantly less carbon than mature boreal forest (Moran et al. In Review).

Although we know disturbances can decrease carbon storage in forests, we do not currently have a way of predicting the consequences of this across the broader landscape. This is partly because we do not have accurate predictions of carbon storage at the spatial resolution at which gaps are formed by disturbances (Hall et al. 2016; Senf et al. 2017; Ballantyne et al. 2021). The difference between carbon estimates from individual global carbon budget models and field measurements can be large (Piao et al. 2013; Bradshaw and Warkentin 2015; Kalliokoski et al. 2018; Ťupek et al. 2019), possibly exceeding an order of magnitude (Bradshaw and Warkentin 2015; Ballantyne et al. 2021). There is especially high uncertainty in carbon storage estimates across the latitudes that span the boreal forest, in part because of limited coverage of the boreal zone by applicable forest inventories (Piao et al. 2013; Schimel et al. 2015). While remote sensing allows for more extensive assessment, the lack of adequate, local, *in situ* measurements of forest characteristics prohibits proper calibration and validation of remote sensing models against regional allometries, limiting the accuracy of their carbon storage estimates (Schimel et al. 2015). Additionally, the highest resolution available for aboveground and belowground carbon storage estimates across Canada is 250 m by 250 m (6.25 ha; Sothe et al. 2022), whereas gaps can occur at a scale of tens of metres (Charron and Hermanutz 2016; Quirion et al. 2021). There are estimates of carbon at 30 m resolutions for the National Parks of Canada (Sharma et al. 2023), however, these are only for forested areas and, therefore, exclude many gaps. There is, therefore, a need to measure and predict carbon storage across boreal landscapes using models of intermediate complexity, with finer resolutions, and that combine remote sensing with *in situ* data (see Heckford et al. 2022 for an example of in situ modelling, but only of foliar carbon). This approach can help inform management at the scale at which disturbances occur, and at which management is implemented (e.g., across municipalities, forest management areas, or national parks).

Previous research provides insights on which remote sensing variables may be related to forest carbon and disturbances. Trees are a large component of aboveground carbon storage in the boreal forest, and differ considerably between mature forest and gaps (Bergeron and Fenton 2012; Kurz et al. 2013; Charron and Hermanutz 2016; Sánchez-Pinillos et al. 2019); trees are abundant, large, and old in mature forests whereas forbs, shrubs, grasses, and small, young trees are common in gaps. Thus, characteristics such as forest height, canopy cover, and stand age can be used to help measure biomass, and therefore, carbon (Lefsky et al. 2005; Saatchi et al. 2011; Wu et al. 2015; Sothe et al. 2022). Vegetation indices, which are measures of how green the vegetation is throughout the year, can help delineate areas dominated by different vegetation types (e.g., coniferous forest, deciduous forest, shrubland, grassland; Clerici et al., 2012; DeFries et al., 1995; Guzinski, 2010; Na-U-Dom et al., 2017) and can help infer the productivity of an area (Li et al. 2007; Huang et al. 2019). Consequently, remotely-sensed vegetation indices have been used to estimate aboveground biomass and carbon storage in many forest ecosystems (Dong et al. 2003; González-Alonso et al. 2006; Blackard et al. 2008; Yuan et al. 2016). Topography may also play a role in carbon storage and affect the development of gaps. For example, slope, elevation, and aspect can influence dominant vegetation types (Zinko 2004; Zhao et al. 2014), vegetation productivity and growth (Boucher et al. 2006; Mao et al. 2019), rates of cycling (Kobler et al. 2019), and horizontal movement of elements (Shen et al. 2011).

Topography can also influence gap formation or continuation by determining exposure to extreme weather conditions (Kramer et al. 2001; Ruel et al. 2002; Mitchell 2013) and because it can influence habitat use by ungulates (McLaren and Mercer 2005; Poole and Stuart-Smith 2006; Jung et al. 2018; Milne-Rostkowska et al. 2020) influencing the vegetation's exposure to herbivory.

Our goal was to assess the influence of forest disturbances on carbon across a boreal landscape. Specifically, our objectives were to use remote sensed data and in situ measurements to (i) predict carbon stored across the landscape (Figure 2.1); (ii) to predict the distribution of gaps formed by disturbances; and (iii) to assess the relative impacts of disturbances and subsequent moose herbivory on carbon stocks. Taken together, this allows us to quantify the total potential impacts of combined disturbances on the carbon stocks of these boreal forests.

Trees are a major component of boreal forest carbon storage (Bradshaw et al. 2009; Kurz et al. 2013) and measures of forest biomass and productivity can relate to tree size and abundance (Lefsky et al. 2005; Saatchi et al. 2011; Wu et al. 2015; Sothe et al. 2022). Consequently, we hypothesize that the main spatial determinates of total carbon storage (objective i) will be measures of forest biomass and productivity (Santoro et al. 2018; Sothe et al. 2022; Currie et al. 2023). We also hypothesize that whether a stand is mature forest or a gap (objective ii) will be related to measures of forest biomass and productivity because these can help differentiate betweeen the vegetation types present in mature forest and gaps (Hall et al. 2016; Senf et al. 2017; Santoro et al. 2018). We also expect that because moose preferentially browse the tree species common to Newfoundland boreal forests, as opposed to grasses and forbs, and can delay or disrupt regeneration of tree biomass (Hjeljord et al. 1990; Schwartz 1992; Arsenault et al. 2016; Leroux et al. 2021b; Petersen et al. 2023), gaps exposed to browsing by moose will have less carbon than gaps that are free from moose herbivory, relative to mature forest.

2.3. Methods

Our three objectives (Figure 2.1) rely on common data sources, with analyses outlined in Figure 2.2. For objective i, we model the relationship between the carbon measured at our field plots and a suite of remote sensed predictor variables, for each study area. For objective ii, we model stand condition (mature forest or gap), identified at the same field sites as carbon, as it relates to the same remote sensed predictor variables, for each study area. We then projected the top resulting models for objective i and ii across the landscape to predict carbon stocks and mature forest/gap across the study areas. Additionally, to address objective iii, we assessed the differences between carbon measured at a subset of our field plots in mature forests and plots in gaps with and without moose herbivory. Finally, we combine these results to quantify the potential impacts of combined disturbances on carbon storage across the two parks. We conducted spatial data preparation in QGIS version 3.36.1-Maidenhead (QGIS Development Team 2024), and statistical analyses in R Version 2024.04.2+764 (R Core Team 2023).

2.3.1. Study areas

We conducted our study in the two national parks on the island of Newfoundland, Canada; Terra Nova National Park and Gros Morne National Park. Within the parks, more than 50% of the terrestrial landscape is classified as boreal forest (Baldwin et al., 2020), dominated by balsam fir and black spruce stands with fewer mixedwood and deciduous stands (Forest Inventory Program, 2022). In both parks the most prevalent disturbance is insect defoliation (Arsenault et al. 2016). Additionally, both parks have areas of windthrow due to high winds, Terra Nova National Park is occasionally affected by forest fires (Arsenault et al. 2016), and Gros Morne National Park permits domestic wood harvesting (Legislative Services Branch 2009). On top of these gap forming disturbances, both parks had hyperabundant moose populations (McLaren et al. 2004). Because of the impact of moose on the park ecosystems (Gosse et al. 2011), the parks have permitted hunting of moose beginning in 2011, and moose are now managed at densities approximating those on the surrounding landscape (Parks Canada 2019, 2021).

2.3.2. Carbon and disturbance field data collection

2.3.2.1. Site selection

We measured carbon stocks, and recorded stand condition (mature forest or gap) at 92 plots in Gros Morne and Terra Nova National Parks on the island of Newfoundland, Canada, during the summers of 2022 (n = 40) and 2023 (n = 52; Appendix 2.1; Table S2.1). We selected plot locations to capture the ranges of environmental predictor variables across the landscape (Appendix 2.1.; Table S2.1). These included forest gaps that resulted from insect defoliation, forest fires, windthrow and domestic wood harvesting, as well as mature forest stands, and spanned a range of moose densities. We also sampled 10 plots in long-term moose exclosures (i.e., fences that exclude moose;), which had been erected 24-27 years prior to our data collection. These exlosures measured 35 m x 35 m in Terra Nova National Park and 15 m x15 m in Gros Morne National Park. These exclosure plots were not included in the analysis for objectives i. and ii., but were required for the analysis for objective iii. Most of our sites were accessed on foot, so were located within 1500 m of a road or trail given the rough terrain. However 10 of the more remote sites were accessed by boat or helicopter.

2.3.2.2. Stand condition

Stand condition (i.e., mature forest or gap) was assessed as a three step approach. First, before going in the field stand condition was assessed visually via Google Earth satellite imagery and considered mature if the area looked predominantly dark green with large trees present, and considered an area with previous disturbance (i.e., a gap) if the area was a patch of lighter geen or grey and lacked large, live (green) trees (Appendix 2.1.; Table S2.2). However, lighter green areas could also be wetlands, or other forms of land that are unlikely to ever be or have been forested. We, therefore, consulted with park staff at each national park to confirm whether they believe our visual classifications of stand conditions and disturbance history were accurate.

2.3.2.3. Site layout

Each plot measured 13 m (East – West) by 15 m (North – South) and included four subplots (Appendix 2.1.; Figure S2.1). We chose the location of the southwest corner so that the entire plot, and therefore, all four subplots, fell within the forest stand of interest (mature or gap). Subplots consisted of one 3 m x 3 m large quadrat (B) with a 0.5 m x 0.5 m small quadrat in each corner (C & D). In 2022 we sampled one 1 m x 5 m transect (A), while in 2023 we sampled a second parallel 1 m x 5 m transect (Aa, Ab) (Appendix 2.1.).

2.3.2.4. Live vegetation > 0.3 m tall

In each 1 m x 5 m transect, we measured the height (metres; using a metre stick) and recorded the species of all live trees and woody shrubs less than 0.3 m tall. For trees and woody shrubs between 0.3 m and 3 m tall we also measured the basal diameter (centimetres; using callipers) and orthogonal diameters (diameters at widest part measured perpandicular to each other; centimetres; using a measuring tape). For trees taller than 3 m we measured the diameter at breast height (centimetres; using DBH tape).

2.3.2.5. Live vegetation < 0.3 m tall

In all four 0.5 m x 0.5 m small quadrats of each subplot, we measured the height (centimetres; using a measuring tape), basal diameter (centimetres; using callipers), and orthogonal diameters (centimetres; using callipers), and recorded the species of each tree or woody shrub under 0.3 m tall. We also recorded the percent cover of forbs, grasses, ferns, brambles (annual vegetation with thorns), lichens, mosses, bare dirt, bare rock, leaf litter, and needles. Total percent cover could exceed 100%.

2.3.2.6. Deadwood

In each 3 m x 3 m large quadrat, we measured the length (centimetres; using a measuring tape) and orthogonal diameters (centimetres; using callipers) of dead trees with a diameter of at least 0.1 m. Following the methods of Richardson *et al.* (2009) our measurements did not include parts of a dead tree that tapered to less than 10 cm or exited the large quadrat. We also recorded whether the dead tree was softwood or hardwood, the class of deadwood following the level of decay classifications of Harmon *et al.* (2011), and whether it was standing, fallen, or a stump.

2.3.2.7. Allometric equations

We used allometric equations to calculate biomass estimates from the in-field measurements of live vegetation and deadwood (Appendix 2.2.; Table S2.3). Following standard procedures (e.g., Coomes *et al.* (2002) and Latte *et al.* (2013)) we assumed that the calculated live and dead biomass stocks were 50% carbon. We used aboveground biomass of live vegetation and the equations laid out by Li *et al.* (2003) and Coomes *et al.* (2002), to calculate carbon stocks for roots of live vegetation above 0.3 m, and less than 0.3 m, respectively.

2.3.2.8. Organic soil carbon

In each of the two westernmost small quadrats of each subplot, we took two soil samples. One sample was taken from the southwest corner of the quadrat, and one was taken from the northwest corner. We sampled the soil using a brass cylinder (0.15 m long and 0.02 m in diameter) which we drove into the ground and pulled out to extract a soil core. We removed the soil from the cylinder by pushing with the handle of a mallet. An abrupt change in colour and texture characterized the boundary between organic and inorganic soil. However, if we did not reach inorganic soil with one core, we repeated the process until we found the boundary. We recorded the depth of the organic soil layer (centimetres; using a measuring tape; Soil Classification Working Group, 1998) from the cores and stored the organic soil layer in a plastic bag and froze the samples at -20˚ C until processing.

We used the dry weight and percent carbon of soil samples to calculate the organic soil carbon stock. For this, we first dried each soil sample to constant weight in an oven at 60˚ C and then combined them by subplot and ground them. We used a Retsch GM 300 Grinder to grind and homogenize the 2022 soil and an OMNI International Bead Mill Homogenizer to grind and homogenize the 2023 soil samples. Next, we sent the ground samples to the Agriculture and Food Laboratory at the University of Guelph to determine percent carbon using a combustion method. Finally, we calculated the amount of carbon in each soil sample by multiplying dry weight by percent carbon. Of our 736 soil samples, 10 from 2023 were burnt in the drying process and were therefore unusable; reparations to obtain substitute values are outlined in Appendix 2.3.

2.3.2.9. Leaf litter carbon

We gathered all leaf litter in the small southwest quadrats and froze the samples at -20˚ C until further processing. We used the dry weight and percent carbon of these leaf litter samples to calculate carbon content. First, we dried each leaf litter sample in a 60˚ C oven until constant weight (dry weight). We then ground and homogenized the 2022 leaf litter samples with a Retsch GM 300 bead mill grinder. We sent the ground samples to the Agriculture and Food Laboratory at the University of Guelph to determine percent carbon using a combustion method. Because there was relatively little variation in carbon content of leaf litter between samples in 2022, instead of grinding and sending away the 2023 leaf litter samples, we used the percent carbon results from 2022, split by national park and disturbance type, to estimate percent carbon content of litter samples from 2023 (Appendix 2.3.; Table S2.4). We then calculated the amount of carbon in each leaf litter sample by multiplying the dry weight by percent carbon.

2.3.2.10. Total carbon

At each subplot, we converted measurements of carbon to grams of carbon per m^2 and summed to estimate total mass of carbon per square meter in each subplot. We then calculated the mean total grams of carbon per square meter across the four subplots from each plot, as our response variable for carbon stock models.

2.3.3. Predictor variables data collection

We compiled remote sensed data and aerial moose survey data that, based on recent research (see introduction), may affect carbon storage or mediate the effect of disturbance on carbon storage (see Table 2.1 for full list of candidate predictor variables). We searched for datasets in the Open Government Portal, Earthdata, and the datasets sent to us by Parks

Canada that had a spatial coverage that included the national parks in Newfoundland, had a similar spatial resolution (~ 25-30 m), and were of adequate quality (e.g., minimal cloud cover, Table 2.1). Relative categorical classifications of moose density data were obtained from Parks Canada and were collected via aerial winter surveys using a stratified random block design in 2015 (Gasaway et al. 1986; Parks Canada 2019, 2021). We did not include disturbance presence or absence, or type as a predictor variable in the models of carbon storage because of inadequate spatial data on disturbance history across much of the unsampled areas of the park. We projected all datasets to EPSG: 26921 – NAD83/UTM zone 21N and resampled (i.e., upscaled finer resolution data and rasterized vector data; see Appendix 2.4. for details on alterations to specific datasets) to 30 m georeferenced units using nearest neighbour resampling. We then aligned the rasters to the same georeferenced extent that encompassed both national parks and all sampling sites with the warp function in QGIS. We also created a subset of each dataset encompassing only each national park individually, using clip to mask. To retrieve data at each sample site, we overlaid the centroid location of the four subplot geographic coordinates for each site, and used the point sampling tool to extract the values from each raster at that location (Appendix 2.4; Table S2.5).

2.3.4. Statistical Models

2.3.4.1. Variable reduction

We assessed collinearity between candidate predictor variables based on pairwise complete observations for each complete data source, using *stats* package version 4.3.2 (R Core Team 2023) and *PerformanceAnalytics* package version 2.0.4 (Peterson and Carl 2020). We assessed collinearity across the values of predictor variables at each site for both national parks combined, and for each national park individually (Appendix 2.5.; Table S2.6). We removed one variable in any pair having a Pearson correlation coefficient >0.7 (Dormann et al. 2013) in the analyses of the combined or individual national parks. Of any two colinear variables, we retained the variable of higher quality (i.e., less missing data or cloud cover) or the variable that was continuous rather than categorical (Appendix 2.4.).

We further reduced the number of variables considered for developing our full model to reduce bias and increase precision of parameter estimates (Peduzzi et al. 1996; Vittinghoff and McCulloch 2007). The maximum number of variables we considered in each model was eight, so we dropped two categorical variables: land type classification and dominant tree type. However, we kept moose densities because, although it was also categorical, it was our only predictor variable pertaining to moose and we wanted to retain this variable in our analyses. Our final reduced set of variables included: forest height, enhanced vegetation index yearly median, enhanced vegetation index yearly amplitude, number of green days, slope, elevation, aspect, and moose densities (Table 2.1). These variables were then scaled for each national park, without centering, using the scale function in R.

2.3.4.2. Carbon stock model

To assess the relationship between carbon storage and remote sensed predictor variables (objective i), we developed a suite of generalized linear models with gamma error distributions and log link functions for each national park (i.e., Terra Nova National Park and Gros Morne National Park). The national parks were assessed separately because of differences in dominant tree species, disturbance histories, and moose densities. However, we observed similar results when we analyzed the national parks together (see Appendix 2.6.; Table S2.7). Our response variable was mean total carbon stocks measured at our field sites, excluding sites in moose exclosures, and the predictor variables were as outlined above (Table 2.1). All models were created using the glm function in *lme4* package version 1.1-35.4 (Bates et al. 2015). For both national parks, the suite of models included a null model (i.e., intercept-only model), a full model (i.e. global model), and a set of reduced models including univariate models for each variable (Appendix 2.7.; Table S2.8). We created an initial reduced model using the step function in *stats* package version 4.3.2 (R Core Team 2023), then simpler reduced models by removing one variable at a time to create all possible combinations of variables within the reduced model created by step function.

Our model selection involved two steps. First, we used Akaike's information criterion corrected for small sample sizes (AICc) to select a set of top models. In this set we included models with a ΔAICc lower than 4, and which ranked above the null model. We used the aictab function from the *AICcmodavg* package version 2.3-3 (Mazerolle 2020) to calculate ΔAICc and rank models. Next, we used k-fold cross validation to select the model with the smallest AICc that validated most often. Our k-fold cross validation consisted of k set at 9 (TNNP) and 10 (GMNP); so that all groups were of approximately equal size for either national park, as required by the cv.glm function in the *boot* package version 1.3-28.1 (Davidson and Hinkley 1997; Canty and Ripley 2020) that was used for cross validation. Detailed instructions of our cross-validation procedure are available in Appendix 2.8.

2.3.4.3. Gap or mature model

To assess the relationship between mature forest/gap and the selected remote sensed predictor variables (objective ii, Table 2.1), we developed a suite of generalized linear models with binomial error distributions (gap = 0, mature = 1) and logit link functions, for each national park independently. We created all models using the glm function in the *brglm2* package version 0.9.2 (Kosmidis 2023) and fit using Firth's bias reduction. Creation of potential models, model reduction, and model selection followed the approach outlined for the carbon stock models above.

2.3.4.4. Spatial model area

For each national park, we delineated the area for prediction using carbon stock models and mature forest/gap models based on ecoregions, human use, and the sampled range of values of predictor variables. Specifically, any waterbodies, un-treed areas (i.e., Long Range Mountains Ecoregion and wetlands in GMNP; identified based on the park's geospatial landcover database), roads, and areas developed by humans (as identified based on the park's geospatial landcover database) were excluded from the prediction space because we had no inference for these areas. Finally, we removed areas where the value of predictor variables (from top models for carbon or mature forest/gap) was outside the range of values observed at locations we sampled (Table 2.1). As a result, we could predict across 266 km^2 (72%) of the 368 km^2 of land in Terra Nova and 762 km^2 (42%) of the 1805 km^2 of land in Gros Morne.

2.3.4.5. Predictions

We used the predict function in the *terra* package version 1.7-55 (Hijmans et al. 2021) to predict total carbon stock and probability that an area is mature forest across our predictable space (see above) in each national park. We also calculated the standard errors of the 95% confidence intervals and 95% prediction intervals across the national parks (Appendix 2.9.). We then used the standard errors to calculate 95% confidence intervals and 95% prediction intervals, respectively.

2.3.5. Effect of combined disturbances on carbon

We compared carbon stocks in sites with different disturbance histories across the two national parks (objective iii). Because of the limited number of exclosures in each national park, we combined the data from the two national parks. We used ANOVA and Tukey's test of honest significant difference to test whether there were differences in average total carbon stocks between plots in mature forest (n = 30, had no recent disturbances), in gaps formed by disturbances that had subsequent moose herbivory (n = 53), and in gaps formed by disturbances that did not have moose herbivory (n = 10, moose exclosures). The sites in gaps were not statistically different in their age in years ($p > 0.8$; Appendix 2.1). We conducted our ANOVAs using aov and anova functions, and the Tukey test was conducted using TukeyHSD function, all in the *stats* package version 4.3.2 (R Core Team 2023).

2.3.6. Total impact on carbon storage of combined disturbances

We calculated the total potential carbon stocks lost across each national park as a consequence of moose herbivory in disturbed areas. First, we took the mean difference between total carbon densities in sites in mature boreal forest and sites in gaps formed by disturbances that had subsequent moose herbivory, from the above Tukeys' test of honest significance. We then multiplied this by the area predicted to be over 50% likely to be a gap from objective ii.

2.4. Results

2.4.1. Carbon

2.4.1.1. Total carbon stock

In Terra Nova National Park, we measured an overall average of 19 600 g/m^2 of total carbon stock per site. In gaps sites there was an average 9300 g/m^2, with a range of 1 350 g/m^2 to 49 200 g/m^2. And, at mature sites there was an average 39 400 g/m^2 of total carbon stock per site, with a range of 9200 g/m^2 to 210 000 g/m^2. In Gros Morne National Park, we measured an overall average of 15 300 g/m^2 of total carbon stock per site. In gaps sites there was an average 6500 g/m^2, with a range of 1 970 g/m^2 to 15 800 g/m^2. And, at mature sites there was an average 28 000 g/m^2 of total carbon stock per site, with a range of 9200 g/m^2 to 150 000 g/m^2. We found living biomass contributed the most to measured carbon stocks (Table 2.2).

2.4.1.2. Top models of total carbon stock

The top model for total carbon stock in Terra Nova National Park was the same as the top model for total carbon stock in Gros Morne National Park, and included environmental variables describing forest characteristics (Table 2.3). In Terra Nova National Park, the model that validated most often for total carbon stock included forest height and Enhanced vegetation index yearly amplitude (EVIamp; $R^2 = 0.42$;). The model that validated the next most often included only forest height (Table 2.3). In Gros Morne National Park, the model that validated most often for total carbon stock also included forest height and EVIamp ($R^2 = 0.51$; Table 2.3). The only other competing candidate model to validate for total carbon stock in Gros Morne National Park included forest height (ΔAICc = 0.9; $R^2 = 0.48$; Table 2.3). In both national parks (Figure 2.3), we observed that total carbon stock was positively related to forest height (beta$_{\text{forestheight}}$_TN$_C$ = 1.2, SE$_{\text{forestheight}}$_TN$_C$ = ±0.4, beta$_{\text{forestheight}}$_GM$_C$ =0.89, SE$_{\text{forestheight}}$_GM$_C$ = ±0.22) and negatively related to EVIamp (beta$_{\text{EVIamp}}$_TN$_C$ = -0.25, SE$_{\text{EVIamp}}$_TN$_C$ = ± 0.46, beta$_{\text{EVIamp}}$_GM$_C$ = -0.56, SE$_{\text{EVIamp}}$_GM$_C$ = ±0.43).

2.4.1.3. Predictions of total carbon stock across national parks

Our carbon predictions were created using the top model of total carbon stock for each national park, both of which included forest height and EVIamp. In Terra Nova National Park we predicted that a total of 4740 billion g (4.74 megatonnes) of carbon stored in forests across the national park and that carbon stocks ranged from 4 720 g/m^2 to 62 700 g/m^2, with an average of 17 800 g/m^2 (Figure 2.4. A & C). In Gros Morne National Park we predicted a total of 12 000 billion g (12 megatonnes) of carbon stored across the national park and that carbon stocks ranged from 3 780 g/m^2 to 70 400 g/m^2, with an average of 15 800 g/m^2 (Figure 2.4. A & C).

2.4.1.4. Errors in predictions:

In Terra Nova National Park, the standard errors of the 95% confidence interval for individual cells ranged from 0.22 to 0.66 and the residual standard error was 1.31 (Appendix 2.9.; Figure S2.2). This corresponds to an lower 95% confidence interval that spanned 1660 g/m^2 to 23 000 g/m^2 and a upper 95% confidence interval that spanned 11 200 g/m^2 to 175 000 g/m^2 (Appendix 2.9.; Figure S2.3). The standard error of the 95% prediction interval in Terra Nova National Park ranged from 1.32 to 1.47 (Appendix 2.9.; Figure S2.2). Therefore, the lower 95% prediction interval spanned 296 g/m^2 to 3 960 g/m^2, and the upper 95% prediction interval spanned 75 400 g/m^2 to 994 000 g/m^2 (Appendix 2.9.; Figure S2.3). In Gros Morne National Park the standard errors of the 95% confidence intervals ranged from 0.13 to 0.062, and the residual standard error was 0.94 (Appendix 2.9.; Figure S2.2). This corresponds to an lower 95% confidence interval that spanned 1 810 g/m^2 to 34 000 g/m^2 and a upper 95% confidence interval that spanned 7 740 g/m^2 to 145 000 g/ m^2 (Appendix 2.9.; Figure S2.3). The standard errors of the 95% prediction interval in Gros Morne National Park, therefore, ranged from 0.95 to 1.12 (Appendix 2.9.; Figure S2.2). Therefore, the lower 95% prediction interval ranged from 520 g/m^2 to 9720 g/m^2, and the upper 95% prediction interval spanned 27 500 g/m^2 to 510 000 g/m^2 (Appendix 2.9.; Figure S2.2).

2.4.2. Gap vs Mature

2.4.2.1. Top models of gap vs mature

Environmental variables describing forest characteristics were included in the top models for gap vs mature in both Terra Nova National Park and Gros Morne National Park (Table 2.3). The top model for gap vs mature in both national parks included forest height and EVIamp, (TN, $R^2 = 0.33$; GM, $R^2 = 0.37$; $\Delta\text{AIC}_\text{C} = 0.35$; Table 2.3). There was a model that validated just as often, and had a lower AIC_C for Terra Nova National Park, which included forest height, EVIamp, length of green season, and aspect (ΔAICc = 0.00; $R^2 = 0.43$;Table 2.3). While that model had a lower AICc, predictor variables length of green season and aspect appear to be uninformative because their confidence intervals overlap 0 when included in any model (Leroux 2019). There were no other models within ΔAICc of 4 or less for Gros Morne National Park (Table 2.3). In both national parks (Figure 2.5), the probability that an area was mature forest was positively related to forest height ($\text{beta}_{\text{forestheight\_}}\text{TN}_\text{M} = 2.49$; $\text{SE}_{\text{forestheight\_}}\text{TN}_\text{M} = \pm0.96$; $\text{beta}_{\text{forestheight\_}}\text{GM}_\text{M} = 2.88$; $\text{SE}_{\text{forestheight\_}}\text{GM}_\text{M} = \pm \pm0.87$) and negatively related to EVIamp ($\text{beta}_{\text{EVIamp\_}}\text{TN}_\text{M} = -3.88$; $\text{SE}_{\text{EVIamp\_}}\text{TN}_\text{M} = \pm1.65$; $\text{beta}_{\text{EVIamp\_}}\text{GM}_\text{M} = -3.9$; $\text{SE}_{\text{EVIamp\_}}\text{GM}_\text{M} = \pm1.64$).

2.4.2.2. Predictions of gap vs mature across national parks

We predicted that ~ 60% of the predictable area in Terra Nova National Park (159 of 266 km^2) and ~50% of the predictable areas in Gros Morne National Park (379 of 762 km^2) had a greater than 0.5 probability of being a disturbed gap (Figure 2.4; Table 2.3).

2.4.2.3. Errors in predictions

Given that our models were fit with a binomial distribution, and a logit link, our residual standard error was equal to 1 in both national parks. In Terra Nova National Park, the standard errors of the 95% confidence interval for individual cells ranged from 0.52 to 2.22 (Appendix 2.9.; Figure S2.4). This corresponds to an lower 95% confidence interval that spanned 0.000016 to 0.74 and a upper 95% confidence interval that spanned 0.09 to 1 (Appendix 2.9.; Figure S2.3). The standard error of the 95% prediction interval in Terra Nova National Park ranged from 1.13 to 2.44 (Appendix 2.9.; Figure S2.4). Therefore, the lower 95% prediction interval spanned 0.000011 to 0.6, and the upper 95% prediction interval spanned 0.13 to 1(Appendix 2.9.; Figure S2.3). In Gros Morne National Park the standard errors of the 95% confidence intervals ranged from 0.44 to 1.91 (Appendix 2.9.; Figure S2.4). This corresponds to an lower 95% confidence interval that spanned 0.000041 to 0.95 and a upper 95% confidence interval that spanned 0.06 to 1 (Appendix 2.9.; Figure S2.3). The standard errors of the 95% prediction interval in Gros Morne National Park, therefore, ranged from 1.1 to 2.15 (Appendix 2.9.; Figure S2.4). The lower 95% prediction interval ranged from 0.000025 to 0.91, and the upper 95% prediction interval spanned 0.094 to 1 (Appendix 2.9.; Figure S2.3).

2.4.3. Effect of combined disturbances on carbon

There was significant difference in total carbon stocks between sites in mature forest, sites in disturbed areas without moose browsing and sites in disturbed areas with moose browsing (Figure 2.6, $p < 0.001$). Mature forest sites had significantly more total carbon stock than disturbed sites with moose browsing ($p < 0.001$), with mature sites having on average 1600 more grams of cabron per m^2 than disturbed sites with herbivory. However, mature forest sites did not have significantly different carbon than disturbed sites without moose browsing (p = 0.35). Total carbon stock in disturbed sites without moose browsing was also not significantly different than disturbed sites with moose herbivory (p = 0. 47).

2.4.4. Total impact on carbon storage of combined disturbances

We calculated the total carbon stocks that could be hindered from being stored across each national park as a potential consequence of moose herbivory in gaps to be about 3230 billion g or carbon (3.23 megatonnes) in Terra Nova National Park, ranging from 1310 billion grams (1.31 megatonnes) if moose have less effect in disturbed gaps, to 5140 billion grams (5.14 megatonnes) at maximum effect in disturbed gaps. This equates to 68% of the carbon stocks estimated to be currently stored in Terra Nova National Park. In Gros Morne National Park the total effects were about 7680 billion g of carbon (7.68 megatonnes), ranging from 3110 billion grams (3.11 megatonnes) if moose have less effect, to 12 000 billion grams (12 megatonnes) at maximum effect. This equates to 64% of the carbon stocks estimated to be stored in Gros Morne National Park at present.

2.5. Discussion

Our goal was to examine and quantify how disturbances affect carbon storage across a maritime boreal landscape. We did this by making fine scale predictions of carbon stocks and forest gaps across a boreal landscape using remotely sensed data paired with data collected in field. We found that the same remotely sensed variables which measure forest biomass and productivity were related to both total carbon and the probability a site was a mature forest or a gap. Specifically, our models predicted less carbon in areas predicted to be gaps, and more carbon in areas predicted to be mature forest (Figure 2.4). These areas with more carbon and mature forests were in stands with taller trees and where greenness and therefore productivity changes less throughout the year (ie lower enhanced vegetation index yearly amplitude;

EVIamp). Evidence from in situ data also suggests that moose herbivory may impede the reaccumulation of carbon in boreal forests after gap forming disturbances in some cases. Consequently, these combined disturbances may contribute to about 40% less carbon being stored across the two national parks we studied.

Around 50% of forest biomass and carbon is stored in the largest 1% of trees globally (Lutz et al. 2018; Allen et al. 2023) and forest height is a key measure of tree size while also indicating the presence or absence of trees (Lefsky et al. 2005; Saatchi et al. 2011; Wu et al. 2015; Sothe et al. 2022). Thus, as we expected, remote sensed measures of forest height were important predictors of carbon stocks in both national parks (Table 2.3; Figure 2.3). Our results are consistent with other studies which found that canopy height was an important variable for predicting aboveground carbon at a broader resolution for the Canadian boreal forest (Sothe et al. 2022), and was related to forest biomass across each forest biome in China (Wu et al. 2015).

Large trees in our maritime boreal forest system are predominantly coniferous (Brandt et al. 2013; Department of Fisheries Forestry and Agriculture of Newfoundland and Labrador 2022). Accordingly, forest stands have consistent greenness, and thus, inferred productivity (Shi et al. 2017; Huang et al. 2019), throughout the year (i.e., there is no large change in productivity measured by spectral signatures due to deciduous leaf senescence; DeFries et al. 1995, Sims et al. 2006, Guzinski 2010, Clerici et al. 2012, Na-U-Dom et al. 2017). In contrast, areas with few trees and less biomass (Sothe et al. 2022) such as grasslands or deciduous shrublands, have large fluctuations in greenness and productivity throughout the seasons which follow phenological patterns of leaf growth and senescence (DeFries et al. 1995; Sims et al. 2006; Guzinski 2010; Clerici et al. 2012; Na-U-Dom et al. 2017). Therefore, a measure of change in greenness throughout the year, such as the enhanced vegetation index yearly amplitude that we employed here, could help discern areas having large trees and forest cover and therefore more carbon from areas with fewer trees and therefore less carbon. As anticipated, enhanced vegetation index yearly amplitude was negatively correlated with carbon stocks across both national parks (Table 2.3; Figure 2.3). Metrics of seasonality derived from vegetation indices have also been used to estimate carbon and aboveground biomass in other systems, such as deciduous forests of the Mediteranean (Chrysafis et al. 2017) and temperate continental forests in North America (Zhu and Liu 2015). In the Brazilian savannah, metrics of seasonality derived from EVI, such as amplitude and rates of change, were also important predictors of carbon storage, with larger changes in vegetation between seasons related to lower carbon estimates (Schwieder et al. 2018).

Globally, forests are impacted by discrete events in time that cause loss of plant biomass, refered to as disturbances (Seidl et al. 2011; van Lierop et al. 2015). By killing and/or removing trees, disturbances create gaps in the canopy, directly reducing forest height in an affected area. As such, gaps have lower forest heights in the years following the disturbance event (Kurz et al. 2013). We were, therefore, able to use forest height to predict where disturbances common to the broeal forest (i.e., insect defoliation, forest fires, wind blowdown, and logging) have created gaps across the landscape (Table 2.3; Figure 2.5). Additionally, by removing competition from adult trees, many disturbances allow early successional species (e.g., brambles; e.g., *Rubus* spp., forbs; e.g. *Poa* spp., laurel; e.g., *Kalmia* spp.; , blueberries; e.g., *Vacciniam* spp.) to proliferate. While mature boreal forest in our study area, and indeed throughout much of the circumpolar boreal biome, is typically dominated by evergreen conifers (International Boreal Forest Research Association 2022), these early successional species are often deciduous. Therefore, also as expected, we found that gaps often have larger changes in greenness throughout the year than the mature forest (Table 2.3; Figure 2.5; DeFries et al. 1995, Sims et al. 2006, Evrendilek and Gulbeyaz 2008, Guzinski 2010, Clerici et al. 2012, Na-U-Dom et al. 2017). While commonly used to delineate deciduous versus coniferous forests (DeFries et al. 1995; Sims et al. 2006; Evrendilek and Gulbeyaz 2008; Guzinski 2010; Clerici et al. 2012; Na-U-Dom et al. 2017), seasonality of vegetation indices have also been relied on to monitor disturbances across many biomes including boreal and temperate forests, the Arctic, and the plains in Canada (Coops et al. 2009), boreal forests in Germany (Gnilke and Sanders 2022), tropical forests of the Amazon (Ferreira et al. 2010), and taiga forests of Siberia (Cuevas-González et al. 2009).

Because disturbances can cause the shift in vegetation structure, from many large mature trees to smaller early successional species associated with areas of lower carbon stocks, disturbances may be responsible for establishing transient areas having less carbon. It is likely that gaps formed by disturbances may initially decrease carbon storage through a decrease in forest height and a shift to vegetation with higher seasonality. Despite initially decreasing carbon storage, the transient occurrence of these areas with smaller trees and early successional species is ecologically important because it generates a patchwork of diverse habitat and ecosystem services across the landscape (Pickett et al. 1985; Engelmark 1999b; Bergeron and Fenton 2012; Kristensen et al. 2022). However, some gaps do not seem to be regenerating (Figure 2.6), and the continuation of lower carbon stocks even 20-25 years after the initial disturbance may not be attributable to gap forming disturbances, but rather herbivory.

We found that gaps that had moose herbivory excluded for 20-25 years after the initial disturbance had similar average total carbon stocks per plot as mature forest (Figure 2.6). In contrast and as expected, the gaps that experienced prolonged moose browsing had significantly lower average total carbon stocks per plot than mature forests (Figure 2.6). Therefore, without moose herbivory, gaps may be able to recover pre-disturbance levels of carbon stocks (Leroux et al. 2020), whereas, moose herbivory may be slowing or impeding the recovery of carbon stocks for decades and possibly longer after a disturbance.

Consequentially, if areas we predicted to be gaps were released from herbivory and were able to regenerate into mature forest, carbon storage across the forest ecosystems in the parks may increase by as much as 60% within a few decades. This is consistent with other reports of moose significantly reducing aboveground biomass and suppressing growth and regeneration of trees in boreal (Ellis and Leroux 2017; Kolstad et al. 2018; Petersen et al. 2023; Swain et al. 2023) and temperate forests (Allen et al. 2023). We also found no significant difference between average total carbon stocks at plots in gaps with versus without herbivory, implying a gradient of carbon recovery across gaps. This may be in part because of heterogenous effects of moose on carbon recovery after disturbances, potentially dependant on legacy effects of disturbances, original forest type, and residual large trees that survived the disturbance (Mason et al. 2010; Smith et al. 2010; Allen et al. 2023).

Because of the evidence suggesting moose are impeding the recovery of carbon stocks in gaps, one may therefore expect areas of high moose densities to correlate to areas having less carbon due to the continued existence of gaps. However, moose densities were not an important variable in any top model for carbon or mature forest/gap (Table 2.3). One potential reason these findings are incongruous is that the moose densities available for inclusion in our models only date back to 2015, while many of the gaps were formed by insect outbreaks in the 1980 or 1990s (Arsenault et al. 2016). Not only have moose densities likely changed over time naturally in response to environmental conditions or food availability, population reduction programs (via hunting) were also initiate in both natinal parks in 2011 (Parks Canada 2019, 2021), leading to a rapid drop in moose populations. Thus, the moose densities available for our model may not relate well to the browsing history in the disturbed areas or over the longer term, which likely had more influence on the forest successional trajectory than contemporary moose densities (Mason et al. 2010). Moose population data from a more relevant timeframe may help account for some of the unexplained variation in our predictions.

In both national parks, and in both models of carbon and mature forest/gap, uncertainty in our predictions stems from variation in our parameter estimates and residual variation (Appendix 2.9.; Figure S2.3). Thus, to reduce uncertainty in our predictions we could both increase sampling to reduce parameter uncertainty (Goodman 2002; Ng and Chick 2006), and also iteratively update the parameters considered in the models as new spatial data become available to potentially explain some of the residual variance (Dietze et al. 2018; Barros et al. 2023). For example, higher resolution maps of soil characteristics may allow us to explain some of the variation in soil carbon, such as soil depth, as found by Sothe et al (2022). As it stands, none of our current predictor variables explain the variation in soil carbon better than chance (Appendix 2.10.) and so variation in soil carbon is likely contributing to the unexplained variance. Unfortunately, we were not able to propagate uncertainty in the predictor variables into the confidence or prediction intervals, because this information was not available. Quantifying uncertainty in modeling efforts to come would benefit from remote sensing products with available uncertainty data.

Our average estimates of carbon stocks in Terra Nova National Park (19 000 g/m^2) and Gros Morne National Park (15 300 g/m^2) are similar to previous values obtained using other prediction methods. While our overall estimates are slightly lower than the estimates created using a process-based model by Sharma et al (2023; 23 800 g/m^2 in Terra Nova National Park; 24 800 g/m^2 in Gros Morne National Park), their estimates are only across forested areas while we included gaps. If we exclude areas we predicted are more likely to be gaps, our estimates of carbon densities are actually larger in Terra Nova National Park (24 500 g/m^2) and more similar in Gros Morne National Park (21 500 g/m^2) to the estimates of Sharma et al. (2023). Our estimates are also lower than those of Sothe et al. (2022 ;27 400 g/m^2 in Terra Nova National Park; 26 500 g/m^2 in Gros Morne National Park). However, their soil organic carbon component included soil to a depth of 30 cm, contributing to a soil organic carbon estimates (23 200 g/m^2 in Terra Nova National Park; 22 500 g/m^2 in Gros Morne National Park) larger than the largest soil organic carbon density we measured at any single site (19 704 g/m^2 in Gros Morne National Park).

In conclusion, we have provided predictions of carbon storage as well as the probability an area is mature forest or a gap using models of intermediate complexity, at a 30 m resolution, and that combine remote sensing with in situ data. These predictions, in combination with our assessment that moose may be impeding the recovery of carbon stocks in disturbed areas, can help inform management of disturbances to influence carbon storage across the boreal forest. For example, our predictions of where carbon is stored and where gaps have been formed could delineate candidate areas for remediation measures, such as tree planting (Parks Canada 2021), and targeted moose population reduction. We do not recommend limiting natural disturbances that cause gaps, because these play an important role in creating a heterogenous tree age structure across the landscape, which is important for maintaining biodiversity and ecosystem resilience (Pickett et al. 1985; Engelmark 1999b; McCarthy and Weetman 2006; Bergeron and Fenton 2012; Rodríguez and Kouki 2017). While these specific conculsions may not be transferable to areas outside our study, given suffient, local in situ forest data, the framework developed to create models of intermediate complexity, with relevant spatial resolutions, and that combine remote sensing and in situ data should be reproducible for other areas of boreal forest.

2.6. Statements & Declarations

2.6.1. Acknowledgements

We would like to acknowledge that this work was conducted on the ancestral lands of the Mi’kmaq, with whom we strive to reach true reconciliation by conducting inclusive and equitable science, and the Beothuk, who were rendered culturally extinct by colonial actions (Tuck 2022). We thank R. Moran for designing and implementing the first year of data collection. Alongside R. Moran, we would like to thank H. Adams, J. Hussey, J. Ball, J. Scott, and D. Bath for their assistance in field work and data collection in the first year, and L. McDaniel and N. van Miltenburg in the second year. We thank the staff from Terra Nova and Gros Morne National Parks for their knowledge and resources in planning and executing this research. We would like to thank Renee Wissink (Parks Canada), Brian McLaren (Lakehead University), and Luise Hermanutz (Memorial University) for guiding the establishment of exclosures in TNNP, and Kevin Connor (University of New Brunswick), Carson Wentzell and Tom Knight (Parks Canada) for overseeing the development of exclosures in GMNP. In the decades since their establishment these exclosures have been maintained by many Resource Conservation staff at each national park. Finally, thank you to my committee members, Y. Wiersma and A. Hurford for providing feedback throughout.

2.6.2. Funding

This research was funded by Parks Canada and the Natural Sciences and Engineering Research Council of Canada (Canada Graduate Scholarship to ERW and Alliance grant to SJL & YW). Some of the data presented here was accessed under the Open Licence – Parks Canada Agency.

2.6.3. Competing Interests

The authors have no relevant financial or non-financial interests to disclose.

2.6.4. Author contributions

SL, YW, and DW conceived of the project; RM led sampling design, field sampling and laboratory work in year 1. EW led sampling design, field sampling and laboratory work in year 1. EW and SL conducted data analyses, interpreted results, and prepared the manuscript, with input provided by YW and DW.

2.6.5. Data availability

The data and R code required to run our analyses are available at https://figshare.com/projects/Predicting_carbon_storage_in_maritime_boreal_forests_under_combines_disturbances/229326. Predictor variable data for the two parks is available from their corresponding sources in Table 2.1.

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2.8. Tables

Table 2.1. Candidate predictor variables considered for inclusion in models of carbon and mature forest/gap. Rows continued in next table.

Variable	Units	Kind	Source	Website	Range sampled (TN; GM)	Range in study area (TN; GM)	Included in full model?	Citation
Forest height	Metres	Vegetation	Global Forest Canopy Height	https://glad.umd.edu/dataset/gedi	0 - 12; 0 - 14	0-12; 0-21	Yes	(Potapov et al. 2021)
Enhanced vegetation yearly amplitude[1]	Spectral Index	Vegetation	Landsat Surface Reflectance-derived Enhanced Vegetation Index	https://espa.cr.usgs.gov/	450 - 3799; 500 - 5703	41 – 5087; 16 – 9636	Yes	(Masek et al. 2006; Vermote et al. 2016)
Enhanced vegetation yearly median[2]	Spectral Index	Vegetation	Landsat Surface Reflectance-derived Enhanced Vegetation Index	https://espa.cr.usgs.gov/	2450 - 5199; 600 - 5994	214 – 5445; 696 – 6315	Yes	(Masek et al. 2006; Vermote et al. 2016)
Length of green season[3]	Days	Vegetation	Multi-Source Land Surface Phenology Yearly North America	https://lpdaac.usgs.gov/products/mslsp30nav011/	54 - 191; 54 - 147	53 – 244; 28 – 192	Yes	(Friedl 2021)

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[1] Enhanced Vegetation Yearly Amplitude measures the difference between the maximum EVI and minimum EVI within the year. As EVI is a measure of greenness or productivity, EVIamp can be interpreted as the magnitude of change in productivity throughut the year.

[2] Enhanced Vegetation Yearly Median measures the median EVI within the year. As EVI is a measure of greenness or productivity, EVImed can be interpreted as the average productivity throughut the year.

[3] Length of green season is the number of days in the year that the area was considered green according to the greenup and greendown days from MSLSP30.

Variable	Units	Kind	Source	Website	Range sampled (TN; GM)	Range in study area (TN; GM)	Included in full model?	Citation
Forest age class	Categorical	Vegetation	Parks Canada	Obtained directly from Parks Canada	NA	1 – 5; 1 - 6[4]	No, removed during correlation analysis	
Dominant tree type	Categorical	Vegetation	Parks Canada	Obtained directly from Parks Canada	NA	NULL, White birch, Balsam fir, Not sufficiently restocked, Coniferous shrub, Black spruce	No, removed during parameter reduction (section #?)	
Land type class	Categorical	Vegetation	Global Land Cover Mapping and Estimation Yearly	http://www.cec.org/north-american-environmental-atlas/land-cover-30m-2020/	NA	1, 6, 8, 14, 16, 17, 18; 1, 6, 8, 14, 16, 17, 18[5]	No, removed during parameter reduction (section #?)	(Pasos 2020)
Slope	Percent	Topography	Canadian Digital Elevation Model	https://open.canada.ca/data/en/dataset/7f245e4d-76c2-4caa-951a-45d1d2051333	0 - 41; 0 - 70.01517	0 - 68; 0 - 160	Yes	(Natural Resources Canada 2011)
Aspect	Degrees from South	Topography	Canadian Digital Elevation Model	https://open.canada.ca/data/en/dataset/7f245e4d-76c2-4caa-951a-45d1d2051333		0 – 215; 0 – 802	Yes	(Natural Resources Canada 2011)

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[4] Forest age classes: TN: 1 = 0 – 20 years, 2 = 21 – 40 years, 3 = 41 –60 years, 4 = 61 – 80 years, 5 = 81 + years
GM: 1 = 0 – 20 years, 2 = 21 – 40 years, 3 = 41 –60 years, 4 = 61 – 80 years, 5 = 81 – 100, 6 = 101 – 120 years

[5] Land classifications: 1 = Temperate or sub-polar needleleaf forest, 6 = Mixed Forest, 8 = Temperate or sub-polar shrubland, 14 = Wetland, 16 = Barren lands, 17 = Urban, 18 = Water

Variable	Units	Kind	Source	Website	Range sampled (TN; GM)	Range in study area (TN; GM)	Included in full model?	Citation
Elevation	Metres	Topography	Canadian Digital Elevation Model	https://open.canada.ca/data/en/dataset/7f245e4d-76c2-4caa-951a-45d1d2051333	5 – 234; 5 – 444	0 – 359; 0 – 359	Yes	(Natural Resources Canada 2011)
Moose density	Categorical	Moose	Parks Canada	Obtained directly from Parks Canada	L:M:H:XH; L:H:VH	L:M:H:XH; L:H:VH[6]	Yes	(Parks Canada 2019, 2021)

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[6] Moose densities: L = Low, M = Medium, H = High, XH = Extra High, VH = Very High

Table 2.2. Mean and standard deviation of carbon stocks measured across park and stand condition in grams per square metre. The stocks are living biomass carbon (sum of live vegetation > 30 cm, live vegetation < 30 cm, and roots), dead biomass carbon (sum of deadwood and litter), soil organic carbon, and total carbon.

	Mean carbon stocks (g/m^2)			
Stand condition	Living biomass carbon	Dead biomass carbon	Soil organic carbon	Total carbon
Terra Nova National Park				
Mature Forest	31 028.49 (± 56 382.59)	1143.78 (± 1751.99)	7228.09 (± 4233.04)	39 400.36 (± 54 992.63)
Gap	4737.39 (± 10 287.71)	704.9 (± 1062.48)	3868.6 (± 2076.74)	9310.89 (± 10 212.22)
Overall	13 751.48 (± 35 458.41)	855.37 (± 1329.73)	5020.43 (± 3347.46)	19 627.28 (± 35 438.43)
Gros Morne National Park				
Mature forest	22 542.37 (± 31 440.92)	483.26 (± 359.21)	4937.72 (± 3863.68)	27 963.35 (± 30 892.92)
Gap	1797.29 (± 2746.13)	758.99 (±871.29)	3920.45 (± 6476.73)	6476.56 (± 3645.56)
Overall	10 339.38 (± 22 496.89)	645.46 (± 714.63)	4339.32 (± 3044.21)	15 324.16 (± 22 439.21)

Table 2.3. Results of generalized linear models of mean total carbon stocks at each site, and mature forest/gap, as they relate to remote sensed variables. Models included have a ΔAICc < 4. K: number of parameters, LL: log-likelihood (measure of model fit), ΔAICc: change in Aikike's Information Criterion corrected for small sample sizes relative to top model, R^2: Nagelkerke's pseudo R^2 (proportion of variation in data explained by the model), FHT: forest height, EVIamp: enhanced vegetation index yearly amplitude, EVImed: enhanced vegeation index yearly median, SLO: slope, ASP: aspect, ELE: elevation, LGS: number of days spent green in year.

				Coefficients: estimate (± standard error)							Cross validation
k	LL	ΔAICc	R^2	Intercept	FHT	EVIamp	EVImed	SLO	ASP	LGS	Number of times validated out of 100
Carbon stocks											
Terra Nova National Park											
3	-372.08	0	0.40	8.6 (±0.38)	1.30 (±0.39)	-	-	-	-	-	47
4	-371.24	0.87	0.43	8.37 (±0.42)	1.14 (±0.42)	-	-	0.42 (±0.41)	-	-	21
4	-371.75	1.91	0.42	8.89 (±0.59)	1.2 (±0.4)	-0.25 (± 0.46)	-	-	-	-	77
5	-370.13	1.39	0.47	8.81 (±0.557)	0.89 (±0.41)	-0.48 (±0.43)	-	0.63 (±0.40)	-	-	11
Gros Morne National Park											
5	-521.49	0.00	0.56	8.13 (±0.83)	0.96 (±0.23)	- 0.64 (± 0.43)	1.19 (± 0.65)	-	-	-	0
4	-523.55	1.66	0.52	7.36 (± 0.73)	1.17 (±0.22)	-	1.21 (±0.66)	-	-	-	5
4	-523.80	2.16	0.51	9.28 (±0.51)	0.89 (±0.22)	-0.59 (±0.43)	-	-	-	-	100
3	-525.43	3.06	0.48	8.69 (±0.20)	1.06 (±0.21)	-	-	-	-	-	95
Probability area is mature forest											
Terra Nova National Park											
6	-6.97	0.00	0.43	8.25 (±5.53)	3.14 (±1.34)	-5.79 (±2.55)	-	-	-2.48 (±1.55)	-5.37 (±3.47)	100
4	-9.79	0.35	0.33	0.093 (±1.3)	2.49 (±0.96)	-3.88 (±1.65)	-	-	-	-	100
5	-9.14	1.61	0.36	0.64 (±1.38)	2.64 (±1.03)	-3.41 (±1.4)	-	-	-1.1 (± 0.94)	-	100
5	-9.29	1.90	0.35	2.53 (±3.02)	2.45 (±1.00)	-4.61 (±1.96)	-	-	-	-1.96 (±2.25)	100
Gros Morne National Park											
4	-15.00	0.00	0.37	0.66 (±1.6)	2.88 (±0.87)	-3.9 (±1.64)	-	-	-	-	100

2.9. Figures

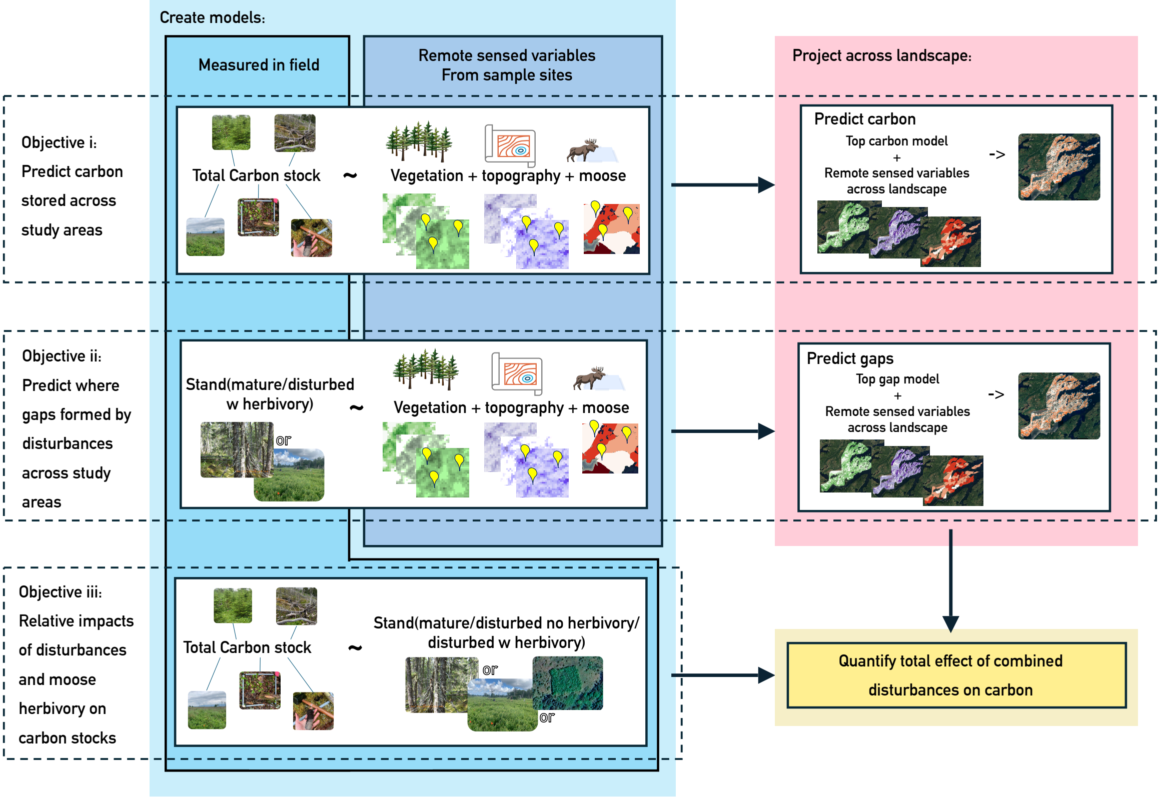


Figure 2.1. Conceptual diagram of workflow to meet our objectives

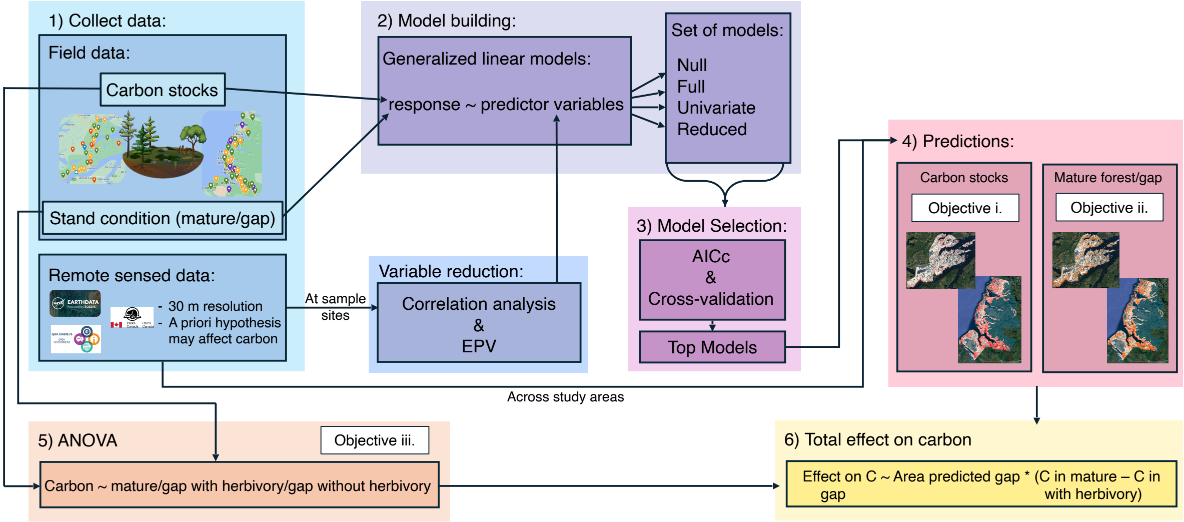


Figure 2.2. Conceptual diagram of analyses used to achieve our three objectives (see Figure 2.1). Outlines flow of data, statistical methods, and outputs. Event per Variable (EPV); Aikike's Information Corrected Criterion (AICc)

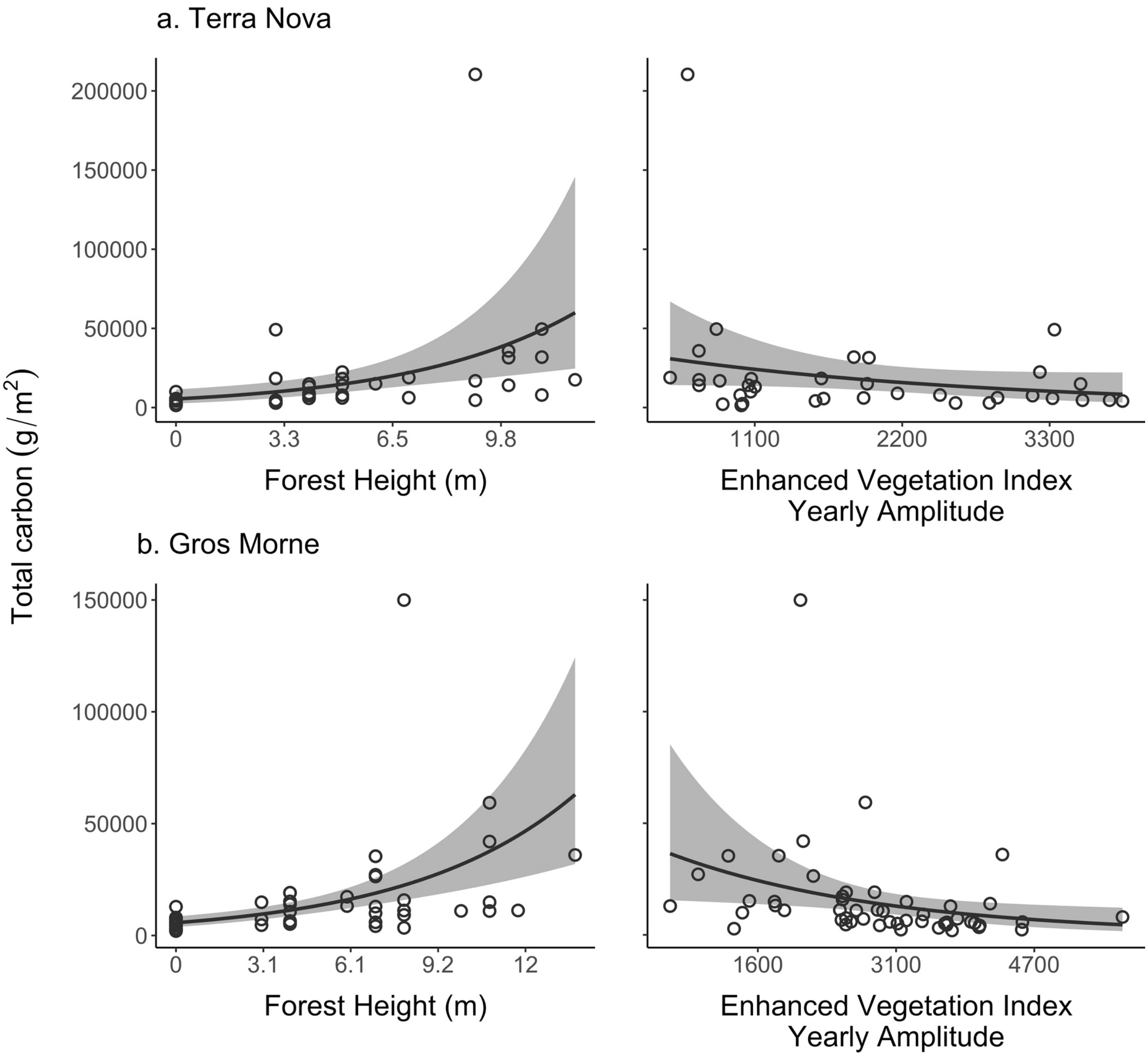
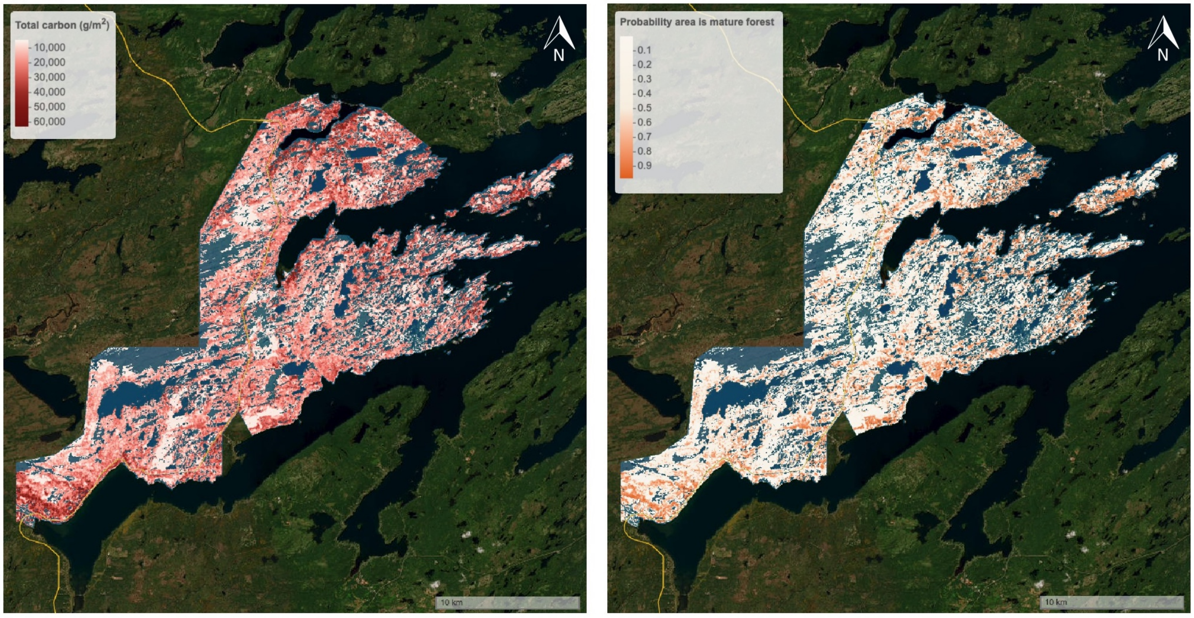


Figure 2.3. Relationship between average total carbon stocks and remote sensed variables included in the top models for (a) Terra Nova National Park and (b) Gros Morne National Park as depicted by the black line, with the 95% confidence interval in light grey. Each point is the total carbon stock in g/m^2 for each plot, averaged across each subplot

a. Terra Nova



b. Gros Morne

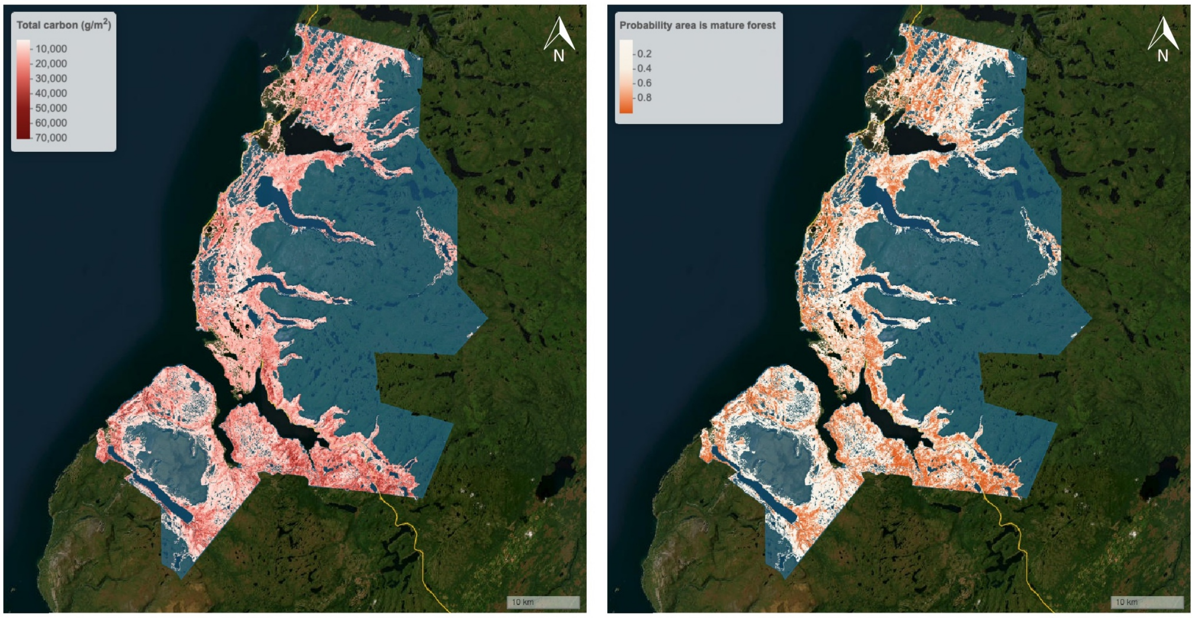


Figure 2.4. Predictions of total carbon stocks per m^2 (left) and probability area is mature forest (right) in each 30 m x 30 m cell for (a) Terra Nova National Park and (b) Gros Morne National Park. Predictions are made using the top model for total average carbon stocks and probability area is mature forest/gap in each national park. See https://emmwilson.github.io/interactive_maps/ for interactive versions of all maps presented here and in Appendix 2.9.

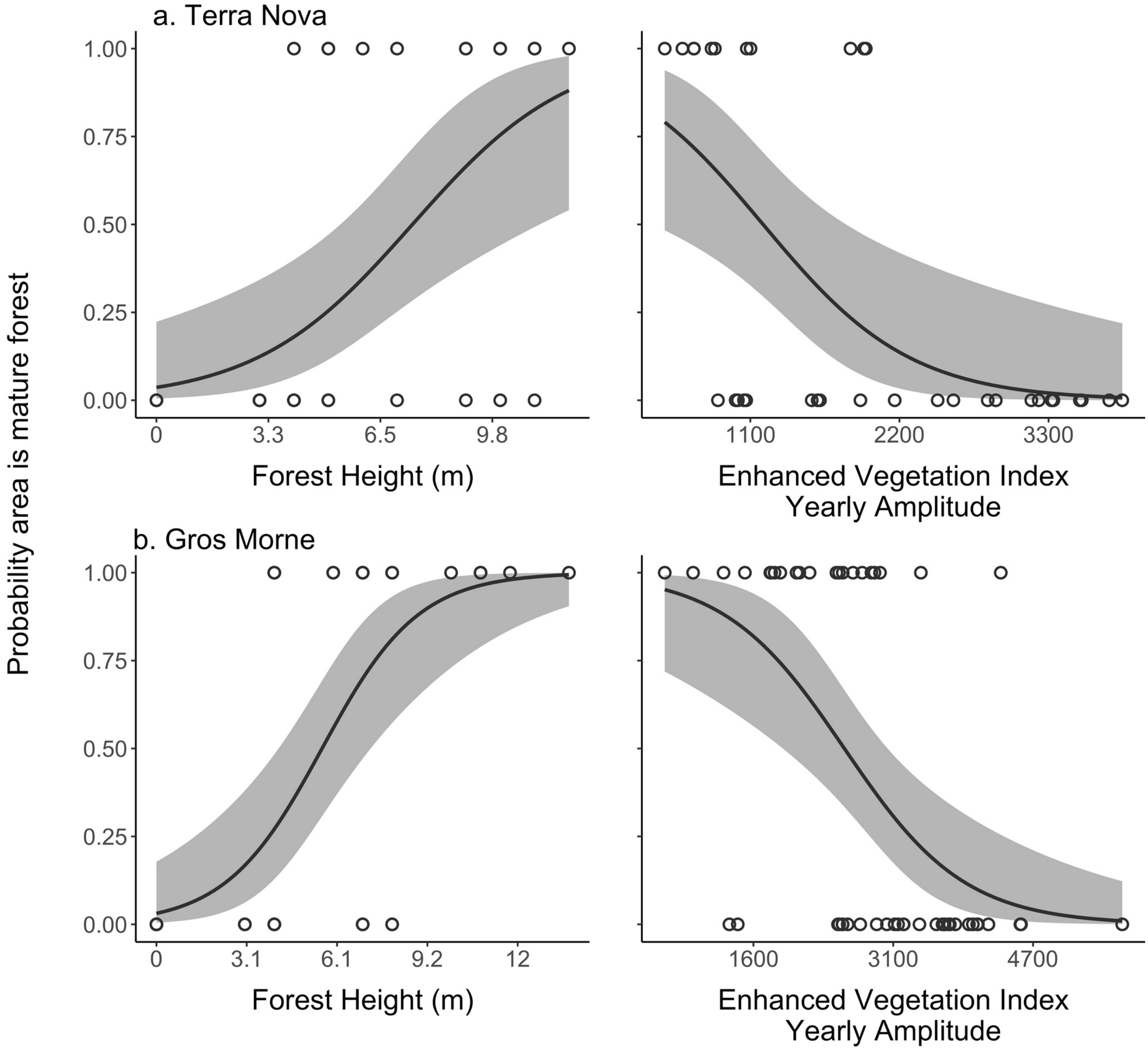


Figure 2.5. Relationship between probability plot is mature forest and remote sensed variables included in the top models for (a) Terra Nova National Park and (b) Gros Morne National Park as depicted by the black line, with the 95% confidence interval in light grey. Each point is the total carbon stock in g/m^2 for each plot, averaged across each subplot

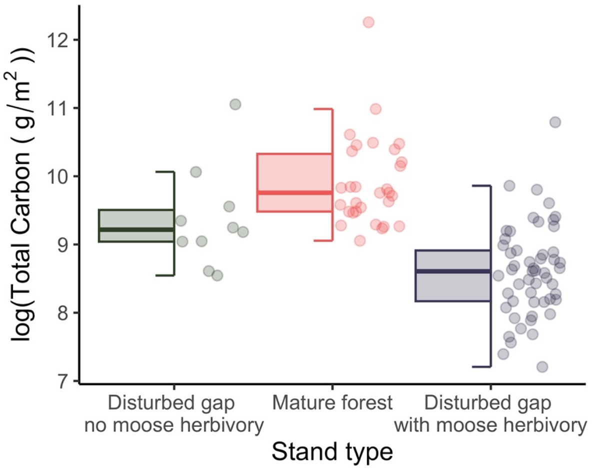


Figure 2.6. Box plot of average total carbon on natural log scale at sites in gap without moose herbivory, mature forest, and gap with moose herbivory. Points denote average total carbon stocks measured at each plot on natural log scale

2.10. Appendices

Appendix 2.1. Sampling sites

Additional information on about sampling sites, including identifying information about subplots (Table S2.1), classification of sites as mature or disturbed (Table S2.2), and layout of each site (Figure S2.1).

Sites in gaps, with exclosures and without, do not differ significantly in age when comparing age in years from ABoVE: stand age from 2020 (Landsat-derived locally-calibrated estimates of tree canopy cover (TCC) and forest stand age; Feng et al. 2022) using a two way anova in R. This data set was not used as a predictor variable for our models because it was missing data for many areas of each national park.

Table S2.1. Information on sample plots, including: park sampled in (Terra Nova: TN, Gros Morne: GM), Year sampled, unqiue plot ID, coordinates, disturbance history, open plot or exclosure, and inclusion in analyses

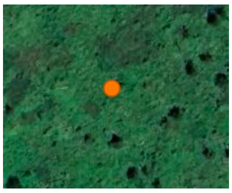
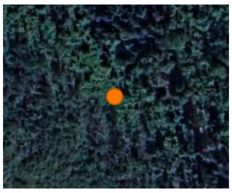
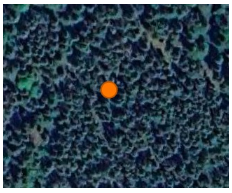
Park	Year	Plot ID (park, year_n_exclosure/ctrl/open)	Coordinates		Disturbance history	Open/Exclosure	Used in analysis 1 & 2	Used in analysis 3
GM	2022	GM_2022_1_OPEN	449165.51	5521521.89	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_1_EX	449149.987	5521509.49	Insect	EX	No	Yes
GM	2022	GM_2022_2_OPEN	433963.256	5497043.15	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_3_OPEN	441502.019	5484819.6	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_4_OPEN	433339.253	5496745.19	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_5_OPEN	443483.445	5483779.72	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_5_EX	443484.587	5483762.35	Insect	EX	No	Yes
GM	2022	GM_2022_6_OPEN	454739.784	5473772.31	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_7_OPEN	432355.902	5504544.98	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_8_OPEN	436696.167	5505446.12	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_9_OPEN	436266.718	5500136.95	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_10_OPEN	436498.602	5500149.02	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_11_OPEN	434447.913	5496789.35	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_12_OPEN	432989.618	5497932.93	Insect	OPEN	Yes	Yes
GM	2022	GM_2022_13_OPEN	437379.604	5490438.51	Mature	OPEN	Yes	No
GM	2022	GM_2022_13_EX	432989.618	5497932.93	Mature	EX	No	Yes
GM	2022	GM_2022_14_OPEN	449772.683	5478583.07	Mature	OPEN	Yes	Yes
GM	2022	GM_2022_15_OPEN	454953.494	5474507.53	Mature	OPEN	Yes	Yes
GM	2022	GM_2022_16_OPEN	436907.175	5505267.59	Mature	OPEN	Yes	Yes
GM	2022	GM_2022_17_OPEN	450046.843	5520040.06	Mature	OPEN	Yes	Yes
GM	2022	GM_2022_18_OPEN	439942.923	5490067.83	Mature	OPEN	Yes	Yes
GM	2022	GM_2022_35_OPEN	432960.26	5495894.62	Mature	OPEN	Yes	Yes

GM	2022	GM_2022_36_OPEN	433429.97	5497876.81	Insect	OPEN	Yes	Yes
TN	2022	TN_2022_19_OPEN	724763.392	5377455.05	Insect	OPEN	Yes	Yes
TN	2022	TN_2022_19_EX	724755.373	5377408.01	Insect	EX	No	Yes
TN	2022	TN_2022_20_OPEN	713900.46	5367730.69	Insect	OPEN	Yes	Yes
TN	2022	TN_2022_20_EX	713871.756	5367793.93	Insect	EX	No	Yes
TN	2022	TN_2022_21_OPEN	713871.756	5367793.93	Insect	OPEN	Yes	Yes
TN	2022	TN_2022_21_EX	723512.387	5387417.58	Insect	EX	No	Yes
TN	2022	TN_2022_22_OPEN	730157.643	5383171.87	Insect	OPEN	Yes	Yes
TN	2022	TN_2022_22_EX	730148.744	5383234.16	Insect	EX	No	Yes
TN	2022	TN_2022_23_OPEN	724026.443	5387375.58	Insect	OPEN	Yes	Yes
TN	2022	TN_2022_24_OPEN	716590.663	5366904.3	Insect	OPEN	Yes	Yes
TN	2022	TN_2022_25_OPEN	722111.819	5379544.51	Fire	OPEN	Yes	Yes
TN	2022	TN_2022_25_EX	722788.246	5379561.56	Fire	EX	No	Yes
TN	2022	TN_2022_26_OPEN	713038.112	5376799.28	Fire	OPEN	Yes	Yes
TN	2022	TN_2022_27_OPEN	721018.254	5370831.33	Fire	OPEN	Yes	Yes
TN	2022	TN_2022_28_OPEN	721609.475	5386088.72	Fire	OPEN	Yes	Yes
TN	2022	TN_2022_29_OPEN	722188.259	5370987.15	Fire	OPEN	Yes	Yes
TN	2022	TN_2022_30_OPEN	717899.043	5379742.58	Fire	OPEN	Yes	Yes
TN	2022	TN_2022_31_OPEN	732425.636	5387188.52	Mature	OPEN	Yes	Yes
TN	2022	TN_2022_31_EX	732413.837	5387151.49	Mature	EX	No	No
TN	2022	TN_2022_32_OPEN	720467.378	5370625.25	Mature	OPEN	Yes	Yes
TN	2022	TN_2022_33_OPEN	708699.834	5363953.18	Mature	OPEN	Yes	Yes
TN	2022	TN_2022_34_OPEN	729898.21	5383298.32	Mature	OPEN	Yes	Yes
TN	2022	TN_2022_34_EX	729933.761	5383349.72	Mature	EX	No	No
GM	2023	GM_2023_1_OPEN	438785.93	5491739.12	Logging	OPEN	Yes	Yes
GM	2023	GM_2023_2_EX	434058.651	5498584.27	Insect	EX	No	Yes
GM	2023	GM_2023_3_OPEN	433972.398	5498654.73	Insect	OPEN	Yes	Yes

GM	2023	GM_2023_5_OPEN	424040.286	5484245.28	Insect	OPEN	Yes	Yes
GM	2023	GM_2023_6_OPEN	444593.321	5478876.83	Insect	OPEN	Yes	Yes
GM	2023	GM_2023_7_OPEN	432092.76	5482467.78	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_9_EX	435968.348	5514194.97	Logging	EX	No	Yes
GM	2023	GM_2023_10_OPEN	435992.346	5514184.63	Logging	OPEN	Yes	Yes
GM	2023	GM_2023_11_OPEN	450928.359	5479173.01	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_13_OPEN	443562.842	5514252.7	Insect	OPEN	Yes	Yes
GM	2023	GM_2023_14_OPEN	444533.159	5513941.13	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_15_OPEN	447554.751	5474862.7	Insect	OPEN	Yes	Yes
GM	2023	GM_2023_16_OPEN	439431.869	5515187.14	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_18_OPEN	445927.851	5533722.23	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_19_OPEN	445862.556	5475105.14	Insect	OPEN	Yes	Yes
GM	2023	GM_2023_20_OPEN	445336.909	5526541.65	Logging	OPEN	Yes	Yes
GM	2023	GM_2023_21_OPEN	453514.636	5477358.68	Logging	OPEN	Yes	Yes
GM	2023	GM_2023_22_OPEN	419735.451	5478665.99	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_24_OPEN	441239.992	5490541.15	Insect	OPEN	Yes	Yes
GM	2023	GM_2023_25_OPEN	452691.717	5533268.45	Insect	OPEN	Yes	Yes
GM	2023	GM_2023_26_OPEN	453479.726	5532676.61	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_27_OPEN	435093.937	5512114.9	Logging	OPEN	Yes	Yes
GM	2023	GM_2023_29_OPEN	436023.271	5499287.93	Insect	OPEN	Yes	Yes
GM	2023	GM_2023_31_OPEN	452376.374	5479424.92	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_34_OPEN	436816.132	5485717.36	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_35_OPEN	440454.961	5486838.86	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_36_OPEN	431121.026	5500784.98	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_37_OPEN	435337.43	5493711.75	Logging	OPEN	Yes	Yes
GM	2023	GM_2023_38_OPEN	434206.648	5475767.26	Logging	OPEN	Yes	Yes
GM	2023	GM_2023_39_OPEN	446997.728	5481923.08	Mature	OPEN	Yes	Yes

GM	2023	GM_2023_40_OPEN	439530.993	5511345.68	Insect	OPEN	Yes	Yes
GM	2023	GM_2023_41_OPEN	440741.325	5511530.28	Mature	OPEN	Yes	Yes
GM	2023	GM_2023_42_OPEN	434132.245	5509276.3	Mature	OPEN	Yes	Yes
TN	2023	TN_2023_1_OPEN	725291.45	5388082.94	Mature	OPEN	Yes	Yes
TN	2023	TN_2023_2_EX	721631.073	5373989.34	Insect	EX	No	Yes
TN	2023	TN_2023_3_OPEN	721634	5373939.23	Insect	OPEN	Yes	Yes
TN	2023	TN_2023_5_OPEN	724300.362	5362179.85	Fire	OPEN	Yes	Yes
TN	2023	TN_2023_6_OPEN	724436.656	5392377.41	Insect	OPEN	Yes	Yes
TN	2023	TN_2023_7_OPEN	735568.434	5380674.36	Fire	OPEN	Yes	Yes
TN	2023	TN_2023_9_OPEN	737065.741	5386722.25	Mature	OPEN	Yes	Yes
TN	2023	TN_2023_12_OPEN	711558.037	5368547.87	Insect	OPEN	Yes	Yes
TN	2023	TN_2023_13_OPEN	718853.915	5378045.34	Wind	OPEN	Yes	Yes
TN	2023	TN_2023_14_OPEN	728209.767	5392129.29	Insect	OPEN	Yes	Yes
TN	2023	TN_2023_16_OPEN	724800.531	5376679.87	Mature	OPEN	Yes	Yes
TN	2023	TN_2023_17_OPEN	723229.57	5381706.9	Insect	OPEN	Yes	Yes
TN	2023	TN_2023_19_OPEN	710879.4	5365304.42	Mature	OPEN	Yes	Yes
TN	2023	TN_2023_20_OPEN	719665.243	5375320.91	Mature	OPEN	Yes	Yes
TN	2023	TN_2023_22_OPEN	717583.43	5367455.6	Insect	OPEN	Yes	Yes
TN	2023	TN_2023_23_OPEN	715081.911	5367139.71	Insect	OPEN	Yes	Yes
TN	2023	TN_2023_24_OPEN	719013.196	5367452.18	Insect	OPEN	Yes	Yes
TN	2023	TN_2023_25_OPEN	723222.052	5388835.4	Mature	OPEN	Yes	Yes
TN	2023	TN_2023_26_OPEN	724542.228	5384293.72	Mature	OPEN	Yes	Yes
TN	2023	TN_2023_27_OPEN	723038.55	5382895.6	Mature	OPEN	Yes	Yes

Table S2.2. Examples of sites in mature forest and gaps with photos taken at each site from both study areas, and a satellite image of the same locations. Coordinates in EPSG:4326 – WGS 84

Classification	Image of site on location	Satellite Image 0 10 20 m	Park (Coordinates)
Gap			Terra Nova (48.6441278,-53.9529835)
			Terra Nova (48.5349013,-53.8087273)
			Gros Morne (49.6427477,-57.8861476)
			Gros Morne (49.4310087,-57.9073801)
Mature Forest			Terra Nova (48.4055927,-54.1504819)
			Gros Morne (49.9446296,-57.6483700)

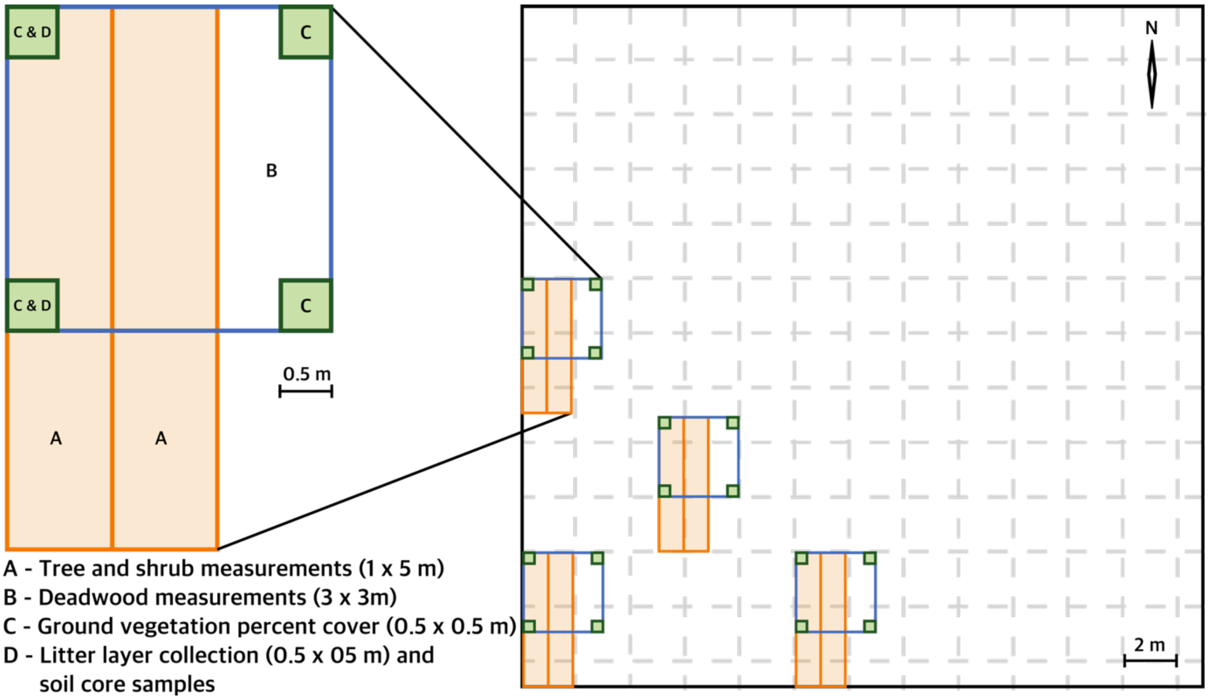


Figure S2.1. Layout of sublots within each 12 x 15m plot, and transects and quadrats within each subplot

Appendix 2.2 Allometric equations

Table S2.3. Published allometric equations used to calculate the biomass of each carbon stock as outlined in Moran et al. in revision

Carbon Stock	**Subgroup**	**Sources**	**Equation Used**	**Notes**
Trees	NA	Lambert et al., 2005	$Y_{wood} = \beta_{wood1} * D \wedge (\beta_{wood2}) * H \wedge (\beta_{wood3})$ $Y_{bark} = \beta_{bark1} * D \wedge (\beta_{bark2}) * H \wedge (\beta_{bark3})$ $Y_{branches} = \beta_{branches1} * D \wedge (\beta_{branches2}) * H \wedge (\beta_{branches3})$ $Y_{foliage} = \beta_{foliage1} * D \wedge (\beta_{foliage2}) * H \wedge (\beta_{foliage3})$ $Y_{total} = Y_{wood} + Y_{bark} + Y_{foliage} + Y_{branches}$	Y_i represents the dry biomass of each compartment. Parameters varied according to species. See Table 4 in reference for parameters.
Woody shrubs (30 cm to 3 m height)	Blueberry & black huckleberry	Chen et al., 2009	Biomass = 10543 *area of cover*average height	See Table 2 in reference for parameters.
	Canada yew		Biomass = 2699.5 *area of cover*average height	
	Labrador tea		Biomass = 1093 *area of cover*average height	
	Currant, wild raisin & rhodora		Biomass = 1197.1 *area of cover*average height	
	Laurel		Biomass = 1216.4 *area of cover*average height	
	Alder	Flade et al., 2020	Biomass = 185.0650 * (volume^0.9760)	See equation 7 and Table S3 in reference.
	Red elderberry	Flade et al., 2020; Smith & Brand, 1983	Biomass = 232.2120 * (volume^0.6290) OR Biomass = 33.016 *(Basal_Diameter^2.407)	See equation 7 and Table S3 in Flade et al., 2020 and Table 1 (*Shepherdia canadensis*) in Brown, 1976.
	Soapberry, mountain holly, pin cherry & serviceberry	Flade et al., 2020	Biomass = 232.2120 * (volume^0.6290)	See equation 7 and Table S3 in reference.
	Willow	Flade et al., 2020	Biomass = 262.4690 * (volume^0.7850)	
	Creeping juniper	Smith & Brand, 1983	Biomass = 59.205*(Basal_Diameter^2.202)	See Table 1, *Juniperus communis*.
Dominant herbaceous vegetation	Forbs	Guevara et al., 2021	Biomass = a* (percent cover^b)	See Table 3 in reference for parameters.
	Graminoids			
	Ferns			
Saplings	NA	Conti et al., 2019	Biomass = exp(-2.869 + 2.584*Ln(basal diameter)	See Model 3 of Table 1 in reference.
Deadwood	Standing	Harmon et al., 2011 & Richardson et al., 2009	Volume = 0.0000598(dbh^2*height)^0.946 Biomass = volume * average density	Average density values varied by decay class and hardwood/ softwood classification.
	Fallen		Volume = (pi/32) [(a+b)^2 + (c+d)^2]	Second pair of measurements was assumed to be the same as the first if it was not possible to measure.

			Biomass = volume * average density	
	Stumps		Volume = (pi/32) [(a+b)^2 + (c+d)^2] Biomass = volume * average density	Second pair of measurements was assumed to be the same as the first. Standing deadwood average density values were used for stumps.
Ground vegetation	Forbs	Guevara et al., 2021	Biomass = a* (percent cover^b)	See Table 3 in reference for parameters.
	Graminoids			
	Ferns			
	Brambles			
	Bryoids	MacDonald et al., 2012	Biomass = 5.534 * percent cover	See Figure 2 in reference for linear regression plot.
Woody shrubs (<30 cm height)	Evergreen shrubs	Chen et al., 2009	Biomass = 1216.4 *area of cover*average height	See Table 2 in reference for parameters.
	Deciduous shrubs		Biomass = 1197.1 *area of cover*average height	
	Blueberry		Biomass = 10543 *area of cover*average height	
	Labrador Tea		Biomass = 1093 *area of cover*average height	
Tree root biomass	Softwoods	Li et al., 2003	Root biomass softwoods = 0.222 * Aboveground biomass softwoods	
	Hardwoods		Root biomass hardwoods = 1.576 * (aboveground biomass hardwoods)^0.615	
Root biomass of woody shrubs (30 cm to 3 m), saplings, & herbaceous plants	NA	Coomes et al., 2002	Root biomass of shrubs = 0.25 * aboveground biomass of shrubs	

Appendix 2.3. Calculating carbon content of soil and litter samples

Table S2.4. Percent carbon content of litter samples by study area and disturbance type in 2022. GM: Gros Morne National Park, TN: Terra Nova National Park.

Study Area	Disturbance Type	Percent C (%)
GM	Insect or Logging	49.63552
GM	Mature	52.38194
TN	Insect or Wind	50.08425
TN	Fire	51.22821
TN	Mature	51.13708

Reparations for unusable soil samples:

All soil samples from plot 35 and from one subplot in plot 41, from Gros Morne in 2023, were burnt in the drying process and were therefore not eligible to have carbon content analyzed. We interpolated the missing soil sample from plot 41 as the mean soil content of the other samples in plot 41 (value = 34750.57 g per 9 m^2). Plot 35 was in a mature forest in Gros Morne in 2023, and so, we made missing values of carbon content for plot 35 equal to the median soil content of sites in mature forests in Gros Morne in 2023 (value = 43049.19 g per 9 m±2). When the analysis for total carbon stocks in Gros Morne was run without plot 35, the model that validated most often remained the same.

Appendix 2.4. Predictor variables

Alterations to datasets:

We converted aspect from the Canadian Digital Elevation Model (Canada 2011) to absolute number of degrees form South. Additionally, when slope is zero aspect cannot exist, creating NAs in the dataset, which cannot be accounted for in our models. Therefore, we set any NA aspect to 0.01˚from S.

We created the predictor variable "length of green season" by calculating the number of days between when an area became green again after winter and when leaves stopped being green in the fall. An area was considered to have become green when there was an initial increase in greenness of 15% from USGS's Multi-Source Land Surface Phenology Yearly North America (Friedl 2021). An area stopped being green when there was a subsequent 10% decrease in greenness from USGS's Multi-Source Land Surface Phenology Yearly North America. Some cells had no data because of cloud cover. We fill no data cells using the QGIS function GDAL Fill no data, interpolated over 10 cells.

Several sites were located slightly outside of the National park borders (TN_2022_26, TN_2022_27, TN_2022_30, TN_2023_05 ; Table S2.4) in order to sample additional areas that had been recently burned. Information provided from the parks (forest age class, dominant tree type, and moose densities classifications) were therefore not available for these sites. For forest age class and dominant tree type at these sites we used information from provincial forestry surveys (Parks Canada 2018), ensuring age classes and tree type classifications aligned. Moose densities for these sites were taken from the closest adjacent moose density classification from inside the park. Forest age class, dominant tree type, and moose densities classifications were also provided as vectors and we therefore converted them to rasters using

Table S2.5. Value of predictor variables at centroid of each sample plot used for objectives 1 and 2 (coordinates of centroid in Table S2.1)

Plot ID (park, year, n, exclosure/ctrl/open)	Forest height (m)	Enhanced vegetation index yearly amplitude (spectral index)	Enhanced vegetation index yearly median (spectral index)	Aspect (|˚ from S|)	Elevation (m)	Slope (Percent)	Forest age class	Canopy cover (percent	Moose density classification	Length of green season (days)	Dominant tree type
GM_2022_1	0	3190	4545	29.35776	36	22.92799	1	23	2	110	NULL
GM_2022_2	0	3619	4536	18.43495	113	7.28688	1	29	1	88	NULL
GM_2022_3	0	1298	4280	7.65065	57	36.94329	1	13	3	96	NULL
GM_2022_4	8	4076	4089	64.98311	106	13.06099	4	41	1	82	White birch
GM_2022_5	4	3249	3266	32.00539	87	11.99036	1	33	3	81	NULL
GM_2022_6	4	4202	5206	60.94539	122	7.94269	1	34	1	86	NULL
GM_2022_7	0	2950	4083	0.1	60	0	1	17	1	77	NULL
GM_2022_8	0	3831	3671	64.98311	206	13.0795	1	14	2	84	NULL
GM_2022_9	0	3770	4066	63.43495	163	7.0125	1	26	2	78	NULL
GM_2022_10	0	4028	4274	156.80141	171	4.5327	1	19	2	83	NULL
GM_2022_11	0	3711	4336	104.93142	106	25.37465	1	40	1	89	NULL
GM_2022_12	3	2566	3811	108.43494	80	2.55846	1	51	2	81	NULL
GM_2022_13	8	2051	3634	69.77515	81	16.26212	4	61	1	92	Balsam fir
GM_2022_14	7	891	3872	21.80141	76	6.34008	4	66	2	54	Balsam fir
GM_2022_15	11	1757	2919	104.74356	186	16.00147	5	62	1	75	Balsam fir
GM_2022_16	11	2082	3314	71.56505	215	2.56184	5	52	2	112	Balsam fir
GM_2022_17	7	573	3142	28.61046	22	15.55681	4	58	2	114	Balsam fir
GM_2022_18	11	2787	3977	50.71059	23	20.73335	5	59	3	104	Balsam fir
GM_2022_35	10	1869	4018	33.69006	86	4.64836	4	51	1	99	Balsam fir
GM_2022_36	0	3753	4051	108.43494	106	2.55846	1	27	2	79	NULL
TN_2022_19	4	3490	3271	157.61987	181	10.8079	1	56	3	98	Not sufficiently restocked

Plot ID (park, year, n, exclosure/ctrl/open)	Forest height (m)	Enhanced vegetation index yearly amplitude (spectral index)	Enhanced vegetation index yearly median (spectral index)	Aspect (|˚ from S|)	Elevation (m)	Slope (Percent)	Forest age class	Canopy cover (percent	Moose density classification	Length of green season (days)	Dominant tree type
TN_2022_20	5	3190	4759	56.7683	15	25.73164	5	64	3	104	Balsam fir
TN_2022_21	3	2818	4509	18.43495	108	16.32625	1	23	3	81	Not sufficiently restocked
TN_2022_22	10	1041	3337	161.56505	6	3.62742	6	66	2	120	Balsam fir
TN_2022_23	3	2568	4949	18.43495	121	7.256	5	32	2	86	Balsam fir
TN_2022_24	3	3297	4577	1.63658	105	18.91599	1	27	3	94	Not sufficiently restocked
TN_2022_25	0	988	2624	23.19859	33	4.50219	1	17	3	153.45364	NULL
TN_2022_26	0	997	3321	168.69006	173	2.82012	0	14	2	145	NULL
TN_2022_27	0	1535	3845	135	110	0.97689	1	32	1	123.12057	Coniferous shrub
TN_2022_28	3	1578	4481	176.18591	84	8.14039	1	35	2	81	NULL
TN_2022_29	0	1595	3599	45	94	0.97689	1	26	2	179	Coniferous shrub
TN_2022_30	0	851	2582	0.1	123	0	1	34	0	177	NULL
TN_2022_31	11	804	3397	33.69006	6	23.00002	6	60	2	105	Balsam fir
TN_2022_32	9	592	3129	28.61046	93	15.38019	5	69	1	139	Balsam fir
TN_2022_33	10	675	2953	33.69006	29	9.1816	6	63	2	143.73402	Balsam fir
TN_2022_34	10	1929	4183	26.56505	16	16.24166	6	66	3	152	Balsam fir
GM_2023_1	0	3151	4888	12.99461	117	14.90134	4	39	2	83	Balsam fir
GM_2023_3	0	3984	3827	135	103	0.99332	1	23	1	71	NULL
GM_2023_5	3	3253	4166	67.83365	150	23.22338	4	31	2	94	White birch
GM_2023_6	4	3429	3497	157.61987	77	10.86614	1	34	2	84	NULL
GM_2023_7	7	1233	3779	71.56505	239	22.96382	5	56	1	94	Balsam fir
GM_2023_10	7	1392	3653	108.43494	21	2.56584	4	53	1	101.44521	Balsam fir
GM_2023_11	4	2891	5087	12.17146	155	29.01454	4	53	2	77	White birch

Plot ID (park, year, n, exclosure/ctrl/open)	Forest height (m)	Enhanced vegetation index yearly amplitude (spectral index)	Enhanced vegetation index yearly median (spectral index)	Aspect (|˚ from S|)	Elevation (m)	Slope (Percent)	Forest age class	Canopy cover (percent	Moose density classification	Length of green season (days)	Dominant tree type
GM_2023_13	7	2624	2331	122.27563	242	34.31638	5	46	2	85	Balsam fir
GM_2023_14	8	2498	2192	164.74487	375	12.89495	6	54	2	100.85822	Balsam fir
GM_2023_15	8	2529	4056	8.74615	41	14.4262	4	53	1	96	Balsam fir
GM_2023_16	4	2569	3006	180	30	2.15983	4	53	1	113	White birch
GM_2023_18	7	1805	3845	21.80141	6	12.71596	5	52	1	105	Balsam fir
GM_2023_19	4	3688	3832	126.8699	93	7.38947	1	23	1	71	NULL
GM_2023_20	0	2516	4248	45	34	1.99398	4	44	1	99	Balsam fir
GM_2023_21	0	5703	3699	73.73979	444	40.57493	1	18	1	81	NULL
GM_2023_22	6	2528	3497	30.96376	63	3.67404	4	50	1	77	Balsam fir
GM_2023_24	7	4084	2797	137.33731	219	47.84767	1	59	3	111	NULL
GM_2023_25	0	4561	3845	153.43495	84	2.73524	1	32	2	79	NULL
GM_2023_26	4	1472	3324	45	71	0.9978	1	37	1	86	NULL
GM_2023_27	0	3709	4133	116.56506	43	3.5135	1	19	1	71	NULL
GM_2023_29	0	4568	3648	45	161	0.99338	1	14	2	83	NULL
GM_2023_31	8	3445	3283	135	174	16.8451	4	64	1	107.61799	Balsam fir
GM_2023_34	4	2987	3327	178.5312	44	21.07474	3	57	1	100	Balsam fir
GM_2023_35	7	2197	3832	74.74489	68	37.17364	4	55	3	147	White birch
GM_2023_36	11	2684	2155	153.43494	16	30.01942	4	62	2	105	Balsam fir
GM_2023_37	0	2568	4535	75.96376	110	27.00381	4	45	2	83	Balsam fir
GM_2023_38	4	3064	2792	175.9144	219	15.2097	1	34	1	65	NULL
GM_2023_39	7	4795	6356	8.74615	218	72.13596	4	40	2	110	White birch
GM_2023_40	3	2765	3465	147.52881	35	8.33671	4	29	3	83	White birch

Plot ID (park, year, n, exclosure/ctrl/open)	Forest height (m)	Enhanced vegetation index yearly amplitude (spectral index)	Enhanced vegetation index yearly median (spectral index)	Aspect (|˚ from S|)	Elevation (m)	Slope (Percent)	Forest age class	Canopy cover (percent	Moose density classification	Length of green season (days)	Dominant tree type
GM_2023_41	12	2925	639	154.33481	44	51.81471	5	63	3	84	White birch
GM_2023_42	6	1767	3638	0.1	16	0	1	53	1	109	NULL
TN_2023_1	4	1089	3611	120.96375	234	4.39255	1	35	2	91	Coniferous shrub
TN_2023_3	4	2140	2896	83.65981	110	22.05243	6	56	2	92	Black spruce
TN_2023_5	4	3283	5335	0	93	6.47948	1	30	2	91	NULL
TN_2023_6	4	3136	5162	9.16235	88	17.23019	1	21	2	88	Not sufficiently restocked
TN_2023_7	0	1057	3883	116.56506	26	6.87178	1	26	2	106	NULL
TN_2023_9	9	829	4641	57.20047	8	39.93323	6	65	1	190	Black spruce
TN_2023_12	5	980	3115	101.30994	88	4.10493	6	39	1	148	Black spruce
TN_2023_13	7	2877	2776	164.0546	150	8.23267	6	47	2	100	Black spruce
TN_2023_14	11	2453	2775	142.59464	55	14.03962	6	65	2	97	Black spruce
TN_2023_16	5	1061	4120	26.56505	152	10.82317	6	56	3	90	Black spruce
TN_2023_17	5	1890	4113	92.12109	61	22.03042	6	47	3	91	Black spruce
TN_2023_19	12	676	3000	14.03624	19	9.23158	6	64	2	147.9597	Black spruce
TN_2023_20	5	676	3340	22.0679	103	23.41991	6	48	1	134	Black spruce
TN_2023_22	3	3504	4490	71.56505	126	4.99998	1	33	1	90	Not sufficiently restocked
TN_2023_23	3	3799	4602	40.03026	62	21.77469	1	16	3	95	Not sufficiently restocked
TN_2023_24	9	3704	4525	18.43495	80	16.31466	1	38	3	106	Not sufficiently restocked
TN_2023_25	11	1818	2468	144.86581	20	21.29179	6	67	3	79	Black spruce
TN_2023_26	7	463	3825	60.25512	23	24.42721	6	64	2	126.29289	Black spruce
TN_2023_27	6	1916	2465	135	101	3.91331	6	37	1	85	Black spruce

Appendix 2.5. Collinearity:

Based on the correlation coefficients from our correlation analysis (Table S2.6), we decided to removed canopy cover and forest age class. We chose to remove canopy cover because it had the most coefficients above 0.7, and also had areas where cloud cover confounded several years of data. Canopy cover had a correlation coefficient above 0.7 with forest height and forest age class across both study areas, and across Terra Nova and in Gros Morne separately. Canopy cover was also highly correlated with land cover type in Gros Morne. We chose to remove forest age class because it had the second most coefficients above 0.7, and was a categorical which would have reduced the number of variables we could include in our models. Additionally, forest age class was originally available in vector form, and consequently the rasterization process would have introduced additional error. Forest age class had a correlation coefficient above 0.7 with canopy cover across both study areas, and across Terra Nova and in Gros Morne separately. Forest age class also had a correlation coefficient above 0.7 with dominant species and forest height in Terra Nova.

Table S2.6. Correlation coefficients between predictor variables across both study areas together (a) and across Terra Nova (b) and Gros Morne (c) separately.

a. Both parks together

Variables	FHT	EVIamp	EVImed	CC	ASP	SLO	ELE	LGS	LCT	SP	Age
FHT		-0.30	-0.30	0.78	0.0029	0.36	-.15	0.18	-0.60	0.34	0.68
EVIamp			0.3	-0.43	0.14	0.16	0.38	-0.53	0.43	-0.0037	-0.50
EVImed				-0.34	-0.48	0.038	-0.041	-0.15	0.33	-0.06	-0.30
CC					0.084	0.25	-0.24	0.23	-0.64	0.27	0.74
ASP						-0.064	0.18	-0.18	-0.24	0.079	0.03
SLO							0.18	0.059	-0.099	0.39	0.23
ELE								0.23	0.094	-0.09	-0.16
LGS									0.062	0.071	0.27
LCT										-0.095	-0.55
SP											0.49
Age											

b. Terra Nova

Variables	FHT	EVIamp	EVImed	CC	ASP	SLO	ELE	LGS	LCT	SP	Age
FHT		-0.15	-0.21	0.81	-0.0065	0.43	-0.5	-0.0013	-0.6	0.45	0.70
EVIamp			0.51	0.31	-0.059	0.093	0.22	-0.57	0.35	-0.064	-0.43
EVImed				-0.30	-0.37	0.28	-0.0052	-0.28	0.10	-0.28	-0.39
CC					0.091	0.44	-0.43	0.12	-0.6	0.49	0.78
ASP						-0.25	0.2	-0.24	0.30	0.25	0.13
SLO							-0.43	-0.052	-0.27	0.36	0.37
ELE								-0.25	0.23	-0.099	-0.39
LGS									0.19	-0.096	0.12
LCT										-0.42	-0.56
SP											0.78
Age											

c. Gros Morne

Variables	FHT	EVIamp	EVImed	CC	ASP	SLO	ELE	LGS	LCT	SP	Age
FHT		-0.39	-.36	0.76	0.022	0.37	0.0046	0.38	-0.66	0.32	0.67
EVIamp			0.22	-0.56	0.24	0.14	0.4	-0.25	0.66	0.021	-0.50
EVImed				-0.38	-0.55	-0.058	-0.058	-0.048	0.6	0.016	-0.25
CC					0.09	0.2	-0.15	0.38	-0.72	0.2	0.72
ASP						-0.0018	0.16	-0.07	-0.18	0.021	-0.014
SLO							0.31	0.31	-0.0015	0.40	0.24
ELE								-0.14	0.026	-0.09	0.014
LGS									-0.20	0.23	0.33
LCT										0.061	-0.55
SP											0.45
Age											

Appendix 2.6. Results for study areas analyzed together.

We created models for carbon and mature forest/gap without splitting the data by study area, following the same model development and selection process as the main manuscript. The results were similar to when we split the plots by park. The model that validated most often for carbon contained forest height and enhanced vegetation index yearly amplitude (EVIamp; R^2=0.47; Table S2.7). The next best competing model based on number of times validating contained only forest height (ΔAICc = 1.34, R^2 = 0.45). We found evidence that carbon was positively correlated with forest height ($beta_{1\_C}$ = 0.99, SE_{1_C} = ±0.2) and negatively correlated with EVIamp ($beta_{1\_C}$ =-0.41, SE_{1_C} = ±0.29).

The top model for mature forest/gap contained forest height and EVIamp (R^2=0.29; Table S2.7). The next competing model contained forest height, EVIamp, and length of green season (ΔAICc = 1.89, R^2=0.29), and all top candidate models validated everytime. We found evidence that the probability an area is mature forest was positively correlated with forest height ($beta_{1\_C}$ = 2.91, SE_{1_C} = ±0.65) and negatively correlated with EVIamp ($beta_{1\_C}$ =-2.84, SE_{1_C} = ±0.93).

Table S2.7. Results for generalized linear models of mean total carbon stocks at each site for both study areas together, and mature forest/gap, as they relate to remote sensed variables. Bold row is the top model chosen. Models included have a ΔAICc < 4. K: number of parameters, LL: log-likelihood (measure of model fit), ΔAICc: change in Aikike's Information Criterion corrected for small sample sizes relative to top model, R^2: Nagelkerke's pseudo R^2 (proportion of variation in data explained by the model), FHT: forest height, EVIamp: enhanced vegetation index yearly amplitude, EVImed: enhanced vegetation index yearly median, LGS: number of days spent green in year.

				Coefficients: estimate (± standard error)					Cross validation
K	LL	ΔAICc	R^2	Intercept	FHT	EVIamp	EVImed	LGS	Number of times validated out of 100
Carbon stocks									
5	-894.94	0	0.50	8.17 (±0.64)	1.06 (±0.20)	-0.51 (±0.29)	1 (±0.58)	-	89
4	**-897.14**	**2.14**	**0.47**	**9.11 (±0.36)**	**0.99 (±0.2)**	**-0.41 (± 0.29)**	**-**	**-**	**100**
4	-897.71	3.28	0.46	7.8 (±0.65)	1.24 (±0.2)	-	0.78 (±0.59)	-	3
3	-898.91	3.48	0.45	8.79 (±1.13)	1.05 (±0.23)	-	-	-	96
Probability area is mature forest									
4	**-29.59**	**0.00**	**0.29**	**-0.63 (±0.9)**	**2.91 (±0.65)**	**-2.84 (±0.93)**	**-**	**-**	**100**
5	-29.44	1.89	0.29	0.37 (±1.94)	2.87 (±0.65)	-3.02 (±1.00)	-	-0.83 (±1.49)	100

Appendix 2.7.

Table S2.8. Full list of potential models for each response variable and study area

Model	Response variable used	Study area	Structure (Response = carbon or mature forest/gap)
Null	Both	Both	Response ~ 1
Full	Both	Both	Response ~ FHT + EVIamp + EVImed + SLO + ASP + ELE + LGS + Moose
Univariate	Both	Both	Response ~ FHT
	Both	Both	Response ~ EVIamp
	Both	Both	Response ~ EVImed
	Both	Both	Response ~ SLO
	Both	Both	Response ~ ASP
	Both	Both	Response ~ ELE
	Both	Both	Response ~ LGS
	Both	Both	Response ~ Moose
Reduced	Carbon	Terra Nova	Response ~ FHT + EVIamp + SLO
	Carbon	Terra Nova	Response ~ FHT + EVIamp
	Carbon	Terra Nova	Response ~ FHT + SLO
	Carbon	Terra Nova	Response ~ EVIamp + SLO
	Carbon	Terra Nova	Response ~ FHT + EVIamp + EVImed
	Carbon	Gros Morne	Response ~ FHT + EVIamp
	Carbon	Gros Morne	Response ~ FHT + EVImed
	Carbon	Gros Morne	Response ~ EVIamp + EVImed
	Mature forest/gap	Terra Nova	Response ~ FHT + EVIamp + ASP + LGS
	Mature forest/gap	Terra Nova	Response ~ FHT + EVIamp + ASP
	Mature forest/gap	Terra Nova	Response ~ FHT + EVIamp + LGS
	Mature forest/gap	Terra Nova	Response ~ FHT + ASP + LGS
	Mature forest/gap	Terra Nova	Response ~ FHT + EVIamp
	Mature forest/gap	Terra Nova	Response ~ FHT + LGS
	Mature forest/gap	Terra Nova	Response ~ FHT + ASP
	Mature forest/gap	Gros Morne	Response ~ FHT + EVIamp

Appendix 2.8. Cross-validation:

To aid in model selection (Yates et al. 2023), we performed k-fold cross validation using the cv.glm function in the boot package (Davidson and Hinkley 1997; Canty and Ripley 2022) for each model in the set of top models. As per Leroux et al. (2017), we compared the estimates of the true cross validation prediction error generated from our real data, to those generated when performing cross validation on models run with re-shuffled response variables. The estimates of the true prediction error were highly variable and we therefore generated 100 estimates to use for comparison. Prediction error for reshuffled data was estimated 100 times, reshuffling the data each time, generating a distribution from which we could extract the 95% confidence interval of the prediction error. We then counted the number of times the 100 estimates of the true prediction error were below the lower 95% confidence interval for the estimates from reshuffled data.

Appendix 2.9. Calculating standard errors of the 95% confidence intervals and prediction intervals.

Standard errors of the 95 % confidence and prediction intervals were calculated at the link scale for estimates of carbon (log link) and mature forest/gap (logit link) across each study area (Figure S2.1). We used predict() in terra (Hijmans 2023) to generate the standard error of the 95% confidence intervals and the residual standard error. Then, we calculated the standard error of the 95% prediction intervals using equation S2.1. Obtaining the standard errors allowed us to calculate 95% confidence intervals and prediction intervals for every estimate of carbon and mature forest/gap across both study areas, on the scale of the response variables (Figure S2.2). The 95% confidence intervals for carbon were calculated for each cell using equation S2.2. The 95% confidence intervals for probability area was mature were calculated for each cell using equation S2.3. The 95% prediction intervals for carbon were calculated for each cell using equation S2.4. The 95% prediction intervals for probability area was mature were calculated for each cell using equation S2.5.

$$Standard\ error_{PI_{C\ or\ Gap}} = \sqrt{estimate_{C\ or\ Gap}^{2} + residual\ standard\ error_{C\ or\ Gap}^{2}}$$ (Eq. S2.1)

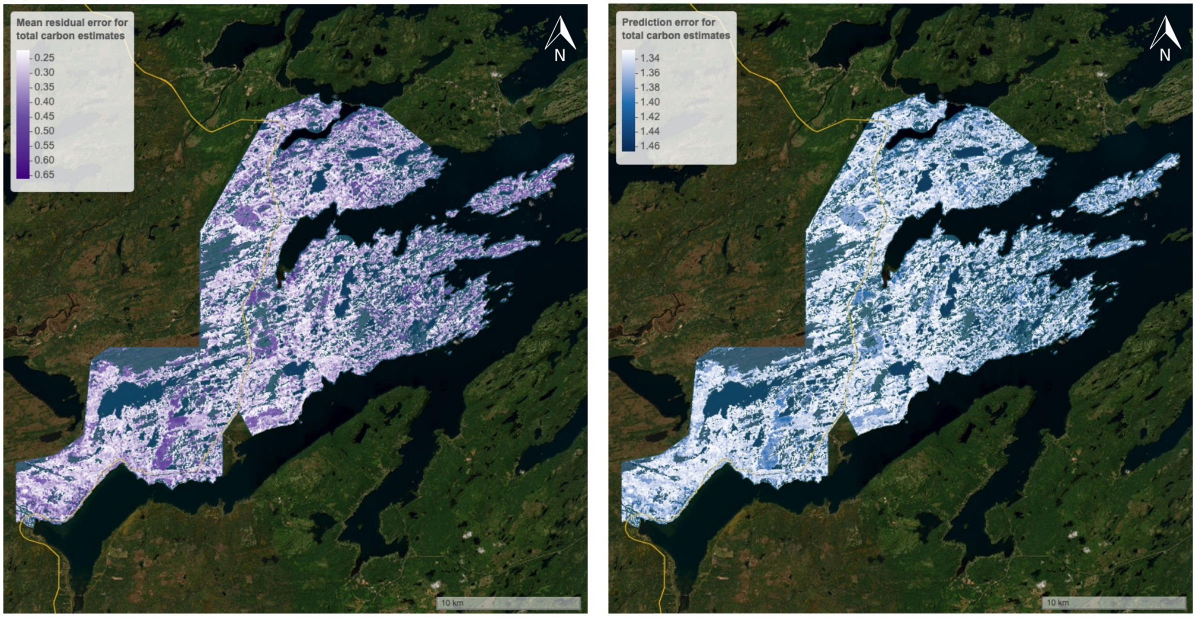
$$95\%\ CI_{C} = e^{estimate \pm 1.96 * standard\ error_{CI}}$$ (Eq. S2.2)

$$95\%\ CI_{Gap} = \frac{1}{1-e^{-(estimate \pm 1.96 * standard\ error_{CI})}}$$ (Eq. S2.3)

$$95\%\ PI_{C} = e^{estimate \pm 1.96 * standard\ error_{PI}}$$ (Eq. S4)

$$95\%\ PI_{Gap} = \frac{1}{1-e^{-(estimate \pm 1.96 * standard\ error_{PI})}}$$ (Eq. S5)

a. Terra Nova



b. Gros Morne

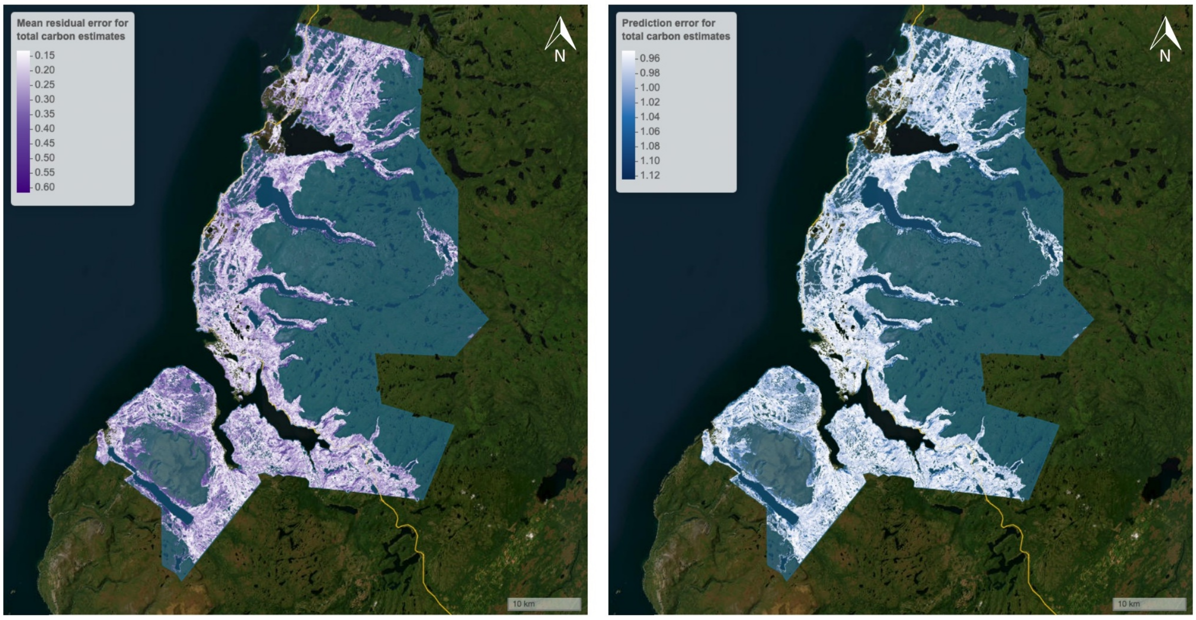


Figure S2.2. Standard error of the confidence intervals (left) and standard error of the 95% prediction interval (right) for total carbon stocks per m^2 in each 30 m x 30 m cell for Terra Nova (top) and Gros Morne (bottom). See https://emmwilson.github.io/interactive_maps/ for interactive versions of all maps presented

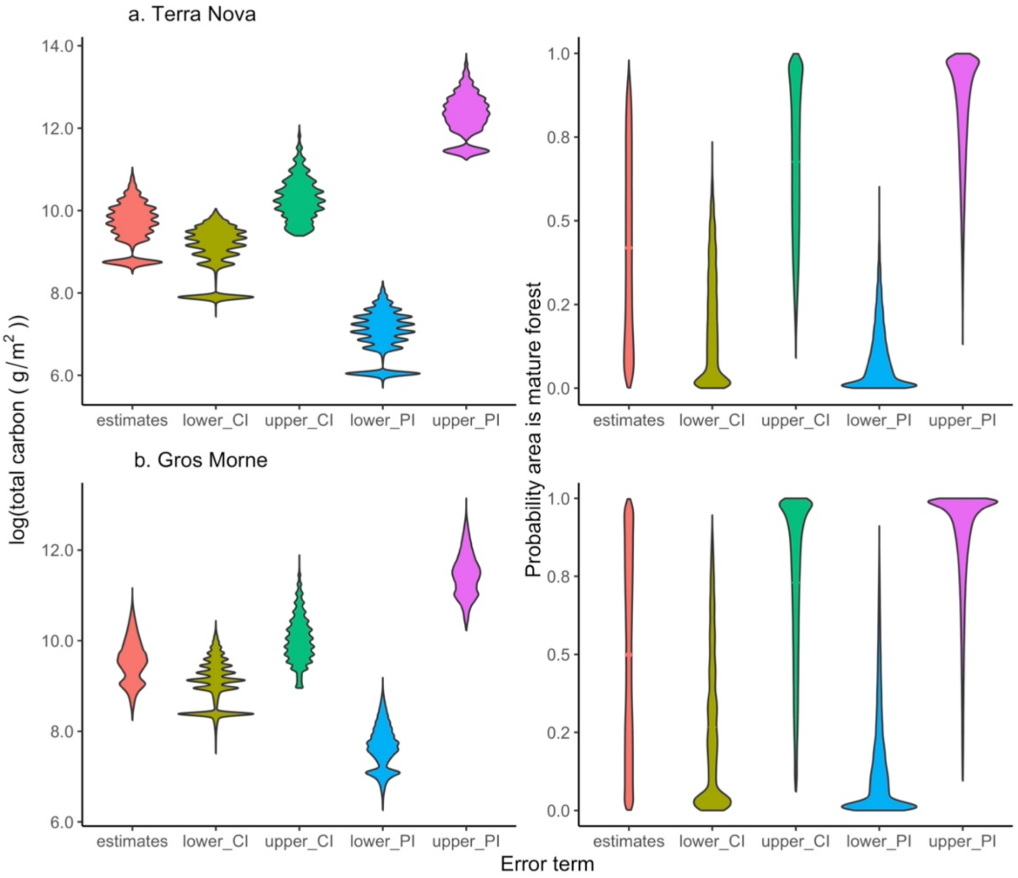
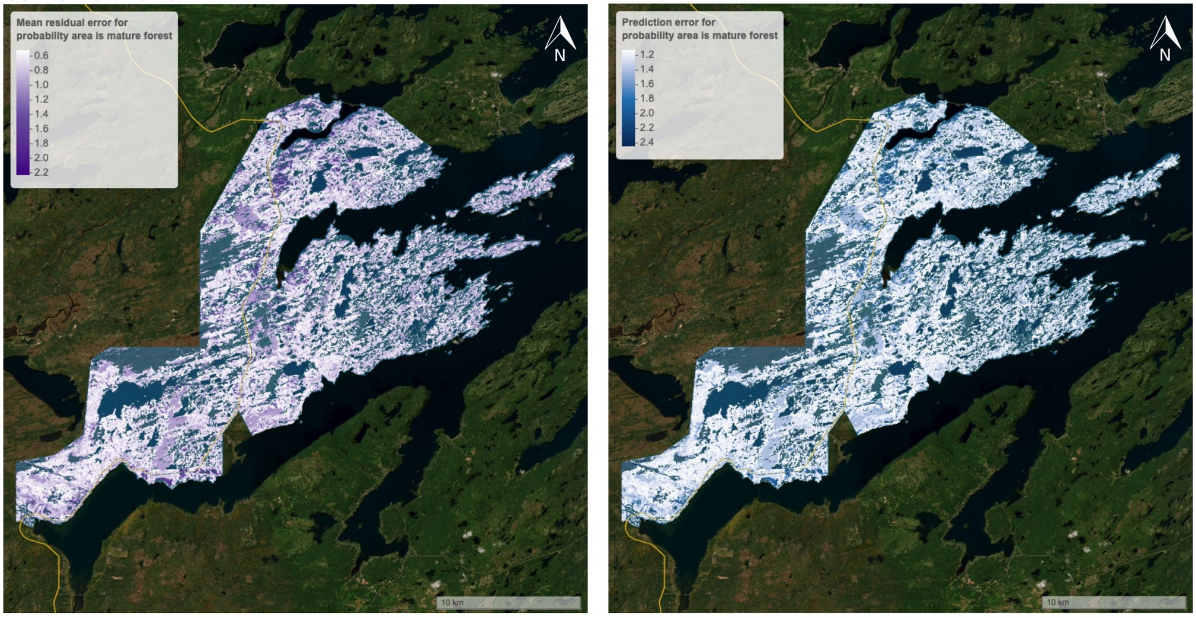


Figure S2.3. Distributions of estimates, lower and upper 95% confidence intervals, and lower and upper 95% prediction intervals of carbon stocks and probability an area is mature forest for (a) Terra Nova and (b) Gros Morne National Parks

a. Terra Nova



b. Gros Morne

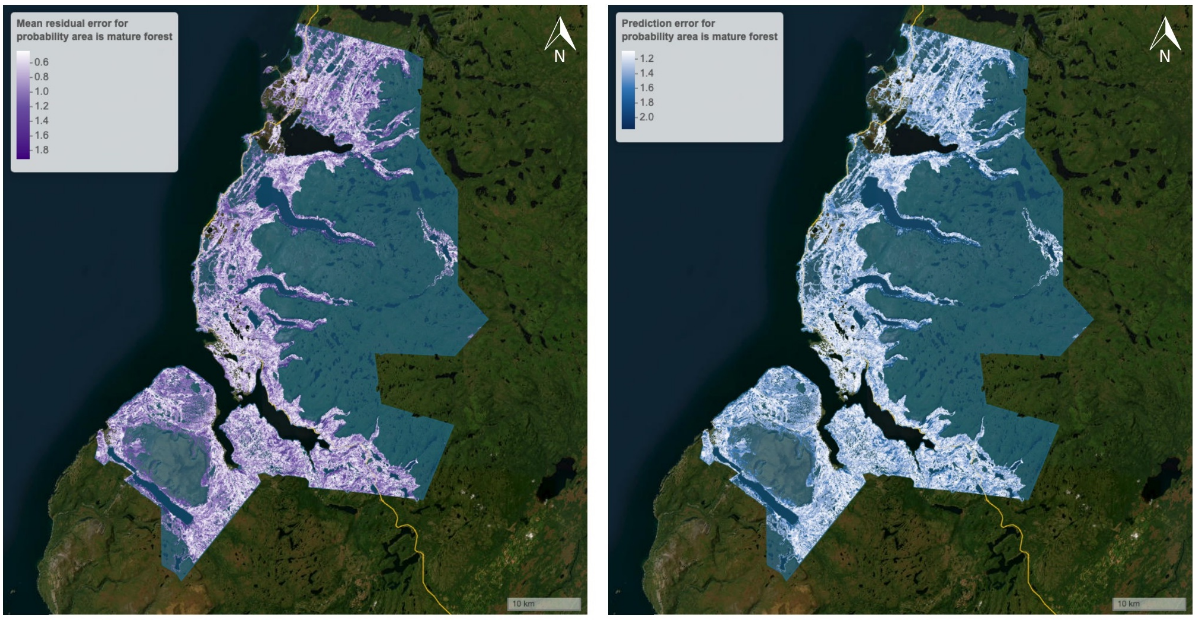


Figure S2.4. Standard error of the confidence intervals (left) and standard error of the 95% prediction interval (right) for probability area is mature forest in each 30 m x 30 m cell for Terra Nova (top) and Gros Morne (bottom). See https://emmwilson.github.io/interactive_maps/ for interactive versions of all maps presented

Appendix 2.10. Results for soil carbon (*Error! Reference source not found.****).***

We created models for just soil carbon following the same model development. We found that the only two models were better than random, the model containing only enhanced vegetation index yearly amplitude (ΔAICc = 0, $R^2 = 0.09$) and the model containing only forest height (ΔAICc = 5.22, $R^2 = 0.04$).

Table S2. 9. Results for generalized linear models of mean soil carbon stocks at each site for both study areas together, as they relate to remote sensed variables. Text in bold was chosen as top model. Models included have an AICc < than that of the null model, and the null model is also included. K: number of parameters, LL: log-likelihood (measure of model fit), ΔAICc: change in Aikike's Information Criterion corrected for small sample sizes relative to top model, R^2: Nagelkerke's pseudo R^2 (proportion of variation in data explained by the model), FHT: forest height, EVIamp: enhanced vegetation index yearly amplitude, EVImed: enhanced vegetation index yearly median, SLO: slope, ASP: aspect, ELE: elevation, LGS: number of days spent green in year.

				Coefficients: estimate (± standard error)						
K	LL	ΔAICc	R^2	Intercept	FHT	EVIamp	EVImed	SLO	ASP	LGS
Soil carbon stocks										
3	**-787.55**	**0**	**0.09**	**8.81 (±0.16)**	**-**	**-0.43 (±0.16)**	**-**	**-**	**-**	**-**
3	-790.16	5.21	0.05	8.27 (±0.12)	0.2 (±0.12)	-	-	-	-	-
2	-791.79	6.32	0.00	8.44 (±0.07)	-	-	-	-	-	-

Chapter 3: Modeling the mechanisms of regime shifts in eastern boreal forests

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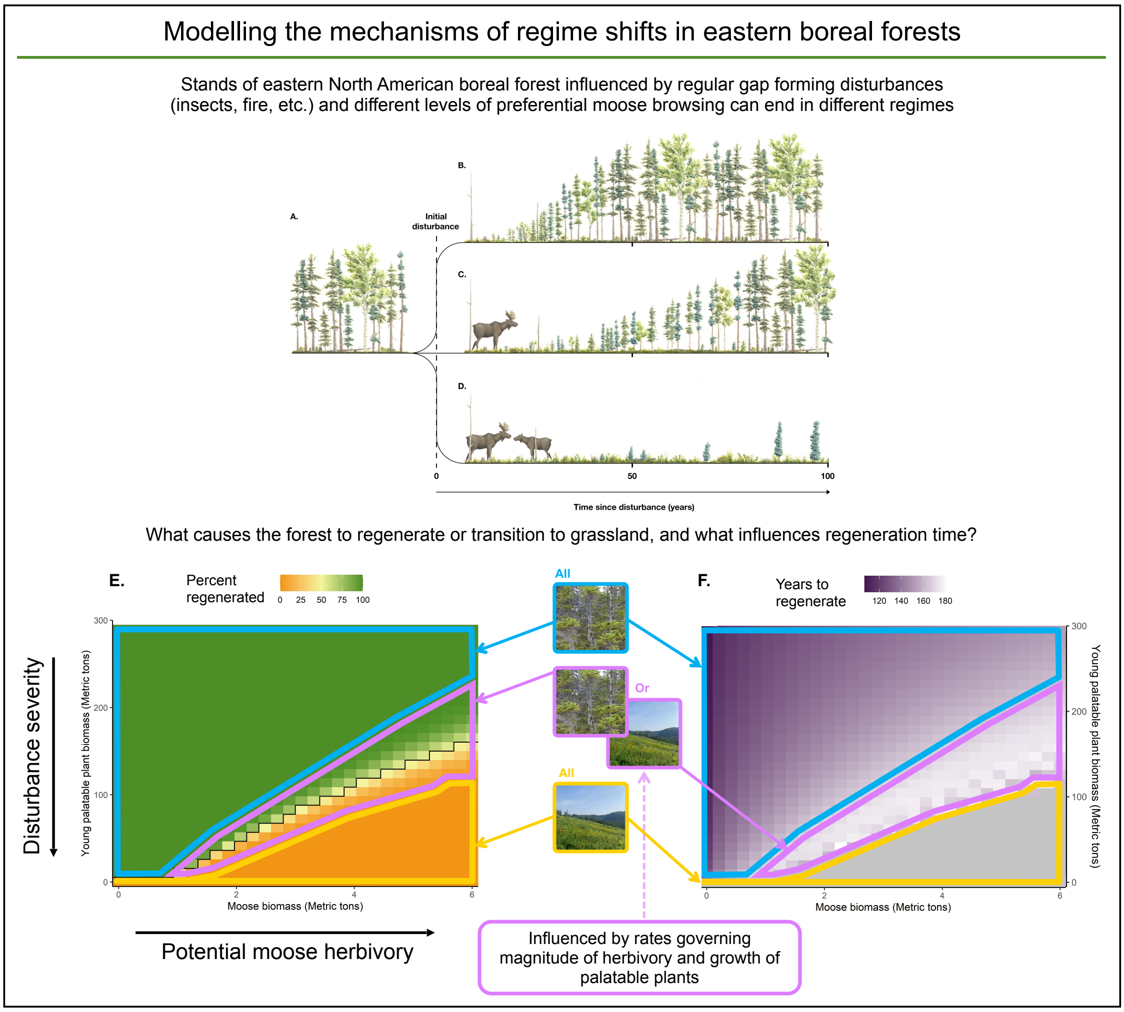
Key words: boreal forest, disturbances, herbivory, regime, mathematical model

3.1. Abstract

Across ecosystems, the transition of systems to new regimes can have consequences for biodiversity, nutrient cycling, carbon storage, and socio-economic relationships. Unfortunately, it can be difficult to resolve what drives the changes in ecosystem conditions. In eastern boreal forests, the conversion to grasslands after a disturbance has often been attributed to hyperabundant moose populations. However, empirical evidence demonstrates variation in moose effects on regeneration of vegetation after disturbances. To try and resolve which drivers result in a boreal regime shift from forest to grassland, we derive a mathematical model of a characteristic eastern North American boreal forest influenced by gap forming disturbances (insects, fire, etc.) and preferential moose browsing. We examine how the regeneration of a disturbed area in this system is affected by initial abundance of young palatable plant biomass and moose biomass, magnitude of herbivory, and growth and competition of plants. Our model demonstrates that the success and timing of boreal forest regeneration after a disturbance can be determined by moose herbivory, both by initial moose biomass and processes governing magnitude of moose consumption. However, if initial young palatable plant biomass is high enough, or growth of young palatable plant biomass fast enough, these can overcome the effects of moose. Therefore, the disturbance type and severity, species composition, or environmental conditions could potentially explain variable empirical results. To ensure forest regeneration after disturbance, we generally recommend maintaining low moose populations. Our model can also be used to generate area specific estimates of management efforts required to ensure forest regeneration and therefore, the maintenance of typical heterogenous forest age structure, biodiversity, wood resources, carbon storage and other ecosystem services.

3.1.1. Graphical abstract



Modelling the mechanisms of regime shifts in eastern boreal forests

Stands of eastern North American boreal forest influenced by regular gap forming disturbances (insects, fire, etc.) and different levels of preferential moose browsing can end in different regimes

What causes the forest to regenerate or transition to grassland, and what influences regeneration time?

Influenced by rates governing magnitude of herbivory and growth of palatable plants

3.2. Introduction

It can be difficult to unravel why systems that have historically demonstrated certain characteristics undergo unexpected and dramatic changes in conditions, and subsequently remain in an alternate regime (Scheffer et al. 2001; Beisner et al. 2003; Scheffer and Carpenter 2003). Extreme changes in the regime of an ecosystem can be driven by discrete events (e.g., forest fires; Dublin et al. 1990, Hayashi et al. 2024), incremental changes in conditions over time (e.g., sea level rise; Hayashi et al. 2024, Steven and Reinette 2017), or a combination of the two (Suding and Hobbs 2009; Johnstone et al. 2016). The identification of the drivers of regime shifts are critical for the conservation and restoration of ecosystems (Scheffer et al. 2001). However, the drivers which result in a regime shift can be difficult to resolve for many ecosystems (Foley et al. 2003; Scheffer and Carpenter 2003; Collie et al. 2004).

Examples of multiple possible regimes exist across many ecosystems (Schröder et al. 2005; Stockholm Resilience Centre), with consequences for biodiversity (Steven and Reinette 2017), nutrient cycling (Rietkerk and van de Koppel 1997), socio-economic relationships (Crépin et al. 2012; Shackleton et al. 2018), and beyond (Scheffer et al. 2001; Crépin et al. 2012). For example, under rapid sea level rise, salt marshes along Northern Atlantic coastlines previously dominated by smooth cordgrass are being replaced by tidal flats devoid of vegetation (Steven and Reinette 2017). This is happening in part because sea level rise has become faster than the rate at which tidal flats can maintain their platform above mean sea level through soil accretion. As a result, biodiversity and ecosystem services, such as protection from storms and filtration of pollution, are lost in this system (Steven and Reinette 2017).

Herbivory can also contribute to the existence of multiple regimes across many systems and at varying scales (Dublin et al. 1990; Augustine et al. 1998; Seabloom and

Richards 2003; Hidding et al. 2013). For example, in the Serengeti-Mara Woodlands of Africa, the combined effect of fires and elephant herbivory likely caused the conversion of woodland to grassland (Dublin et al. 1990; Holdo et al. 2009; Davies and Asner 2019). The influence of elephant herbivory alone would not have been sufficient to cause areas to switch from woodland to grassland, and a discrete change from fire alone was unlikely to sustain the grassland regime (Dublin et al. 1990; Holdo et al. 2009). But, the combination of a discrete fire event followed by elephant herbivory could have caused the transition to and persistence of the alternate grassland regime.

The combination of a discrete event and herbivory has also lead to a drastically different regime than historically expected across the balsam fir dominated eastern boreal forests of North America. Forest clearing disturbances followed by high levels of moose herbivory, enabled by low densities or complete extirpation of predators, have caused parts of the boreal forests of Isle Royale, US (Brandner et al. 1990; McInnes et al. 1992; Rotter and Rebertus 2015), Cape Breton, CA (Smith et al. 2010; Parks Canada Agency 2018), and Newfoundland, CA (Charron and Hermanutz 2016; Leroux et al. 2021b) to transition to grasslands or shrublands, instead of regenerating to mature boreal forest. Consequently, the landscape is able to store less carbon (Moran et al. In Review), has altered ecosystem services and age structure with implications for biodiversity (Fleming and Candau 1998; Connor et al. 2000), and fewer wood resources for harvesting than if the stand were able to regenerate to mature boreal forest.

Forest clearing disturbances, such as insect defoliation, forest fires, wind and logging, are the discrete events that initially create gaps in the eastern boreal forest canopy (Payette 1992; Engelmark 1999b; Reich et al. 2001; Charron and Hermanutz 2016; Boucher et al. 2017; Leroux et al. 2021b). The initial formation of a gap creates an abundance of light and, depending on the remaining vegetation after the disturbance, allows either individuals of overstory species, whose growth has been halted in the understory, to grow to fill the gap (Kneeshaw and Bergeron 1998) or the colonization and accumulation by fast growing, early successional species (Hart and Chen 2006; Bartels et al. 2016). In the latter case, tree seedlings may establish, outcompete early successional species, and eventually return the area to a stand of mature boreal forest (Archambault et al. 1998; Bartels et al. 2016).

However, across parts of the boreal forest, hyperabundant moose populations can impede forest regeneration (Brandner et al. 1990, Smith et al. 2010, Hidding et al. 2013, Rotter and Rebertus 2015, Parks Canada Agency 2018, Leroux et al. 2021). The later successional tree species that would eventually come to dominate stands of mature boreal forest (e.g.,balsam fir and birch) also form much of a moose's diet (Belovsky 1978, Thompson and Vukelich 1981, Cumming 1987, Hjeljord et al. 1990, Schwartz 1992). Therefore, moose present following a disturbance may browse the new growth of these palatable tree species to such an extent that it impedes forest regeneration. Furthermore, by preventing the growth of individuals from the original seed bank, and thus, preventing trees from maturing to add to the seed bank moose impact the future capacity of the forest to regenerate (Gosse et al. 2011; Charron and Hermanutz 2016). In this way, moose can release less browsed grass and shrub species from competition, directing the area towards a regime dominated by shrubs, grasses, and forbs (Brandner et al. 1990; Smith et al. 2010; Hidding et al. 2013; Rotter and Rebertus 2015; Parks Canada Agency 2018; Leroux et al. 2021b). Some established grassland and shrubland species are then difficult for saplings to outcompete (Kupferschmid and Bugmann 2005; Royo and Carson 2006; Gärtner et al. 2014), and also form poor seedbed for tree species (Mallik 2003; Charron and Hermanutz 2016). Therefore, because of herbivory, extirpated seedbanks, poor seedbed quality, and competition, the regeneration of an established grassland to boreal forest is unlikely.

It is not always the case that moose herbivory in disturbed areas impedes the regeneration of boreal forest (Petersen et al. 2023; Moran et al. In Review). A recent analysis of 100 moose exclosure/control plots across the circumboreal region, showed that a few gaps where moose have been excluded actually have lower canopy height and aboveground biomass than similar gaps with moose herbivory (Petersen et al. 2023). Variation in moose effects on forest regeneration following initial disturbance could be a result of varying moose densities throughout the stages of regeneration, differences in remaining vegetation as a legacy of disturbances, and dominant tree species before the disturbance (Mason et al. 2010; Allen et al. 2023; Moran et al. In Review). Models may be useful to resolve the variable experimental findings of the relative impact of different drivers of multiple possible states in boreal forests. Here, we begin to fill this gap by deriving mathematical models to examine what thresholds govern whether the boreal forest regenerates or becomes a grassland following a forest clearing disturbance. In our models, these thresholds may depend on aspects of moose herbivory, competition between forms of vegetation, and intrinsic growth of plant biomass. We parametrized the models with field data and values from literature (Table 3.1), to simulate the effects of moose herbivory and plants growth dynamics on the long-term trajectory of the system.

We hypothesize that stocks of vegetation palatable to moose must remain above a certain abundance, or else herbivory will outpace new growth leading to the extirpation of the palatable vegetation, similar to the response of vegetation to deer herbivory (Augustine et al. 1998). We assume that disturbance could drive the abundance of palatable vegetation below such a threshold. We, therefore, hypothesize that whether a system regenerates or not may be sensitive to the biomass of palatable plants and moose immediately following a disturbance. Additionally, that in the absence of the more competitive palatable vegetation, unpalatable vegetation (grasses and shrubs) would be released from competition leading to the formation of grasslands. However, do the thresholds depend on the initial moose densities and biomass of palatable species, or parameters governing ecological processes such as magnitude of herbivory (e.g., minimum time to eat a unit of plant, efficiency of conversion of plant biomass to moose biomass) or competition between vegetation (e.g., relative growth rates, competative effects)? We aim to answer this research question by simulating the effects of initial conditions (Figure 3.2. Objective i.) and ecological processes (Figure 3.2. Objective ii.) on the regeneration of the system to a mature boreal forest. Understanding the thresholds that determine whether a disturbed area regenerates to a mature boreal forest or not has practical benefits because it can inform how we manage these disturbances (i.e., number of moose hunted, volume of trees needed to plant).

3.3 Methods

3.3.1. Model development

Our goal was to develop a model of a characteristic eastern North American boreal forest, which is influenced by regular gap forming disturbances (insects, fire, etc.) and preferential moose browsing (see Introduction; Figure 3.1). To emulate these dynamics our model included a stock for moose biomass (M), young palatable plant biomass (P_y), mature palatable plant biomass (P_m), and unpalatable plant biomass (U). Young and mature palatable plants are considered to be the same tree species, which form the majority of a moose's diet (Dodds 1960; Belovsky 1978; Thompson and Vukelich 1981; Cumming 1987; Schwartz 1992), but are only accessible to moose when young. Specifically, once these plants reach three metres they are no longer within reach of moose browsing (Nichols et al. 2015). Consequently, in our model, young palatable plant biomass is consumed and mature palatable plant biomass is not. Unpalatable plant biomass (U), on the other hand, includes grasses, forbs and unpalatable shrubs and are not consumed by moose in this model (Dodds 1960;

Belovsky 1978; Thompson and Vukelich 1981; Cumming 1987; Schwartz 1992). While moose may consume some of this plant biomass in nature, it remains a very small part of their annual diet (Dodds 1960; Belovsky 1978; Thompson and Vukelich 1981; Cumming 1987; Schwartz 1992). Growth in the stock of moose biomass depends on a type II functional response of moose biomass to young palatable plant biomass (Lundberg and Danell 1990), based on a handling time (h) and attack rate (a). Consumed young palatable plant biomass is then converted into moose biomass based on a conversion efficiency (e). Loss from the moose stock (e.g., death) occurs at a density dependant rate (l_M). Addition to the stocks of young palatable plant biomass follows logistic growth under the constraints of competition. Specifically, growth is based on a growth rate of young palatable plant biomass (r_{Py}), and constrained by a carrying capacities (k_{Py}), and competition with mature palatable plants and unpalatable species (α_{UPy}). There is also addition to the stock of young palatable plant biomass through the addition of new seed at rate (s). Young palatable plant biomass is lost via consumption from moose (see above), through a death rate (l_{Py}), and as it ages with rate w into the mature palatable plant stock. Following Moen et al. (1998), we assume that the rate young palatable plant biomass matures decreases exponentially based on the proportion of young palatable plant biomass consumed by moose (Equation 3.1; Appendix 3.1.; Figure S3.1).

$$w^{1+3*\left(\left(\frac{a*P_y}{1+a*h*P_y}\right)*M \Big/ P_y+0.01\right)} \quad \text{(Eq. 3.1)}$$

We added a small amount (0.01) to the denominator so this function was never undefined. Addition to the stock of mature palatable plant biomass also follows logistic growth under the constraints of competition based on a growth rate of mature palatable plant biomass (r_{Pm}), and constrained by a carrying capacities (k_{Pm}), and competition with young palatable plants and unpalatable species (α_{UPm}). Further addition to the stock comes as young palatable plants age into the mature plant biomass stock with rate w. Mature palatable plant biomass is lost through a death rate (l_{Pm}). Addition to the stock of unpalatable plant biomass also follows logistic growth under the constraints of competition based on a growth rate (r_U) , and constrained by a carrying capacity (k_U), and competition with young (α_{PmU}) and mature (α_{PyU}) palatable plants. Unpalatable plant biomass is also lost through a death rate (l_U). All together, the system is represented by the series of ordinary differential equations (Eq. 3.2-3.5):

$$\frac{\mathrm{d}M}{\mathrm{d}t} = \left(\frac{a * \mathrm{P}_y}{1 + a * h * P_y}\right) * e * M - l_M * M^2 \quad \text{(Eq. 3.2)}$$

$$\frac{\mathrm{d}P_y}{\mathrm{d}t} = r_{P_y} * P_y * \left(\frac{1 - \left(P_y + P_m + \alpha_{UP_y}\right)}{k_{P_y}}\right) + s * P_m - \left(\frac{a * \mathrm{P}_y}{1 + a * h * P_y}\right) * M -$$

$$w^{1 + 3 * \left(\left(\frac{a * \mathrm{P}_y}{1 + a * h * P}\right) * M \Big/ P_y + 0.01\right)} * P_y - l_{P_y} * P_y \quad \text{(Eq. 3.3)}$$

$$\frac{\mathrm{d}P_m}{\mathrm{d}t} = r_{P_m} * P_m * \left(\frac{1 - \left(P_y + P_m + \alpha_{UP_m}\right)}{k_{P_m}}\right) + w * P_y - \mathrm{l}_{P_m} * P_m \quad \text{(Eq. 3.4)}$$

$$\frac{\mathrm{d}U}{\mathrm{d}t} = r_U * U * \left(\frac{1 - \left(U + \alpha_{P_y U} * P + \alpha_{P_m U} * P_m\right)}{k_U}\right) - \mathrm{l}_U * U \quad \text{(Eq. 3.5)}$$

Evidence from empirical studies demonstrates that eastern North American boreal forests can exist perpetually in different regimes: mature boreal forest (often dominated by adult coniferous trees), and grasslands or shrublands (Thompson et al. 1992; Rotter and Rebertus 2015; Charron and Hermanutz 2016; De Vriendt et al. 2021). We capture these states in our model as follows. A scenario dominated by mature palatable plants is the model's approximation of a mature boreal forest (Figure 3.1. A). Whereas, a scenario where the stocks of palatable plant biomass are near zero is the model's approximation of a recently disturbed area. These disturbed areas have potential to regenerate to a mature forest through the growth of palatable plants (Figure 3.1.B), however, high moose herbivory of young palatable plants can slow (Figure 3.1.C) or stop regrowth and cause the area to be dominated by unpalatable plants (grasses and kalmia; Figure 3.1.D). A scenario dominated by unpalatable plants is our model's approximation of a moose meadow, where after a forest disturbance event the area is perpetually dominated by grasses and shrubs.

3.3.1.1. Assumptions

Based on forest regeneration theory, the first species to colonize a canopy opening should be fast growing but poor competitors (Hart and Chen 2006; Bartels et al. 2016), then slower growing but better competitors will establish afterwards and slowly replace the early set of species (Huston and Smith 1987; McCook 1994; Archambault et al. 1998; Bartels et al. 2016). Similar to the simulations of succession by Huston and Smith (1987), we set the relative growth rates, rates of biomass loss (determined by longetvity), and competitive interactions of the three stocks of plant biomass based on our consideration of whether the stocks were primarly early or later successional species. We assumed that unpalatable plant biomass was primarly composed of early successional species (e.g., blueberry, forbs; Mallik 1995, Royo and Carson 2006, De Vriendt et al. 2021) and that palatable plant biomass was primarily composed of later successional tree species (e.g., balsam fir and black spruce; Brandt 2009). Therefore, we assumed the growth rate of unpalatable plant biomass (U; early successional species) was higher than the growth rate of palatable plant biomass (P_y, P_m; later successional species; $r_U > r_P$; Table 3.2). We also assumed the rate of loss of unpalatable plant was faster than that of palatable plant biomass ($l_U > l_P$), since palatable plant species (trees) are longer lived than unpalatable plant species (grasses and forbs). To characterize the competitive interactions during succession, we assumed that palatable plant biomass could outcompete unpalatable plant biomass, but not the other way around. More specifically, we assumed the competative effect of mature palatable plant biomass on unpalatable plant biomass was larger than that of young palatable plant biomass on unpalatable plant biomass, and that the effect of unpalatable plant biomass on young plant biomass was larger than that of unpalatable plant biomass on mature palatable plant biomass ($\alpha_{UPm} < \alpha_{UPy} < \alpha_{PyU} < \alpha_{PmU}$). We assumed the competitive effect of unpalatable plant biomass on mature palatable plant biomass to be as near to zero as the model could handle without running into precision errors. Our assumptions of competative effects do not consider areas where invasive unpalatable plants may outcompete palatable plants, and thus, this assumption could be relaxed in future models if the specific area of interest requires. Based on observations in the field (Appendix 3.2.), we assumed the carrying capacity of unpalatable plant biomass was less than the carrying capacity of young palatable plant biomass, which was less than the carrying capacity of mature palatable plant biomass (i.e., $k_U < k_{Py} < k_{Pm}$.). Similar to Otto et al. (2007) and Roy et al. (2020), we specified extinction explicitly in our model code. If any stock became smaller than 0.01 $t*km^{-2}$ the value of the stock was changed to 0.

3.3.2. Simulations

3.3.2.1. Determining steady state end conditions

We determined our system had reached steady state when the changes in all stocks between time steps was less than 1e-8, when our system was solved numerically (Soetaert et al. 2008; Soetaert 2008). We then categorized the resulting steady states into two possible regimes based on end conditions. In the first possible regime, mature palatable plant biomass would reach near carrying capacity (Appendix 3.3., Figure S3.2 A). In these scenarios young palatable plant biomass would always be present in lower quantities that depended on parameter values, and moose and unpalatable plant biomass were either present at some intermediate value or extinct. The second possible regime had only unpalatable plant biomass

(Appendix 3.3., Figure S3.2. B). We considered any simulation that ended with mature palatable plant biomass to have regenerated to mature forest, and any simulation that ended with no mature palatable plant biomass to have become a grassland. We numerically solved our system using deSolve::ode (Karline Soetaert et al. 2010) in R Version 2024.04.2+764 (R Core Team 2023). For any scenario where the model regenerated to mature forest, we determined the number of years it took the system to regenerate. We considered a system regenerated when mature palatable plant biomass reached within 1% of the value of mature palatable plant biomass once the system is stable.

3.3.2.2. Effect of initial conditions

To accomplish objective i. and assess the effects of initial conditions on the regeneration of a 1 km^2 disturbed area to mature boreal forest, we simulated the system starting at 900 combinations of initial conditions. We set the different initial conditions to represent possible post disturbance scenarios with different values of remaining young palatable plant biomass and moose biomass. The 900 sets of starting conditions contained all possible combinations of 30 values of remaining young palatable plant biomass (from 0 t; low to 500 t; high) and 30 values of moose biomass (from 0t ; no moose to 6 t; above historic high moose density from McLaren et al. 2009). We set all initial values of mature palatable plant biomass to 0 t; because if any mature plant biomass remained the system would regenerate 100% of the time, and unpalatable plant biomass to 100 t based on data collected in field (Appendix 3.2.). To simulate each initial condition over a range of realistic situations we created 94 random combinations of parameter values (number of combinations determined in Appendix 3.4.; Figure S3.3). Specifically, 150 combinations of parameters were drawn randomly by R from a normal distribution within the range we determined from literature for each parameter (Table 3.1), and filtered to meet assumptions (Table 3.2), leaving

94 combinations. We kept the same 94 random combinations of parameters for each combination of initial conditions. In total, we ran 84 600 simulations to assess the effects of initial conditions.

For each set of initial conditions we counted the number of runs where the system regenerated to mature forest (end condition dominated by mature palatable plant biomass; Figure 3.1. A) or became grassland (end condition dominated by unpalatable plant biomass/without mature palatable plant biomass; Figure 3.1. C). We also calculated the mean number of years it took for the simulations with the same initial conditions to regenerate. We could therefore, compare how changes in initial conditions influenced the probability a disturbed area regenerates and how long it takes to regenerate, across a range of realistic situations.

3.3.2.3. Effect of parameters

For objective ii. we wanted to assess the influence of each parameter, and therefore the influence of moose herbivory and plant growth, on how often the system regenerated to mature forest or became a grassland. This was done by simulating the system setting one parameter at a time at 11 evenly spaced values across its reasonable range, with the rest of the parameters drawn randomly by R from a normal distribution within the range we determined from literature (ranges were determined using minimum and maximum values found throughout literature and empirical data from Chapter 2; Table 3.1). For each level of the parameter being set, we repeated the simulations 150 times, drawing a new random combination of values for the remaining parameters determined from literature for each parameter (Table 3.1), and filtered to meet assumptions (Table 3.1), leaving 94 combinations. Furthermore, for each combination of set parameter values and randomly selected remaining parameter combinations, we started a simulation at each of combinations of initial conditions that didn't have 100% or 0% of simulations regenerating (total of 284 initial conditions). For each parameter, we ran a total of 293 656 simulations (11 * 94 * 284). At each of the 11 values of the parameter being set, for each random combination of remaining parameter values, we calculated the percent of simulations that regenerated to a forest or converted to a grassland and the mean number of years for the simulations to regenerate. We then repeated this whole process for all parameters. We could therefore, compare how changes in biological processes influenced the probability a disturbed area regenerates and how long it takes to regenerate, across a range of realistic situations.

3.4. Results

3.4.1. Effect of initial conditions

3.4.1.1. Mature forest likelihood of regeneration

Our model suggests that the likelihood an area regenerates to mature boreal forest after a forest clearing disturbance depends on the initial ratio of young palatable plant biomass (Py) to moose biomass (Figure 3.3). If at the beginning of a simulation there is enough young palatable plant biomass per moose, a ratio of 37 t of Py for every 1 t of moose or higher and the system will regenerate under all parameter combinations. On the other hand, if at the start of a simulation there is not enough young palatable plant biomass per moose, a ratio of 10 t of Py for every 1 t of moose or lower, the system with be converted to grassland under all parameter combinations. In between these two ratios, there is a gradient of likelihood the system will regenerate. In this mid range (Appendix 3.5.; Figure S3.5), every 1 t increase in initial moose biomass, with initial young palatable plant biomass remaining constant, causes the forest to regenerate, on average, 44% less often. Whereas, every 1 t increase in initial young palatable plant biomass, with initial moose biomass remaining constant, results in the forest regenerating, on average ~ 1.5% more often. Thus, to maintain the same likelihood of regeneration, there must be ~29 t more initial biomass of Py for every 1t increase in initial moose biomass present.

While for some ranges of initial conditions the likelihood of regeneration depends on the values of both moose and Py, there are instances where a change in the initial value of one stock will not change the likelihood the area will regenerate (Figure 3.3). For example, the system will always regenerate if the initial young palatable plant biomass is higher than ~210 t, across all values of initial moose biomass tested. The system will also always regenerate if initial moose biomass is lower than ~0.75 t, unless initial Py is 0 t in which case there is no chance of regeneration.

3.4.1.2. Mature forest regeneration time

For initial conditions that regenerate more than 50% of the time (above a ratio of about 25 t Py to 1 t M), a 1 t increase in young palatable plant biomass, keeping moose biomass constant, will decrease the number of years for the simulation to regenerate by an average of 0.7 years (Figure 3.4). The initial conditions that take the longest to regenerate have the lowest ratios of Py to M that regenerate at least once (10 t Py:1 t M). However, below the ratio where simulations regenerate 50% of the time (about 25 t Py to 1 t M), the pattern is more variable. There seems to be a repetitive pattern, where for some instances regeneration time continues to increase as the ratio young palatable plant biomass to moose biomass decreases, but at the same ratios but with higher moose densities, regeneration time will decrease as the ratio of young palatable plant biomass to moose biomass decreases (Figure 3.4).

3.4.2. Effect of herbivory and plant growth

3.4.2.1. Mature forest likelihood of regeneration

Several parameters can also influence the likelihood of a system regenerating to mature boreal forest after a forest clearing disturbance. Both processes influencing the magnitude of herbivory (conversion efficiency, e; handling time, h; loss rate, l_M), and processes influencing the growth of young palatable (growth rate, r_{Py}; rate grow out of browse zone, w; loss rate l_{Py}) affect the likelihood of regeneration (Figure 3.5).

Three of the four processes in our model that are associated with herbivory substantially influence whether the system will regenerate to mature boreal forest after a forest clearing disturbance (Figure 3.5). The mean percent of simulations that regenerate increases 2.94 times across the range of handling times (h; 0.0208 – 0.0387 t_M * year * t_{Py}^{-1}; Table 3.1). Therefore, at the lowest value of handling time of 0.0208 t_M * year * t_{Py}^{-1}, 21.5% of simulations regenerate, and at the highest value of handling time of 0.0387 t_M * year * t_{Py}^{-1}, 63% of simulations regenerate. The mean percent of simulations that regenerate also increases 1.38 times across the range of rate of moose biomass loss (l_M; 0.2647 – 0.3765 (t_M * year)$^{-1}$). In contrast, mean percent of simulations that regenerate decreases 1.52 times across the range of conversion efficiency (e; 0.01 – 0.03 t_M * t_{Py}^{-1}).

Several processes in our model that are associated with the growth of young palatable plant biomass influence whether the system will regenerate to mature boreal forest after a forest clearing disturbance. The mean percent of simulations that regenerate increases 1.35 times across the range of young palatable plant biomass growth rates (r_{Py}; 0.15 - 0.325 t_{Py} * (t_{Py} * year)$^{-1}$; Figure 3.5), and 6.98 times across the range of rates of young plant biomass maturing to mature plant biomass (w; 0.09 - 0.2 year^{-1}). In contrast, regeneration decreases

1.23 times across the range of loss of mature palatable plant biomass rates (l_{Pm}; 0.005 - 0.02 $year^{-1}$).

3.4.2.2. Mature forest regeneration time

Both processes influencing the magnitude of herbivory (conversion efficiency, e; handling time, h; loss rate, l_M), and processes influencing the growth of young and mature palatable plant biomass (growth rate, r_{Py} & r_{Pm}; rate grow out of browse zone, w; rate of seed addition, s; loss of mature palatable plant biomass, l_{Pm}) affect the likelihood of regeneration (Figure 3.6).

Again, three of the four processes in our model that are associated with herbivory influence the time it takes the system to regenerate to mature boreal forest after a forest clearing disturbance. The mean number of years to regenerate decreases by 16.17 years, or 1.1 times across the range of handling times (h; 0.0208 – 0.0387 t_M * year * t_{Py}^{-1}; Table 3.1). The mean number of years to regenerate also decreases by 7.68 years, or 1.05 times, across the range of rate of moose biomass loss (l_M; 0.2647 – 0.3765 $(t_M * year)^{-1}$). In contrast, the mean number of years to regenerate increases by 9.68 years, or 1.06 times, across the range of conversion efficiency (e; 0.01 – 0.03 $t_M * t_{Py}^{-1}$).

Several processes in our model that are associated with the growth of young and mature palatable plant biomass influence the time it takes the system to regenerate to mature boreal forest after a forest clearing disturbance (Figure 3.5). The mean number of years to regenerate decreases by 16.17 years, or 1.09 times, across the range of rates of young plant biomass maturing to mature plant biomass (w; 0.09 - 0.2 $year^{-1}$), by 3.91 years, or 1.02 times, across the range of seed addition rates (s; 0.0088 - 0.053 tPy * $(t_{Pm} * year)^{-1}$), and by 130.00 years, or 2.12 times, across the range of mature palatable plant biomass growth rates (r_{Pm}; 0.1 - 0.2 $t_{Pm} * (t_{Pm} * year)^{-1}$). In contrast, the mean number of years to regenerate increases by

10.22 years, or 1.06 times, across the range of matrue palatable plant biomass carrying capacities (k_{Pm}; 20000 – 80000 t_{Pm}), and by 104.04 years, or 1.65 times, across the range of mature palatable plant biomass loss rates (l_{Pm}; 0.005 - 0.02 $year^{-1}$). Uniquely, the pattern across the range of young palatable plant biomass growth rates (r_{Py}; 0.15 – 0.325 t_{Py} * (t_{Py} * $year)^{-1}$) is not consistent. The mean number of years to regenerate decreases until rPy = 0.29, then above that the number of years to regenerate increases in both mean and variation. This results in a net increase of 6.97 years, or by 1.04 times, to regenerate across the range of young palatable plant biomass growth rates.

3.5. Discussion

Areas of eastern boreal forests are not regenerating after disturbances, leading to conservation concerns (Gosse et al. 2011; Smith et al. 2015; Parks Canada Agency 2018; Parks Canada 2019, 2021). The inhibition of regeneration and possible transition of these areas to grassland is often attributed to hyperabundant moose populations (Brandner et al. 1990, Smith et al. 2010, Hidding et al. 2013, Rotter and Rebertus 2015, Parks Canada Agency 2018, Leroux et al. 2021; Figure 3.1). However, the effects of moose herbivory in disturbed areas can be variable (Petersen et al. 2023; Moran et al. In Review). Simple models representing explicit interactions between components of a system let scientists investigate ecological processes (Grimm 1994; Odenbaugh 2005) with possible applications to ecosystem management. We derive a model of a characteristic eastern North American boreal forest which is influenced by gap forming disturbances (insects, fire, etc.) and preferential moose browsing. We explored how the initial forest conditions and moose densities as well as ecological processes of herbivory, and plant growth and competition impact the trajectory of forest regeneration. We report scenarios where initial conditions and certain ecological processes determine whether the mature forest regenerates and the time to regeneration. We end by discussing the management implications of these findings.

3.5.1. Effects of initial conditions

3.5.1.1. Mature forest likelihood of regeneration

Regeneration of the system to mature boreal forest can be solely determined by the initial amounts of young palatable plant biomass and moose biomass remaining after a disturbance, specifically when the two stocks are at more extreme magnitudes. If forest clearing disturbances drive abundance of young palatable plant biomass below a certain threshold, relative to moose abundance (below 10 t per t of moose biomass), herbivory will outpace new growth leading to the extirpation of the palatable vegetation. This is similar to the outcomes of simulated and empirical observations of deer herbivory in Minnesota, US (Augustine et al. 1998), and empirical observations of moose herbivory in boreal forests of Isle Royale, US (Brandner et al. 1990,) and Cape Breton Highlands National Parks, CA (Franklin and Harper 2016). In nature, this could occur when a disturbance that is indiscriminate in its removal of biomass, for example severe forest fires, affects an area with relatively high moose populations. Conversely, if enough young palatable plant biomass remains after the disturbance relative to moose populations (above 37 t per t of moose), the moose cannot consume all the young plant biomass, ensuring some plant biomass grows to mature stock and the forest recovers. A scenario where this would be the case is when disturbances that target only mature trees, for example logging, affects an area with advanced regeneration and moderate to low moose populations (Spence and MacLean 2012). Consequently, the severity of disturbance, and abundance of moose following the disturbance, can strongly influence whether the area recovers or not. Previous work also provides evidence disturbance type and severity, moose populations and the interaction between the two can influence the regeneration of boreal forests (Bartels et al. 2016; Andrus et al. 2020). For example, the size of gap formed by disturbance and moose densities have substantial effects on the success of recovery in disturbed areas in both empirical studies (Charron and Hermanutz 2016) and mathematical models (Noonan et al. 2021). High initial moose populations were found to have legacy effects on the ability of gaps to recover, impeding recovery in large gaps even once populations were lowered. Similar legacy impacts of initial conditions of our model could be investigated using time series sensitivity analyses.

3.5.1.2. Mature forest regeneration time

According to our model, gaps in the boreal forest generally regenerate faster when there is a higher ratio of remaining young palatable plant biomass per moose. As remaining young palatable plant biomass increases per moose biomass, more trees are able to outpace herbivory (Augustine et al. 1998) and contribute to regeneration by becoming mature trees. This is consistent with the decreased time to regeneration found in stands with greater surviving juveniles after a disturbance, even under deer browsing in subalpine forests of the southern Rocky Mountains, US (Andrus et al. 2020). In that case, pre-disturbance stand complexity and species diversity also played a role in the time for stands to regenerate (Andrus et al. 2020). Similar to probability of regenerating, the regeneration time after a disturbance can depend on stand or disturbance characteristics, such as amount of advanced regeneration and disturbance severity.

3.5.2. Effects of herbivory and plant growth

3.5.2.1. Mature forest likelihood of regeneration

The likelihood of forest regeneration seems to be influenced by processes that govern the magnitude of consumption by moose, by either influencing the rate of consumption (h) or the amount of moose biomass present (e, l_M). Of these, handling time was the most influential (Figure 3.5 & 6). When the magnitude of consumption by moose is high, it outpaces the growth of young palatable plant biomass and inhibits plant recruitment into mature palatable plant biomass, thus inhibiting forest regeneration. Abundance of palatable species has previously been related to moose browsing intensity (Connor et al. 2000), and the height and density of young palatable species can be strongly impacted by moose herbivory (McInnes et al. 1992; Leroux et al. 2021b; De Vriendt et al. 2021; Buchkowski et al. 2023). Plant species diversity, temperature, and other environmental conditions such as snow depth may also influence bite choices and components of a moose's functional response (Vivås and Sæther 1987; Hjeljord et al. 1990; Lenarz et al. 2009). While we did not directly investigate the influence of such drivers, we hope to have captured their possible impacts by simulating across a range of parameter combinations.

Our model also suggests that the likelihood of a gap regenerating to mature boreal forest is dependent on the intrinsic growth of young palatable plant biomass (r_{py}, w, l_{py}). These rates can determine whether the increase in young palatable plant biomass outpaces herbivory and thus if some trees escape the browse zone (i.e., ~ 3m). The maximum rate at which young palatable plant biomass grows past 3 m, and escapes the browse zone, had the greatest impact on forest regeneration. This maximum maturation rate, as well as growth rate of young palatable plant biomass were also important for return time in a similar model of preferential herbivory with competition of boreal forest tree species (Buchkowski et al. 2023). The growth of young palatable plant biomass, and therefore regeneration time, can then vary in response to species composition (Boucher et al. 2006) and environmental conditions (Mao et al. 2019).

3.5.2.2. Mature forest regeneration time

Our model demonstrates that gap regeneration time also depends on the magnitude of moose herbivory and the intrinsic growth of young and mature trees. This occurs because the relative magnitude of moose herbivory and tree growth determine the ability of young palatable plant biomass to reach a mature state and escape herbivory. Additionally, the faster mature palatable plant biomass accumulates, the sooner the system will regenerate to a mature forest. This is consistent with empirical evidence for increased rate of boreal forest regeneration with site productivity and the speed of tree growth (Mack et al. 2008; Bolton et al. 2015; Boucher et al. 2017). Additionally, regeneration time has previously been shown to be sensitive to processes governing moose herbivory (Buchkowski et al. 2023). Similar stand characteristics (e.g., species composition, environmental conditions) affecting likelihood of regeneration would also influence moose herbivory and plant growth, leading to varying regeneration times.

3.5.3. Model considerations

One distinct alteration from a previous model of selective herbivory in the boreal forest (Buchkowski et al. 2023) is our use of a type II instead of type I functional response of moose herbivory to young palatable plant biomass. Therefore, when the abundance of young palatable plant biomass is too low, the per capita effects of herbivory on young palatable plant biomass is greater than the per capita growth of young palatable plant biomass. Consequently, our use of a type II functional response to model moose response to young palatable plant biomass can potentially lead young palatable plant biomass to extinction. While mechanistic models of type II functional responses (like the Hollings disc equation used here) do describe the response of moose herbivory to overall plant abundance well, future models with explicit plant patch dynamics could account for variation in plant palatability as well as quantity within the simulated area (Lundberg and Danell 1990). By using a model of herbivore-plant patch dynamics, future models of selective herbivory in the boreal forest could explicitly investigate the influence of species composition on herbivore consumption and gap regeneration.

Our model is currently limited to two biotic trophic levels; primary producers and herbivores and is therefore a model of a community. However, models of ecosystems with abiotic interactions can yield very different predictions than community models (Loreau and Holt 2004). What is more, herbivore effects on plants may be mediated by herbivore effects on abiotic conditions. For example, grazing can promote plant primary productivity by increasing nitrogen availability (Holland et al. 1992; de Mazancourt et al. 1998), while trampling can reduce nitrogen availability (Meyer and Leroux 2024). Consequently, the incorporation of an abiotic nutrient compartment, and their interactions with plants and moose into our model could alter the thresholds that determine whether a disturbed area regenerates to a mature boreal forest.

The number of years our simulations took to regenerate is likely much longer than in a real forest. This may be caused by our very conservative threshold to consider a simulation regenerated (within 0.01% of mature palatable plant biomass of the system when stable). Therefore, in some simulations, the forest had to reach up to almost 80 000 t of mature palatable plant biomass, whereas, in reality, some mature forests have as little as 20 000 t of mature palatable biomass (Table 3.1; Appendix 3.2.). The number of years to regenerate can therefore be taken as relative, and the important information to take from the analysis is the relative influence of initial conditions and parameters on regeneration.

3.5.4. Implications

Different empirical studies report varying evidence for the effects of moose herbivory on the regeneration of boreal forests after gap forming disturbances. Classic studies in Isle Royale (Brandner et al. 1990; McInnes et al. 1992) and Cape Breton (Smith et al. 2010; Parks Canada Agency 2018), have observed the formation of meadows, but these are less prevalent in other systems like Newfoundland (Leroux et al. 2021b) and Norway (Kolstad et al. 2018). Recent meta-analysis show a mean negative effect of moose on plant biomass across 100 exclosure/control plots in the circumboreal but there is a striking amount of individual site variability in these patterns (Petersen et al. 2023). We use a simple model of a characteristic eastern North American boreal forest, which is influenced by regular gap forming disturbances (insects, fire, etc.) and preferential moose browsing, to uncover the drivers of forest transition to grassland or mature forest regeneration. We found that, at more extreme initial conditions of moose biomass and remaining young palatable plant biomass (e.g., above 37 t of Py for every 1 t M), initial conditions of the system can be the driving force behind whether the regime shifts or the forest regenerates. However, at more intermediate initial conditions (e.g., M = 3 t, and Py = 60 t) rates determining magnitude of herbivory and young palatable plant biomass growth also determine regeneration. Therefore, previous variable empirical results about the effects of moose on the regeneration of boreal forests after gap forming disturbances may have resulted from disparities in region’s disturbance severity, tree species composition, or environmental conditions that can lead to different moose herbivory and young palatable plant growth.

Our model not only helps interpret variable empirical results but can also inform management. Broadly, to ensure regeneration of boreal forests after disturbances we recommend maintaining low moose populations. Specifically, we predict that gaps should regenerate at moose densities less than 2.4 moose per square kilometer, regardless of disturbance severity or rates of moose herbivory and plant growth. However, as the remaining young palatable plant biomass increases, and some ecological rates changes, the system may be able to support higher moose densities and still regenerate. Influencing ecological processes such as moose death and tree growth through management like hunting, fertilization, and fungicides could help ensure regeneration and decrease the time for forests to regenerate. To make quantitative estimates of required management efforts for specific management areas, decision makers can estimate required efforts off an area's initial conditions of moose biomass or remaining young palatable plant biomass using Figure 3.3. For example, if after a forest fire, an area of 1 km^2 had only 50 t of remaining young palatable plant biomass but high moose biomass of 3 t (about 9 moose), we predict planting at least 75 t of young trees or lowering moose densities by just over a tonne (decrease by about 4 moose/km^2) could help ensure regeneration. Or, estimates could be made more specific to management areas. Specific values for management targets could be obtained by constraining the parameter values to better reflect the area of interest. For example, plant growth parameter values could be based on dominant tree types from forest inventory data, and moose herbivory parameters values could be based on moose habitat use data. Hopefully, this helps manage areas of boreal forest to maintain typical heterogenous age structure, biodiversity, wood resources, carbon storage and other ecosystem services.

3.6. Statements & Declarations

3.6.1. Acknowledgements

We first acknowledge that this work studies the forests towards the east of Turtle Island, which includes the ancestral lands of the Mi'kmaq, Wolastoqiyik, Abenaki, Penobscot, Passamaquoddy, Beothuk, and Innu Peoples. These Peoples have stewarded this land since time immemorial, have cultivated in depth knowledge of the land, and continue to be at the forefront of its conservation. We thank the people involved with field data collection: R. Moran for designing and implementing the first year of data collection, and H. Adams, J. Hussey, J. Ball, J. Scott, and D. Bath, L. McDaniel, and N. van Miltenburg for their assistance with data collection and processing. Park staff and such as D. Whitaker and J. Gosse were also integral for the success of you field work. Thank you to all the current and past members of EEL, who gave insightful feedback throughout the development of the model. Special thanks to A. Arkilanian for helping us get around several coding roadblocks. Finally, thank you to my committee members, Y. Wiersma and A. Hurford for providing feedback throughout.

3.6.2. Data availability

The R code required to run our analyses are available at https://figshare.com/projects/Using_a_mathematical_model_to_determine_drivers_of_regime_shifts_in_eastern_boreal_forests/232208.

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3.8. Tables

Table 3.1. Model parameter definition, units, values, and sources. All parameters based on an area of 1 km^2. t_M is metric tonnes of moose, t_{Py} is metric tonnes of young palatable plants, and t_{Pm} is metric tonnes of mature palatable plants.

Parameter	Definition	Minimum	Maximum	Units	Source
a	Attack rate	0.996	1.005	$(t_M * \text{year})^{-1}$	(Renecker and Hudson 1986; Lundberg and Danell 1990)
h	Handing time	0.0207933	0.038735	$t_M * \text{year} * t_{Py}^{-1}$	(Belovsky 1978; Gross et al. 1993)
e	Conversion efficiency	0.01	0.03	$t_M * t_{Py}^{-1}$	(Humphreys 1979)
l_M	Loss rate of moose biomass	0.2647	0.3765	$(t_M * \text{year})^{-1}$	(Hatter and Bergerud 1991; McLaren et al. 2000)
Mt	Mass of moose	NA		tM	(Gross et al. 1993)
s	Rate of addition of new seed	0.0088	0.053	$t_{Py} * (t_{Pm} * \text{year})^{-1}$	(Rossi et al. 2012; Buchkowski et al. 2023)
r_{Py}	Per capita growth rate of young palatable plant biomass	0.15	0.325	$t_{Py} * (t_{Py} * \text{year})^{-1}$	(Sprugel 1984)
r_{Pm}	Per capita growth rate of mature palatable plant biomass	0.1	0.2	$t_{Pm} * (t_{Pm} * \text{year})^{-1}$	(Coyea and Margolis 1994; Buchkowski et al. 2023)
α_{UPm}	Competitive effect of unpalatable plant biomass on young palatable plant biomass	0	0.0002	$t_U * t_{Py}^{-1}$	NA
k_{Py}	Carrying capacity of young palatable plnat biomass	400	2000	t_{Py}	Field data; Appendix 3.2.; Chapter 2

w	Rate young mature palatable plant biomass grows out of browse zone	0.09	0.2	$year^{-1}$	(Moen et al. 1998; Pothier 2002; Nigh et al. 2009; Prévost and Gauthier 2012)
α_{UPy}	Competitive effect of unpalatable plant biomass on mature palatable plant biomass	0.0005	0.0019	$t_U * t_{Pm}^{-1}$	Field data; Appendix 3.2.; Chapter 2
k_{Pm}	Carrying capacity of mature palatable plant biomass	20000	80000	t_{Pm}	Field data; Appendix 3.2.; Chapter 2
l_{Py}	Loss rate of young palatable plant biomass	0.1	0.3	$year^{-1}$	(Buchkowski et al. 2023)
l_{Pm}	Loss rate of mature palatable plant biomass	0.005	0.02	$year^{-1}$	(McCarthy and Weetman 2006)
r_U	Per capita growth rate of unpalatable plant biomass	0.6	1.3	$t_U * (t_U * year)^{-1}$	(Kumar et al. 2018)
α_{PyU}	Competitive effect of young palatable plant biomass on unpalatable plant biomass	0.001	0.003	$t_{Py} * t_U^{-1}$	Field data; Appendix 3.2.; Chapter 2
α_{PmU}	Competitive effect of mature palatable plant biomass on unpalatable plant biomass	0.004	0.008	$t_{Pm} * t_U^{-1}$	Field data; Appendix 3.2.; Chapter 2
k_U	Carrying capacity of unpalatable plant biomas	300	1200	t_U	Field data; Appendix 3.2.; Chapter 2
l_U	Loss rate of unpalatable plant biomass	0.168	1	$year^{-1}$	(Peters 2002; Kumar et al. 2018)

Table 3.2. Assumptions about the system, and their mathematical representations

Assumption		Mathematical representation
1	Intrinsic growth rate of palatable lower than unpalatable	$r_P < r_U$
2	Rate of biomass loss for mature palatable is lower than for unpalatable	$l_{Pm} < l_U$
3	Competitive effect of unpalatable on mature palatable is less than the effect of unpalatable on young palatable, which is less than the effect of young palatable on unpalatable, which is less than the effect of mature palatable on unpalatable	$\alpha_{UPm} < \alpha_{UPy} < \alpha_{PyU} < \alpha_{PmU}$
4	Competitive effect of unpalatable on mature palatable assumed to be very small	$\alpha_{UPm} \approx 0$
5	Carrying capacity of unpalatable is less than the carrying capacity of young palatable, which is less than the carrying capacity of mature palatable	$k_U < k_{Py} < k_{Pm}$

3.9. Figures

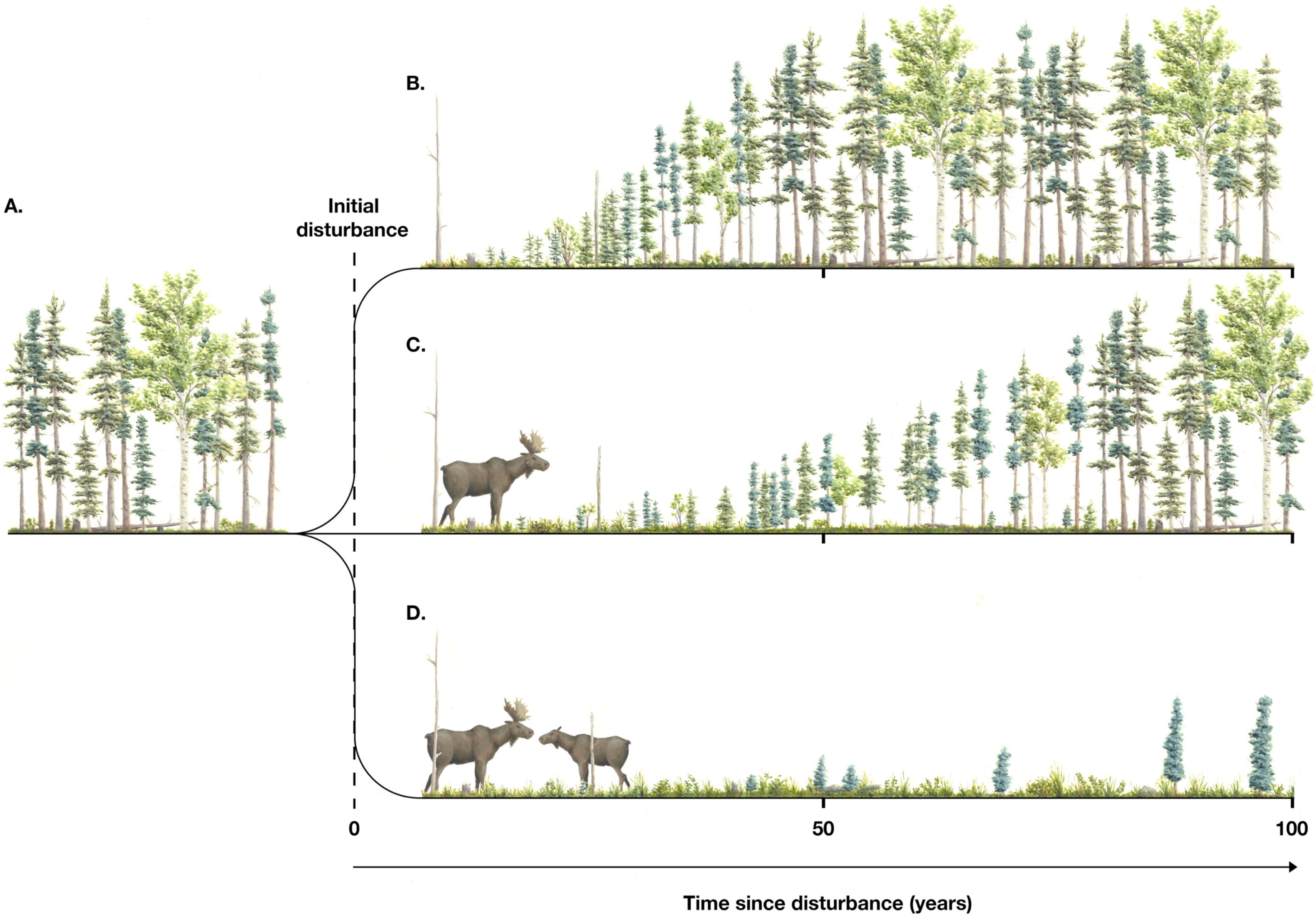

A.
Initial disturbance
B.
C.
D.
0
50
100
Time since disturbance (years)

Figure 3.1. Regeneration trajectories of a characteristic eastern North American boreal forest (A; left) after forest clearing disturbance, under the impacts of no (B; top), low (C; middle), and high (D; bottom) moose herbivory. Moose feed on the canopy forming balsam fir seedlings which has an impact on forest regeneration following an initial disturbance (Leroux et al. 2020). Painted by Emmerson Wilson

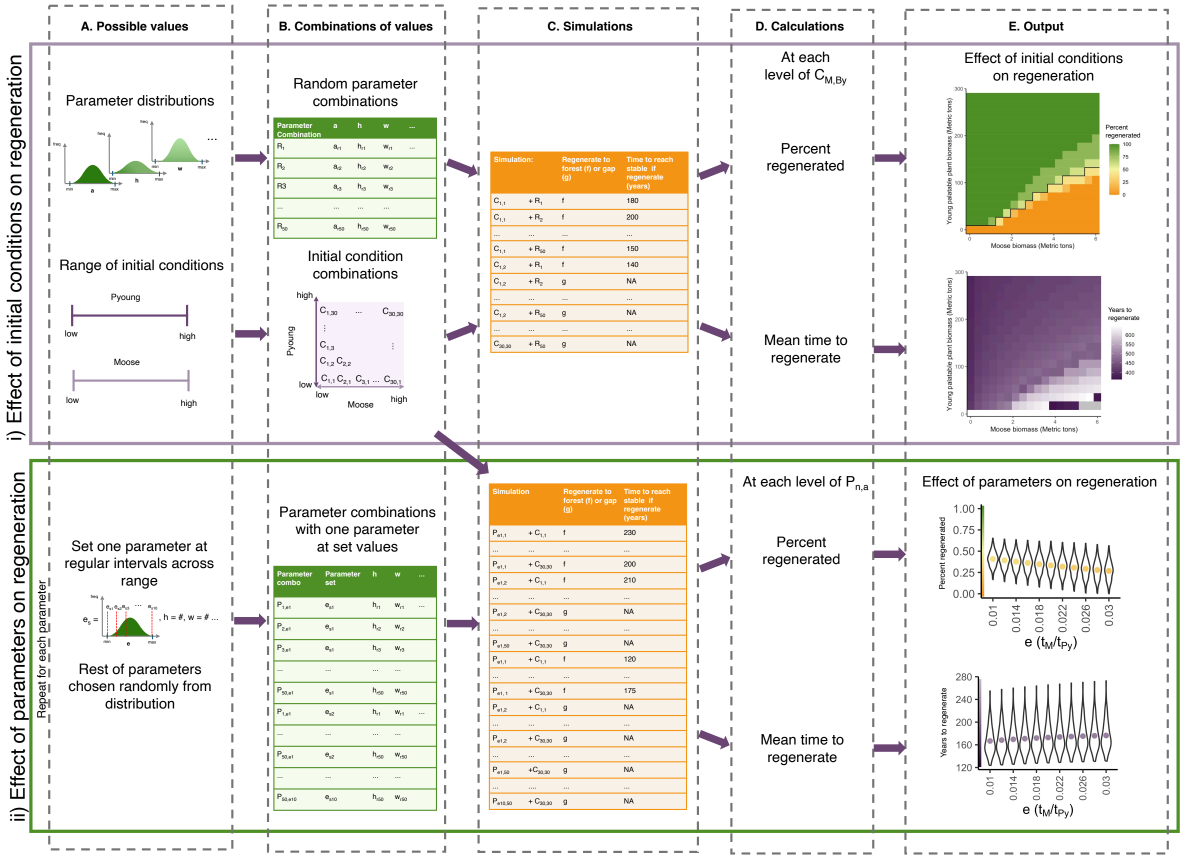


Figure 3.2. Flow diagram of analysis. A. The initial conditions (amount of moose biomass and young palatable plant biomass present at start of simulations) and parameter values (govern the mathematical model of a characteristic eastern North American boreal forest Eq. 3.2 – 3.5) are drawn from ranges of found in-field and in literature. B. The values from A are combined to make combinations of initial conditions, and combinations of parameter values C. The combinations of initial conditions are combined with the parameter values. Simulations using each combination of parameter values is started at each combination of initial conditions. From each simulation we can extract whether the forest regenerates or not and the time it takes to regenerate. D. The values we extract from each simulation are used to

calculate the percent regenerated and mean time to regenerate at the desired grouping level.

E. The output created from the values extracted in step D.

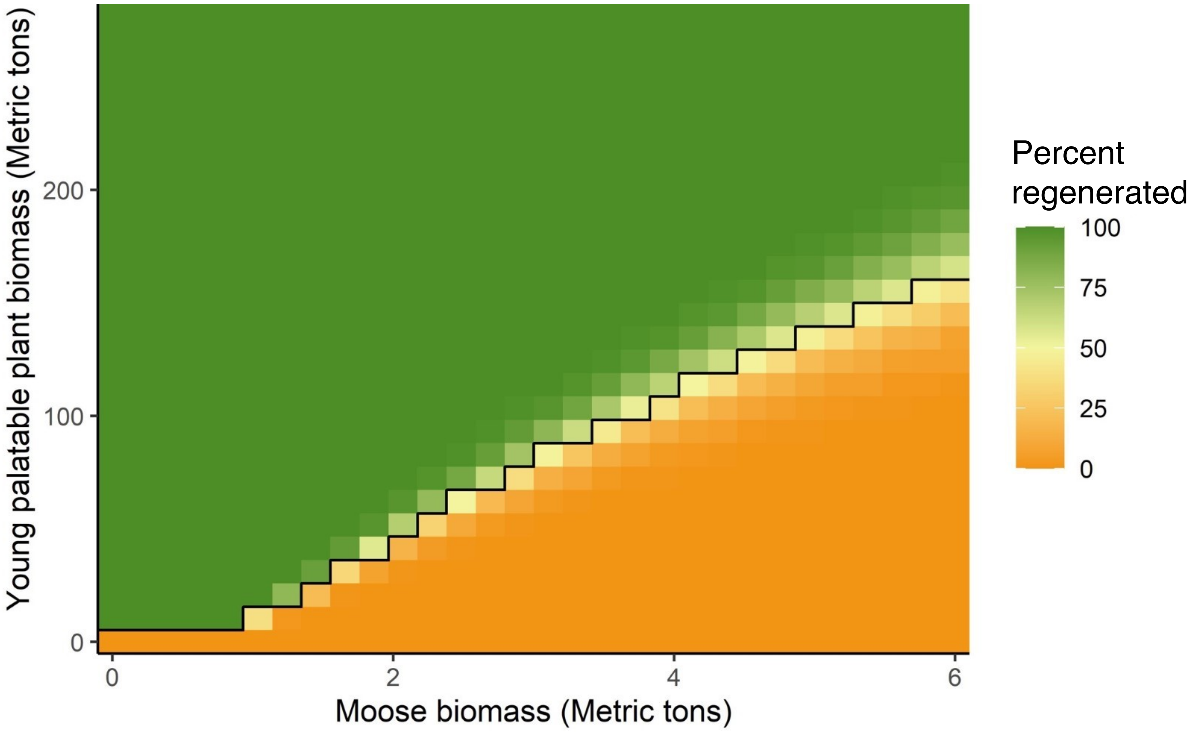


Figure 3.3. Heatmap depicting percent of simulations that regenerated to mature boreal forest for each combination of initial conditions of moose density and young palatable plant biomass for an area of 1 km^2. Each cell is based on 94 simulations, each simulation had a different combination of parameter values randomly selected from a normal distribution with mean, min, max values determined from the literature (see Table 3.1). The set of random combinations of parameters were the same for each combination of initial conditions. At least 50% of simulations regenerated for cells above the black line, less than 50% of simulations regenerated for cells below the black line.

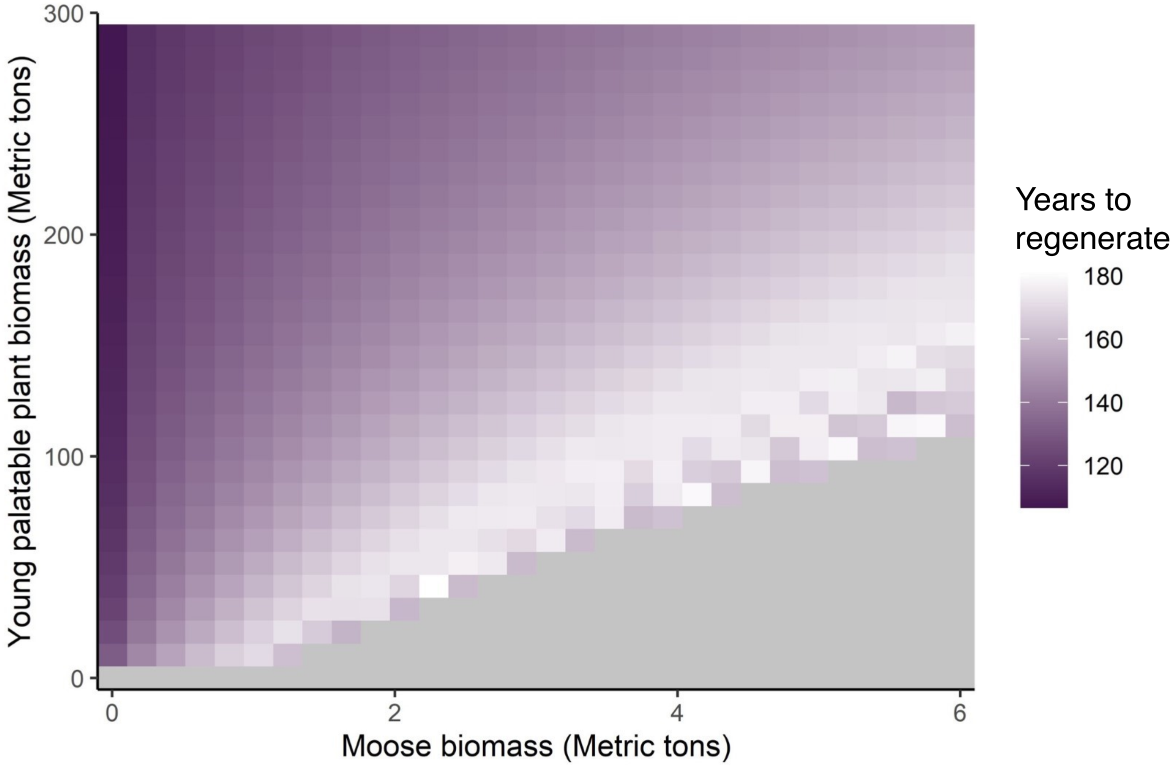


Figure 3.4. Heatmap depicting mean number of years for simulations that recovered to mature forest to reach steady state starting from combination of initial conditions of moose density and young palatable plant biomass for an area of 1 km^2. Each cell is based on 94 simulations, each simulation had a different combination of parameter values randomly selected from a normal distribution with mean, min, max values determined from the literature (see Table 3.1). The set of random combinations of parameters were the same for each combination of initial conditions.

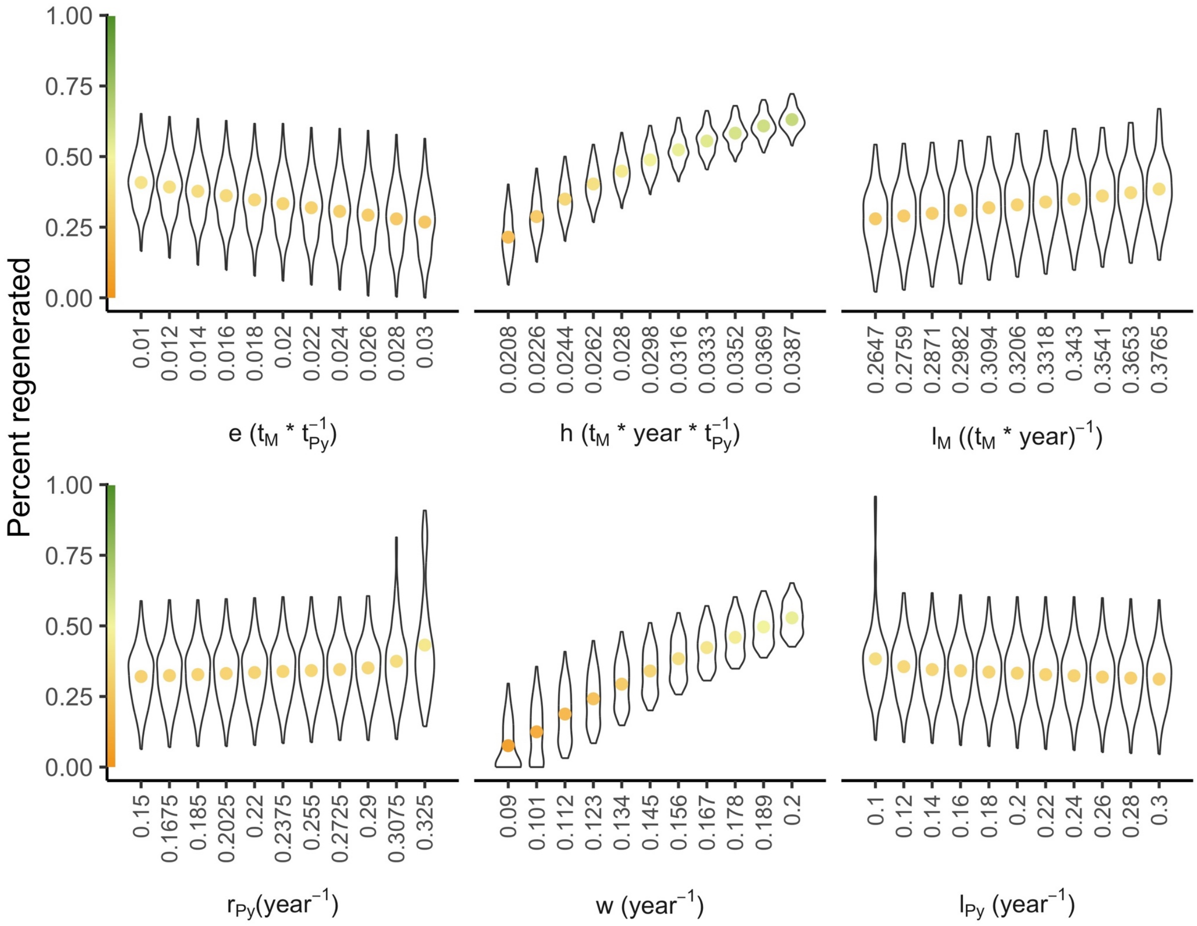


Figure 3.5. Violin plots depicting the effect of increasing the parameter value of interest on the percent of simulations that regenerated to mature boreal forest. Only parameters where increasing the value had a visual impact on percent regenerated are pictured because these are the most influential (example of no visual change in Appendix 3.5., Figure S3.7). The distribution for each level of a parameter encompasses the means of the percent of simulations regenerated for each combination of parameter selected randomly, and is therefore across 94 points. The value of each point is therefore the average of 900 simulations with different combinations of initial conditions of moose and Pyoung for an area of 1 km^2. The coloured dots are the overall mean percent regenerated for all simulations at that value of the parameter. e: conversion efficiency; h: handling time; l_M: loss rate of moose biomass; r_{Py}:

growth rate of young palatable plant biomass; w: maturation rate of young palatable plant biomass to mature palatable plant biomass; l_{Py}: loss rate of young palatable plant biomass.

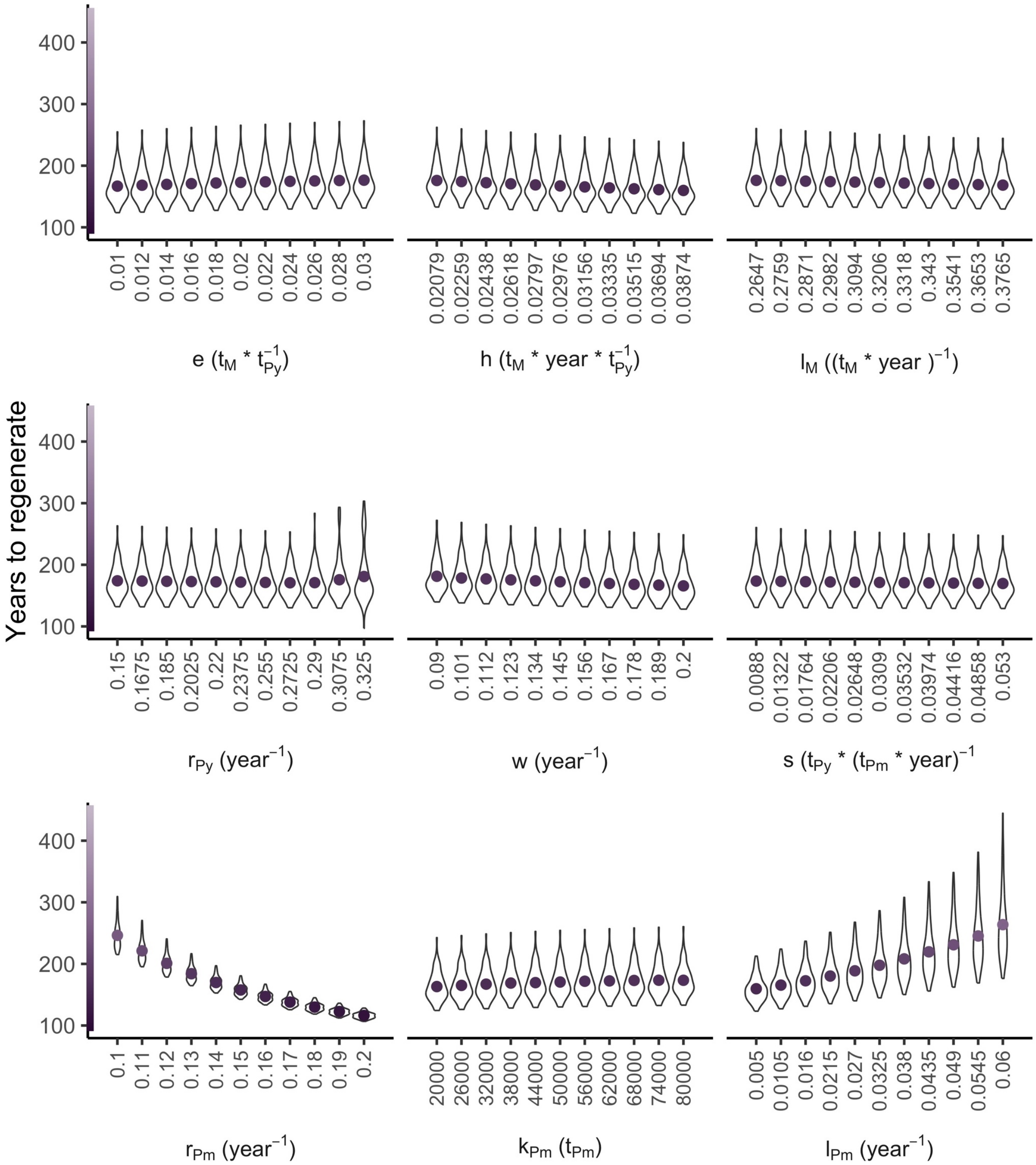


Figure 3.6. Violin plots depicting the effect of increasing the parameter value of interest on the average number of years for simulations that regenerated to mature forest to reach steady state. Only parameters where increasing the value had an impact on percent regenerated are pictured (example of no visual change in Appendix 3.5., Figure S3.7). The distribution for each level of a parameter encompasses the means of the percent of simulations regenerated

for each combination of parameter selected randomly, and is therefore across 94 points. The value of each point is therefore the average of 900 simulations with different combinations of initial conditions of moose and Pyoung for an area of 1 km^2. The coloured dots are the overall mean percent regenerated for all simulations at that value of the parameter. e: conversion efficiency; h: handling time; l_M: loss rate of moose biomass; r_{Py}: growth rate of young palatable plant biomass; w: maturation rate of young palatable plant biomass to mature palatable plant biomass; srate of addition of new seed; r_{Pm}: growth rate of mature palatable plant biomass; k_{Pm}: carrying capacity of mature palatable plant biomass; l_{Pm}: loss rate of mature palatable plant biomass.

3.10. Appendices

Appendix 3.1. Maturation rate

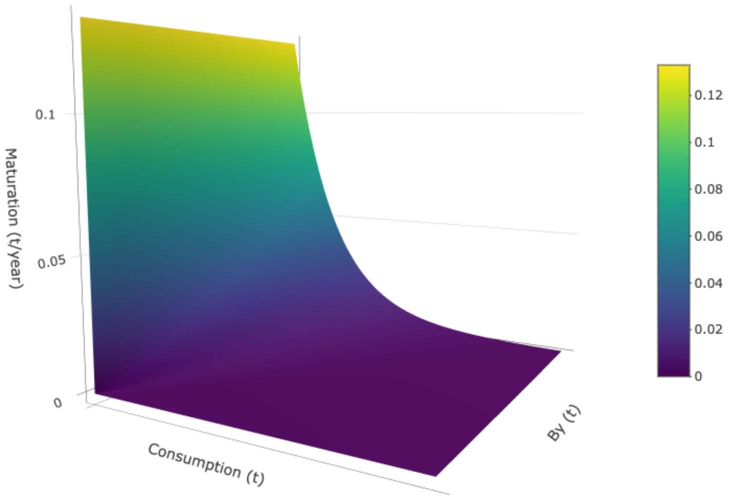


Figure S3.1. Surface plot of the relationship between the proportion of young palatable plant biomass consumed (consumption) to available young palatable plant biomass (P_y), and the rate at which young palatable plant biomass grows into the mature palatable plant biomass stock (maturation). The relationship is represented by equation S3.1, where consumption is equal to equation S3.2. Consequently, when moose densities are high a lot of young palatable plant biomass is consumed, and when young palatable plant biomass is low the rate at which palatable plant biomass grows into the mature stock is impeded. The highest rate of maturation (equal to the value of *w*) occurs when consumption is near zero and young palatable plant biomass is high.

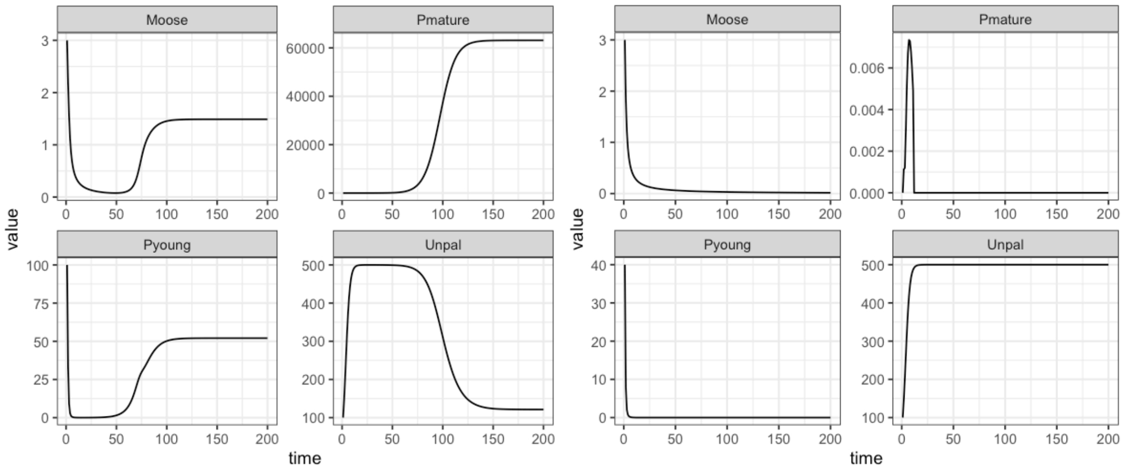
$$Maturation\ rate = w^{1+3*\frac{Consumption}{Py+0.01}} \quad \text{(S3.1)}$$

$$Consumption\ rate = \left(\frac{a*\mathrm{P}_y}{1+a*h*P_y}\right) * M \text{ (S3.2)}$$

Appendix 3.2. Field data

We used in-field measurements of plant biomass from Chapter 2 to calculate carrying capacities and competative interactions of the plant stocks. Carrying capacity of mature palatable biomass was based on the average biomass of mature trees found in 10 sites with most mature tree biomass, of young palatable biomass was based on the average biomass sapling and seedling biomass found in 10 sites with most sapling and seedling biomass, and of unpalatable biomass was based on unpalatable plant biomass found in 10 sites with the most unpalatable plant biomass. The ranges came from the average biomass of interest, in different stand conditions, across the 10 sites with the most biomass of the relevant stock. The competative effects of young and mature palatable plant biomass on unpalatable plan biomass were calculated so that a similar amount unpalatable plant biomass persists in simulated mature dominated end states, as seen in field.

Appendix 3.3. Regimes


A. Regenerated to forest

B. Converted to grassland

Figure S3.2. Example simulations where system ends in one of two possible regimes. Simulations used in our analyses ran to 1000 years instead of the 200 years shown here. A. regenerates to mature boreal forest: mature palatable plant biomass (Pmature) reaches near carrying capacity, young palatable plant biomass (Pyoung) and unpalatable plant biomass (Unpal) present in lower quantities (exact values depend on parameter values) and moose were either present at some intermediate value or extinct (also dependant on parameter values). B. converted to grassland: only unpalatable plant biomass at carrying capacity.

Appendix 3.4. Number of parameter combinations

We wanted to ensure the number of combinations of randomly generated parameter values did not severely change the outcomes of the simulations. To do this we repeated section ‘3.3.2.2. Effect of initial conditions’ 20 times, each with a different number of parameter combinations ranging from 28 to 500 following a gamma distribution (shape = 4, rate = 0.035). These combinations were filtered each time to meet assumptions (Table 3.2). We then compared the number of parameter combinations to the average number of total regenerations. Overall, the percent of simulations that regenerate to mature boreal forest only spanned about 1.5%, from ~76% to ~ 77.5%. We chose to use 150 combinations of randomly generated parameter values because above that the error band always encompasses the mean.

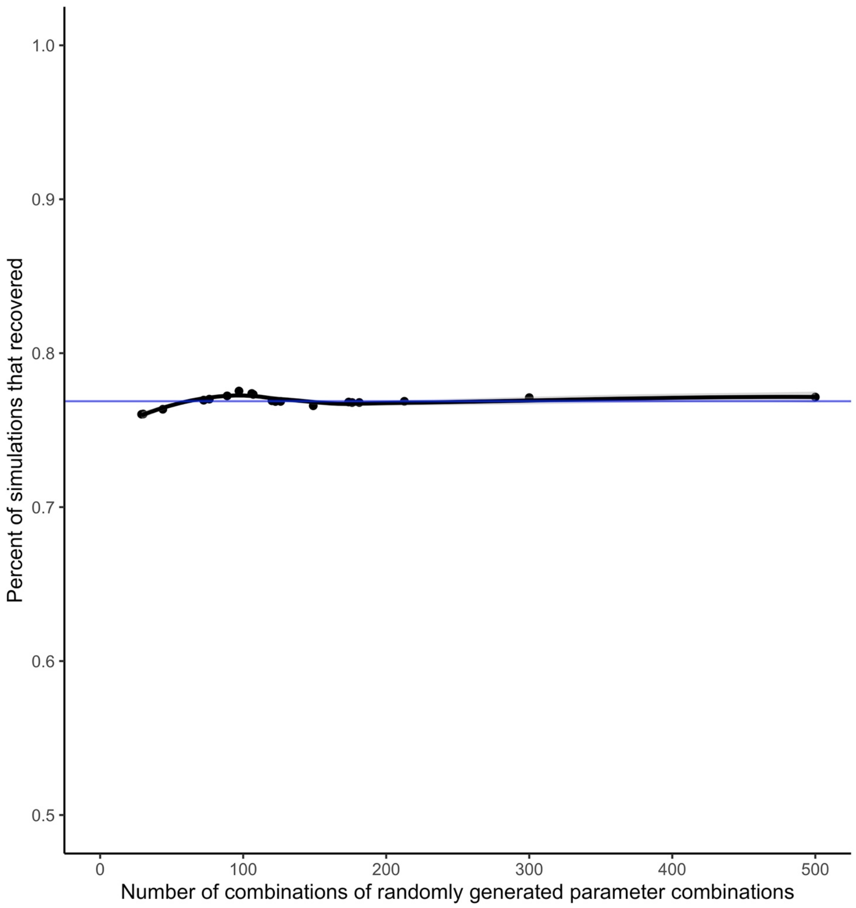
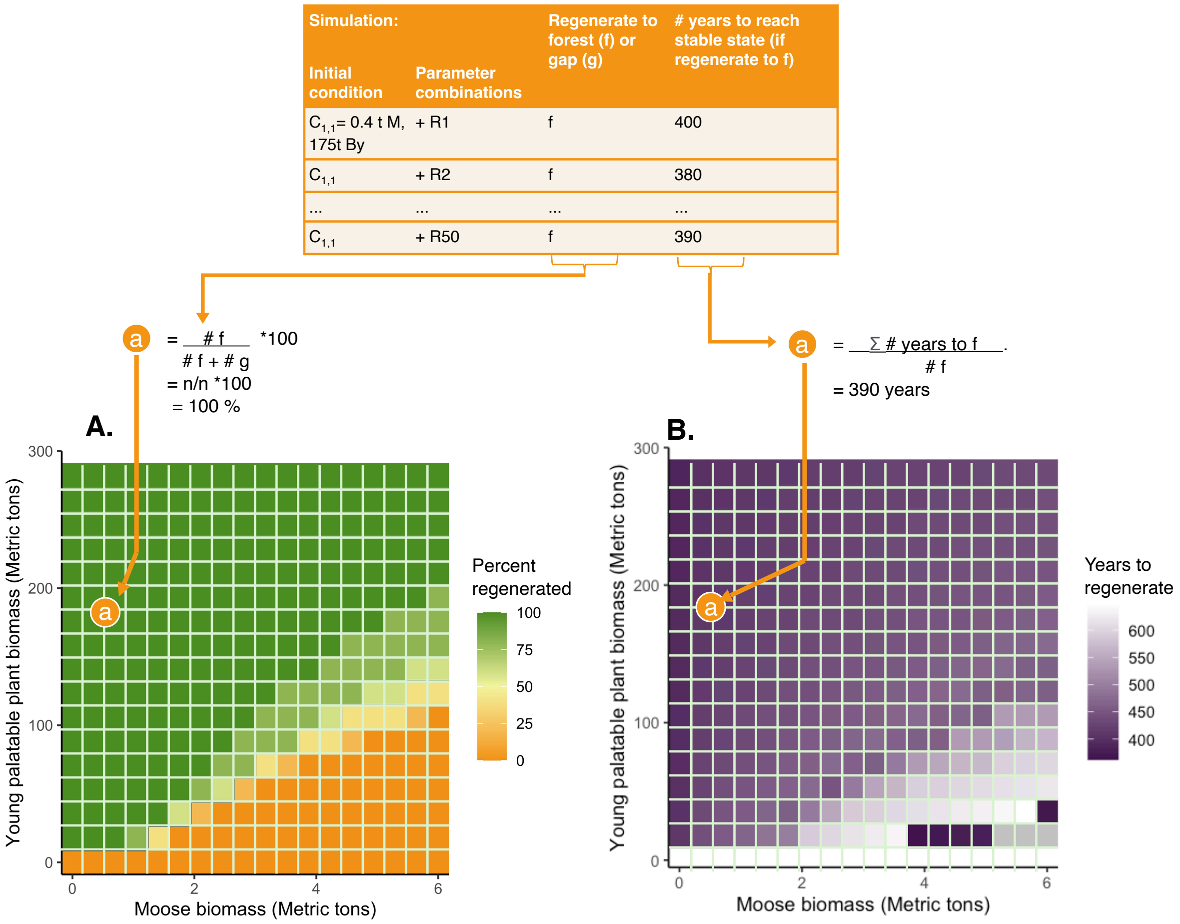


Figure S3.3. Percent of simulations that regenerated to mature boreal forest for each number of combinations of randomly generated parameter values used in section '3.3.2.2. Effect of initial conditions'. Solid line (smoothed conditional mean) and grey band (pointwise confidence interval) generated with ggplot2::geom_smooth (cite) in R. Dashed line is the mean percent simulations that regenerated across all numbers of parameter combinations.

Appendix 3.5: Interpreting figures



Simulation:			
Initial condition	Parameter combinations	Regenerate to forest (f) or gap (g)	# years to reach stable state (if regenerate to f)
$C_{1,1}$= 0.4 t M, 175t By	+ R1	f	400
$C_{1,1}$	+ R2	f	380
...	...	...	...
$C_{1,1}$	+ R50	f	390

Figure S3.4. Conceptual diagram of how each cell for the heatmaps was calculated. Each node of the grid represents n simulations at that value of M and Py. Each of the n simulations was run with a different combination of randomly selected parameter values. Values for nodes in both graphs were calculated from the same set of n simulations (ex: value of 100% for node a in graph A calculated from the same set of n simulations used to calculate value of 390 for node a in graph B, this means the set of n simulations that started at 0.4 t Moose and 175 t of Py all regenerated to mature forest and took on average 390 years to regenerate).

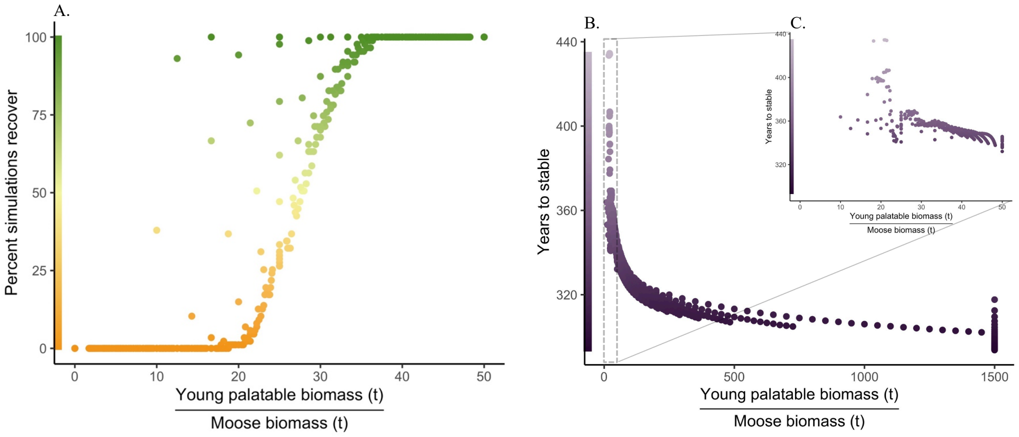


Figure S3.5. A. percent of simulations that regenerated to mature boreal forest and B. mean number of years it took mature palatable biomass to reach within 1% of mature palatable plant biomass found when the simulation reached stable, for simulations that regenerated to mature forest, starting for each ratios of initial young palatable plant biomass to moose biomass up to 50:1 (beyond 50:1 the percent simulations regenerated is always 100). Each point is based on 150 simulations, each simulation had a different combination of parameter values randomly selected from a normal distribution with mean, min, max values determined from the literature (see Table 3.1). The set of random combinations of parameters were the same for each combination of initial conditions. C. shows up to 50 t young palatable plant biomass to 1 t moose biomass versus years to stable.

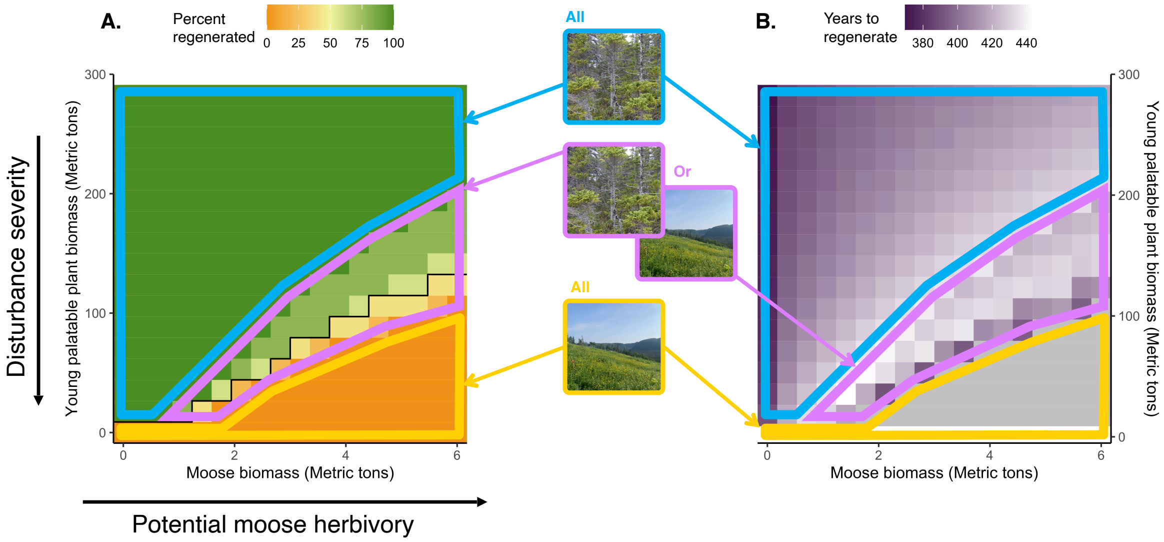


Figure S3.6. Association between results for simulations run across each combination of initial moose biomass and young palatable plant biomass, and the end condition of the system. All simulations that fall within the blue polygon regenerate to a mature boreal forest, all simulations that fall within the purple polygon convert to grassland, and the simulations that fall in the pink polygon can, depending on parameter values, either regenerate to mature forest or convert to grassland. A. shows the percent of simulations that regenerate and B. shows the number of years it took mature palatable biomass to reach within 1% of mature palatable plant biomass found when the simulation reached stable, for simulations that regenerated to mature forest.

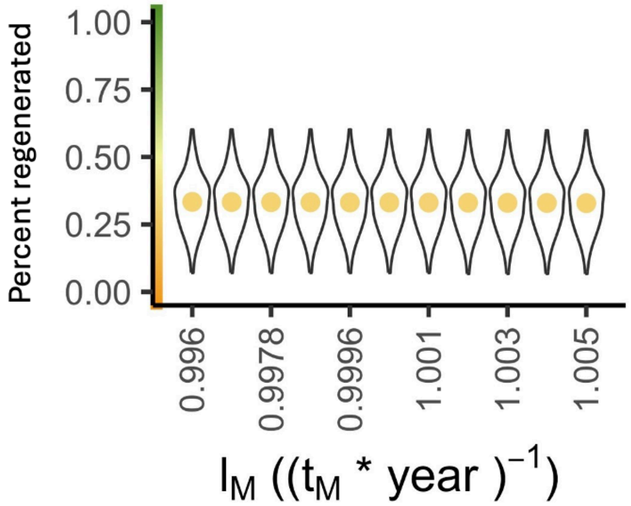


Figure S3.7. Example where there is no visual effect of increasing the parameter value of interest on the percent of simulations that regenerated to mature boreal forest. This is for loss rate of moose. For each point, the simulation started at a different combination of initial conditions of moose and Pyoung. The value of each point is the average of n simulations with a different combination of parameter values randomly selected from a normal distribution we determined using literature.

Chapter 4: General Discussion

Across the boreal forest, a broad range of ecosystem functions are the result of natural patterns of gap formation and forest regeneration across the landscape (Bergeron & Fenton, 2012; Engelmark, 1999; McCarthy & Weetman, 2006; Pickett et al., 1985; Rodríguez & Kouki, 2017). However, because anthropogenic influences (i.e., climate change, forest management, fire suppression, introduced herbivores) have altered the dynamics of key disturbances, the frequency of gap formation and their subsequent ability to regenerate has also been altered (Fleming and Candau 1998; Connor et al. 2000; Dymond et al. 2010; Leroux et al. 2020). This can have consequences for carbon storage, biodiversity and other ecosystem services (Moran et al. In review, Fleming and Candau 1998b, Connor et al. 2000).

4.1. Key Results

In this thesis, we examined responses of the boreal forest to the combination of gap forming disturbances (i.e., insect defoliation, forest fires) and moose herbivory by integrating statistical and mathematical approaches (Connolly et al. 2017; Laubmeier et al. 2020; Schlüter et al. 2023). Specifically, we fit statistical models to field and remotely sensed data to predict how carbon storage is affected by the combined effects of gap forming disturbances and moose herbivory across the landscape. We also used a mathematical model to investigate the specific mechanisms by which disturbances are influencing forest regeneration. By integrating these approaches, and comparing and contrasting results, we provide robust insights on how eastern boreal forests may respond to and recover from combined disturbances, as well as provide valuable and actionable insights for ecosystem management.

4.1.1. Chapter 2

In Chapter 2, we conducted an empirical study to examine the relationship between carbon storage and gaps created by disturbances across the landscape. Using in-field measurements of carbon and assessments of disturbance, as well as remotely sensed predictor data, we created models that predicted carbon storage and the probability an area is disturbed forest across our study areas. This allowed us to assess our hypotheses that carbon storage and the probability an area is a mature forest or disturbed gap, would be related to similar remotely sensed variables describing vegetation. We concluded that both carbon storage and the probability an area is a mature forest were related to forest height and seasonality of vegetation greenness. Therefore, areas predicted to have higher carbon storage were in areas with taller forests whose vegetation changed relatively less throughout the year. These same areas were then also predicted to have a higher probability of being a mature forest.

In Chapter 2, we also examined the combined effects of gap forming disturbances and moose herbivory on carbon storage recovery. By comparing carbon storage in mature forests to disturbed gaps with and without herbivory, we gained evidence supporting the hypothesis that moose impede the regeneration of boreal forests after disturbances (Leroux et al. 2021b). Just 20–25 years after the disturbance, previously disturbed areas from which moose had been excluded had similar carbon storage to areas of mature boreal forest. However, previously disturbed areas where moose were allowed to browse had significantly lower carbon storage relative to areas of mature boreal forest. When extrapolated over the areas we predicted to be gaps, and compared to the total carbon estimated across our study areas, moose herbivory in gaps seems to have impeded 13 megatonnes of carbon storage over the past 20–30 years.

4.1.2. Chapter 3

In Chapter 3, we derived a mechanistic mathematical model to characterize the drivers of regime shifts between mature forest and grassland across the eastern boreal forests. We hypothesized that the success of regeneration of boreal forests after disturbances is governed by aspects of moose herbivory, growth of vegetation, and competition between forms of vegetation. We assessed these hypotheses by running simulations of our model over a range of scenarios that manipulated the initial states, and ecological processes of herbivory and vegetation. We found that when there was sufficient initial young palatable biomass relative to moose, palatable vegetation was able to overcome herbivory and regenerate into mature boreal forest no matter the magnitude of moose herbivory, plant growth or plant competition. However, when the initial amount of young palatable biomass was low relative to moose biomass, moose consumed all the palatable vegetation allowing unpalatable grassland species to establish and therefore transition the area to grassland, no matter the magnitude of moose herbivory, plant competition or plant growth. The magnitude of herbivory (conversion efficiency, handling time, loss rate), and the growth of young palatable biomass (growth rate, rate grow out of browse zone, loss rate) affect the likelihood of regeneration and the time it takes to regenerate at an intermediate range of ratio of initial vegetation to moose.

As expected, we find that initial moose densities, and the magnitude of moose herbivory can impede regeneration of boreal forests after diturbances. However, if the remaining young palatable plant biomass after the disturbance is high enough relative to moose biomass, the growth of young palatable plant biomass is fast enough, or the magnitude of moose herbivory is low despite high biomass, the system may recover even under high moose densities. The characteristics of a stand, like plant species composition or environmental conditions, may therefore explain the variable effects of moose on vegetation regeneration found through empirical studies in the boreal forest (Petersen et al. 2023; Moran et al. In Review).

4.2. Integrating empirical and mathematical approaches

We combined empirical and mathematical approaches to study the disturbance dynamics of eastern boreal forests. A strength of this approach is that our mechanistic mathematical model helps reveal ecological processes responsible for the relationships observed in our empirical study. One such relationship was between tree height and carbon as well as tree height and whether an area was a gap or mature forest. Because processes governing plant growth have such an impact on whether or not the trees after a disturbance can escape herbivory, they are a large determinant of whether or not the area is mature forest or gap, and how much biomass there is. For example, a gap with faster growing trees is more likely to outpace herbivory by moose and therefore have trees that grow taller, escape the browse zone, and recover to a mature forest with more biomass and therefore carbon. The second relationship found in our empirical work was between seasonality of vegetation productivity and carbon as well as seasonality of vegetation productivity and whether an area was a gap or mature forest. While grasslands tend to have larger changes in productivity throughout the year than forested areas (Clerici et al., 2012; DeFries et al., 1995; Guzinski, 2010; Na-U-Dom et al., 2017), they also are dominated by species that are not often browsed by moose (Belovsky 1978, Thompson and Vukelich 1981, Cumming 1987, Hjeljord et al. 1990, Schwartz 1992). By explicitly representing this browsing preference in our model, we demonstrate that the preferential browsing of moose on canopy forming tree species, which also tend to have smaller changes in productivity throughout the year (Clerici et al., 2012; DeFries et al., 1995; Guzinski, 2010; Na-U-Dom et al., 2017), can lead to the formation of grasslands which have less biomass and store less carbon.

By comparing and contrasting results from empirical and mathematical approaches we can also provide more robust insights on how eastern boreal forests respond to combined disturbances. For example, pairing empirical and mathematical approaches could help resolve the variable experimental findings of the relative impact of different drivers of multiple possible states in boreal forests. The variable experimental findings on the effect of moose on forest regeneration (Petersen et al. 2023; Moran et al. In Review) were exemplified in our empirical study: moose densities were not included in predictive models of carbon stocks or probability areas were gaps, but evidence from exclosures suggests moose may impact the recovery of carbon in gaps. We propose several mechanisms that could alter the effects of moose on boreal forest gap recovery.

First, our mathematical model suggests that moose densities immediately following a disturbance can be highly influential in whether the area recovers, and therefore the amount of plant biomass and plant carbon stocks in the area. Consequently, if the spatial data on moose densities available for inclusion in our statistical models were not representative of the levels of herbivory gaps were initially exposed to, then moose's influence on forest recovery and carbon was unlikely accurately represented when developing our statistical models. We may, instead be observing legacy impacts of moose densities that were present when the disturbance initially occurred (Noonan et al. 2021).

Second, the amount of young trees remaining after a disturbance can alter the recovery of a stand irrespective of moose biomass. If the amount of remaining young trees is high enough, gaps can recover even if moose biomass is moderate to high. For example, in logged areas, advanced regeneration can promote stand regeneration even under moose herbivory (Spence and MacLean 2012). Alternatively, if the remaining amount of young trees is too low, gaps are not able to recover even if moose biomass is quite low. Therefore, there are legacy impacts of disturbance type and severity that can negate the impact of moose on boreal forest recovery.

Third, specific ecological processes can drive forest recovery when the initial ratio of plant biomass and moose are intermediate. Our mathematical model, as well as empirical studies, suggest that areas where trees grow faster may be able to escape browsing pressure and regenerate to mature broeal forest more often and faster (Mack et al. 2008; Bolton et al. 2015; Boucher et al. 2017). Similarly, areas that cause moose to have longer handling times, lower conversion efficiency, or higher mortality are also more likely to recover to mature broeal forest. Therefore, the effects of moose on gap formation and carbon storage across the landscape could also be negated by differing magnitudes of moose herbivory or rates of plant growth.

4.3. Future directions

It is unlikely that a single one of the above mechanisms acts across the whole landscape, but rather a mosaic of different levels of initial conditions and ecological processes interact to influence the effect of moose on forest regeneration after disturbances. To further parse out these interactions, we would need empirical studies that explicitly measure moose densities and young tree conditions closer to the time of disturbance as well as estimates of moose herbivory and plant growth throughout regeneration (or lack of regeneration). A chance to measure these in new gaps is close at hand, as there is an ongoing spruce budworm outbreak in western Newfoudland (Parks Canada Agency 2021), which will likely lead to new gaps throughout the landscape. As gaps are formed, initial moose densities and young palatable plant biomass can be measured, and as regeneration progresses, pellet or bite counts can be used to monitor exposure to herbivory, and vegetation can continue to be measured. Furthermore, the development of exclosures as new gaps are formed would create the opportunity to measure growth of vegetation without influence of moose herbivory.

Our models may ultimately be incorporated into an adaptive management framework through a cycle of iterative forecasting (Dietze et al. 2018; Lewis et al. 2022; McIntire et al. 2022; Barros et al. 2023). As management is implemented and outcomes monitored, our models can be reevaluated, allowing our initial understanding of the system to be tested and improved upon (Houlahan et al. 2017) and creating more useful predictions. Specifically, as new in situ data becomes available, both the statistical and mathemeatical models developed in this thesis may be reparameterized or have their structure updated (Dietze et al. 2018; McIntire et al. 2022; Barros et al. 2023). Furthermore, new remotely sensed products may allow additional variation to be accounted for in the statistical models, especially within soil carbon stocks. The forest restoration projects within Terra Nova National Park and Gros Morne National Park (Parks Canada 2019, 2021) gives us a unique ability to confront our predictions with new data under a variety of management scenarios. A primary goal of these projects is reduced moose populations with targeted tree planting in many disturbed gaps throughout these two national parks. Within the areas with different management approaches we could establish continued monitoring of vegetation biomass, stand condition, and moose populations. Data from locations previously not sampled would allow us to validate the predictions from our staitistical models. Meanwhile, new data from locations sampled in this study would allow us to assess the generalizability of our statistical model through time and changes in the landscape. The continued monitoring of these management efforts would also allow us to compare real management outcomes to the predictions from our mathematical model. Therefore, as the forest restoration program progresses we will be able to iteratively evaluate and improve our models to best inform future management.

4.4. Implications

For the areas studied empirically in Chapter 2; Terra Nova National Park and Gros Morne National Park, our empirical and mathematical results support the current efforts of lowering, or maintaining lower, moose populations (Parks Canada 2019, 2021). Going forward, priority should be to ensure reduced moose populations in areas likely to be gaps or newly created gaps, especially ones with low advanced regeneration and with larger extents (Noonan et al. 2021). Depending on the severity of the disturbance, our mathematical model suggests most areas should be able to recover with a moose density of below 2.4 moose per square kilometer. However, in areas with extremely little remaining biomass, and large extents (Noonan et al. 2021), tree planting may also be necessary to increase young tree biomass and ensure recovery. If all current gaps affected by moose herbivory were to successfully recover to mature boreal forest, there is potential for an additional 13 megatonnes of carbon stored across the two parks within the next 20–30 years.

There is also potential for our work to inform broader boreal forest management, by providing a combined empirical and mathematical approach. Following the framework of our empirical study provides spatial predictions of the where and why: where gaps have been formed and the consequences for carbon stocks. Our mathematical work then provides the what: what needs to be done to allow an area to recover, or is the area likely to recover on its own? Hopefully, by promoting recovery of gaps formed by disturbances rather than halting the formation of gaps, we can find a balance between maintaining the ecosystem functions of mature boreal forests humans have come to rely upon, with the ecosystem benefits provided by a landscape containing stands at different stages of regeneration.

4.5. References

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