Drivers of elemental storage and cycling in boreal forests: evaluating the effects of forest disturbances and an introduced ungulate

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ABSTRACT

Selective browsing by ungulates alters forest structure and composition with the potential to suppress forest regeneration. Research suggests that ungulate impacts may be stronger in recently disturbed forests and in novel environments (i.e., introduced ungulates). In this thesis, we used observational and experimental (i.e., paired exclosure-controls) data to test the hypothesis that non-native moose and forest disturbances (i.e., fires and insect outbreaks) have negative impacts on carbon storage (i.e., total, aboveground, and belowground carbon) and plant-available nitrogen in Newfoundland's boreal forests. Using our observational data, we found that forest disturbances were a key driver of carbon storage dynamics, but we did not find a relationship between moose densities and carbon storage. We also found that supply rate of ammonium was negatively correlated with soil temperature and positively correlated with moose density. Using our experimental data, we did not detect any effect of disturbance history or moose presence on carbon storage or ammonium supply rates after 24-27 years of moose exclusion. This work demonstrates the impacts of natural disturbances and herbivory on forest ecosystem functions, such as carbon sequestration. Our findings will help natural resource managers consider the effects of moose and disturbances when developing nature-based solutions to climate change.

DEDICATION

I dedicate my thesis to my parents, James and Andrea Moran. Their constant love and support have allowed me to pursue many adventures while ensuring that home will always be my favourite place.

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CHAPTER 1: General Introduction

1.1. Background to terrestrial carbon and nitrogen cycling

Carbon and nitrogen are essential elements for living organisms, with carbon comprising approximately 50 percent of all dry biomass and nitrogen being necessary for the creation of amino acids, nucleic acids, and chlorophyll (Bar-On et al., 2018; Houghton et al., 2009; Ohyama, 2010; Schlesinger, 1997). While there is an abundance of nitrogen in the atmosphere, it exists largely as nitrogen gas, a form unusable by plants; plant growth is therefore often limited by access to plant-available forms of nitrogen (e.g., nitrate and ammonium; LeBauer & Treseder, 2008; Vitousek & Howarth, 1991). With both carbon and nitrogen being finite resources, their continuous cycling is a crucial ecosystem function.

In terrestrial ecosystems, carbon is fixed from the atmosphere by plants through photosynthesis (Bowyer & Leegood, 1997; Chapin et al., 2011a); conversely, to become available to plants, nitrogen gas must first be fixed by microorganisms (Postgate, 1982; Vitousek et al., 2002) or from the energy produced by lightning (Barth et al., 2023; Scott, 2023). Following consumption, both elements can then move through the food chain, eventually being recycled to soil (Bishop et al., 2021). Carbon and nitrogen may be returned to the atmosphere during a forest fire (Bond-Lamberty et al., 2007; Johnson et al., 2008), or carbon may be released through respiration by organisms and nitrogen via denitrification processes (Chapin et al., 2011b; Nieder & Benbi, 2008; Tiedje et al., 1983).

The availability of nitrogen and carbon in soil is largely dependent on the activity of microorganisms due to their role in fixing and converting elements. Soil abiotic conditions, including pH, temperature, moisture, and texture, impact the composition and abundance of soil microorganisms and therefore the rates of decomposition mediated by these organisms (Abdul Rahman et al., 2021; Islam et al., 2020). Changes in elemental inputs to soil can also impact microbial activity; for example, inputs of low-quality plant material (high C:N ratio) can lead to higher immobilization rates of nitrogen (Parton et al., 2007; Prieto et al., 2019). Additionally, increased microbial activity and decomposition rates may increase losses of carbon dioxide to the atmosphere through respiration (Jílková, 2020; Rui et al., 2016).

Anthropogenic activities affect the cycling of carbon and nitrogen in many ways. Land-clearing (e.g., industrial forestry, mining, agriculture) reduces carbon storage on land through the removal of aboveground biomass (Erb et al., 2018), with impacts on future primary productivity and carbon stored in soil (IPCC, 2000; Wang et al., 2023). Humans have also increased the availability of reactive nitrogen (Galloway et al., 1995), simultaneously promoting carbon storage through plant productivity, while increasing emissions of nitrous oxide (Clark et al., 2023; Zaehle et al., 2011). The burning of fossil fuels has released large amounts of carbon into the atmosphere causing a global increase in temperature (Karl & Trenberth, 2003; Mann et al., 1998; Mitchell, 1989); this has the potential to release carbon stored in long-term reservoirs, such as in permafrost (Dutta et al., 2006; Natali et al., 2021). As global climate changes, terrestrial elemental cycling may be further altered by feedbacks such as more frequent and severe natural disasters including storms, droughts, and forest fires (Flannigan et al., 2013; IPCC, 2012; Xu et al., 2019). This necessitates further research on how forest disturbances may alter the dynamics of elemental storage and cycling.

1.2. Climate Change and Mitigation Strategies

While weather describes daily atmospheric conditions, climate describes average weather conditions over an extended period (Adhikari et al., 2018). As mentioned above, the release of greenhouse gases (e.g., carbon dioxide) driven by fossil fuel combustion, has caused an increase in global surface temperatures, altering global climate patterns (IPCC, 2018; Mann et al., 1998). Climate change will have consequences for vegetation and wildlife, as temperature and precipitation trends change. For example, higher temperatures and reduced summer rainfall were found to negatively impact the survival of common boreal tree species, such as balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*; Collier et al., 2022; Reich et al., 2022). Changes in vegetation will alter the availability and quality of food and habitat for wildlife (Hotta et al., 2019; Martin & Maron, 2012). Climate change may further impact wildlife by changing seasonal conditions (Twining et al., 2022; Walther et al., 2002). For example, snowshoe hare (*Lepus americanus*) mortality is higher in warmer winters with decreased snow cover (Zimova et al., 2016), and the reproductive success of Canada jays (*Perisoreus canadensis*) declines with increasing freeze-thaw events deteriorating crucial food stores (Sutton et al., 2019).

Many technological solutions are being explored to mitigate the impacts of climate change, including the use of renewable energy sources and capturing, using, and storing carbon dioxide from current emissions (Sims, 2004; Wang et al., 2021; Wilberforce et al., 2021). Natural areas play a key role in climate change mitigation through their uptake of carbon dioxide (Drever et al., 2021; Griscom et al., 2017; Sharma et al., 2023). For example, forests store approximately 45 percent of global terrestrial carbon (Bonan, 2008). Forest soils, in particular, can act as a key carbon sink (Lal, 2004), with the long-term storage of carbon promoted where organic material decomposition rates in soils are limited such as in the boreal biome (Harris et al., 2022; Kurz et al., 2013).

1.3. The Boreal Forest Biome as a Global Carbon Sink

The boreal forest is one of the world's largest forested biomes, representing one-third of Earth's remaining forests (Bradshaw et al., 2009). Located in high northern latitudes (typically between 50 and 60° North; Taggart & Cross, 2009), the boreal zone of Canada stretches from the Alaskan border to the island of Newfoundland; it covers 552 million hectares and is comprised of forests, wetlands, lakes, rivers, alpine areas, and heathlands (Brandt et al., 2013; Henry, 2002). Boreal forests experience long winters with persistent snow cover, and so are comprised of cold-tolerant trees, including many coniferous species (e.g., *Abies* spp.*, Larix* spp.*, Picea* spp. *or Pinus* spp.), as well as broadleaf species within the *Betula* and *Populus* genera (Brandt et al., 2013; Taggart & Cross, 2009).

Boreal forests are regarded as one of the world's most important carbon sinks, storing approximately 30 percent of global terrestrial carbon, with much of this carbon stored in peatlands and soils (Beaulne et al., 2021; Bradshaw & Warkentin, 2015; Kasischke et al., 1995). Cold temperatures, low precipitation, and predominately acidic soils slow decomposition rates, and have led to the accumulation of soil organic carbon (Adamczyk, 2021; Deluca & Boisvenue, 2012). For example, while carbon stored in boreal biomass is estimated at less than half of that in the tropical forest, the boreal forest is estimated to store more carbon in soil than both temperate and tropical forests combined (Malhi et al., 1999; Taggart & Cross, 2009). However, heightened anthropogenic pressures (e.g., land-clearing, oil and gas exploration, industrial forestry) and climate change impacts are threatening the integrity and carbon storage capacity of the boreal forest (Bradshaw et al., 2009; Gauthier et al., 2015; Kurz et al., 2013).

1.4. Natural disturbances in eastern boreal forests

Natural disturbances drive cycles of forest renewal and are necessary for the growth of a biodiverse and structurally complex forest (Swanson et al., 2011; Thom & Seidl, 2016). While some wildlife, such as American marten (*Martes americana*) and woodland caribou (*Rangifer tarandus)* are reliant on habitat and food found in mature forests, others, including moose, benefit from an abundance of new growth at early-successional sites (Fisher & Wilkinson, 2005; Gosse et al., 2005; Timmermann & McNicol, 1988). With both early-successional forests and mature forests providing key resources and fulfilling habitat requirements, it is vital to ensure both are present across the landscape (Kuuluvainen & Gauthier, 2018). The species and structural diversity remaining post-disturbance (Senf et al., 2020; Thom & Seidl, 2016) also help to foster resilient forests (Jactel et al., 2017; Seidl et al., 2014).

Common natural disturbances in the boreal forest include insect outbreaks, forest fires, pathogens, and windthrow (De Grandpré et al., 2018; Foster et al., 2022). Outbreaks of defoliating insects (e.g., Eastern spruce budworm (*Choristoneura fumiferana*), Eastern hemlock looper (*Lambdina fiscellaria*)) and forest fires are prevalent natural disturbances in eastern boreal forests, with widespread impacts on forest structure and composition (Bond-Lamberty et al., 2007; Brandt et al., 2013). Both disturbance types have consequences for the carbon cycle and the use of forests to mitigate climate change impacts (Anderegg et al., 2020).

1.4.1. Defoliating Forest Insects

Eastern spruce budworm and Eastern hemlock looper are forest insects native to North America that disturb forests through defoliation (Danks & Foottit, 1989). Both of these insects have cyclical outbreak patterns reaching epidemic levels every ~ 30 years (Eastern spruce budworm) or ~15 years (Eastern hemlock looper; Arsenault et al., 2016; Cooke et al., 2007).

During the larval stage of their lifecycle, Eastern spruce budworm feed on the current- and previous-year needles of coniferous tree species (Otvos & Moody, 1978); Eastern hemlock looper larvae feed on new and old foliage of both coniferous and some hardwood species (e.g., *Betula* spp*.,* and *Acer* spp.; Holmes, 1968; Otvos et al., 1971). Climate change may directly affect the frequency, duration, and distribution of future insect outbreaks as changing temperature patterns shift historical range limits and alter insect phenology (Battisti & Larsson, 2023; Candau & Fleming, 2011); for example, the distribution of spruce budworm is expected to shift northward (Gray, 2008; Régnière et al., 2012).

During outbreaks, defoliation can cause large decreases in tree height and radial growth (Iqbal et al., 2011; MacLean, 1984; Otvos & Moody, 1978). In contrast with spruce budworm, whose defoliation can take 5 to 7 years to cause mortality (MacLean, 1980; Otvos & Moody, 1978), hemlock loopers can cause tree mortality after just one year (MacLean, 2016; MacLean & Ebert, 1999). Insect outbreaks result in higher amounts of standing and fallen deadwood, in turn, increasing rates of decomposition and heterotrophic respiration (Gray, 2008; Hicke et al., 2012); increased inputs of organic matter in the form of insect cadavers and feces may also stimulate these processes (Grüning et al., 2018; Hwang et al., 2022). While outbreaks cause mortality of their host species, they also create openings allowing for the growth of understory vegetation (MacLean, 2016; Swanson et al., 2011), and may promote the growth of non-host species (Hennigar et al., 2007).

Dymond et al. (2010) and Kurz et al. (2008) demonstrated that insect outbreaks, such as spruce budworm and mountain pine beetle, can shift a forest from a carbon sink to a source, through decreased primary productivity and increased heterotrophic respiration. For example, Quirion et al. (2021), found that there was 69% less carbon sequestered by live trees in forests recently disturbed by insects, compared to undisturbed forests. The recovery of carbon stocks post-disturbance is dependent on several factors, including disturbance severity and intensity, as well as the potential for tree regeneration (i.e., quality seed beds and sources; Kurz et al., 2013).

1.4.2. Forest Fires

Forest fires shape boreal forests, burning between 5 and 12 million hectares of the boreal per year (Kasischke, 2000). Some boreal species exhibit adaptations to forest fires, such as the semi-serotinous cones of black spruce (*Picea mariana*) and serotinous cones of jack pine (*Pinus banksiana*). Following a fire, early-successional species take advantage of the increased availability of previously limited resources, such as elements and light (Swanson et al., 2011). Forest fires can provide beneficial ecosystem services by releasing elements into the soil, promoting new growth in forest canopy openings, and reducing fuel-load for future fires (Thomas et al., 2010; Weber & Stocks, 1998). Forest fires may become more frequent, intense, and extensive as the climate continues to change, with higher temperatures leading to drier conditions and a longer fire season (Arsenault et al., 2016; Flannigan et al., 2013; Price et al., 2013). This has the potential to negatively impact the regeneration of dominant boreal species, such as black spruce, with shorter fire cycles reducing seed quantities (Baltzer et al., 2021).

Forest fires release carbon into the atmosphere through the combustion of organic matter, both above- and belowground (Bond-Lamberty et al., 2007; Kasischke, 2000), with the term fire severity often being used to describe the amount of organic matter consumed (Keeley, 2009). During a fire, aboveground (i.e., live vegetation, deadwood, ground litter) and belowground (i.e., organic matter in soil) organic matter may be burned through flaming combustion; belowground and surface fuels may continue to burn through glowing combustion after the fire has passed (Johnson, 1992; Kasischke et al., 1995). Decomposition rates in soil may be altered following a fire, due to changes in soil abiotic conditions and changes to microbial biomass and community composition (Pellegrini et al., 2022). The incomplete burning of biomass can also result in deposits of pyrogenic carbon (e.g., charcoal; Preston & Schmidt, 2006), a persistent carbon stock; however, charcoal may also stimulate microbial activity leading to increased decomposition (Wardle et al., 2008).

1.5. The effects of animals on elemental cycling

Global climate change has driven carbon cycling research, requiring large-scale measurements that increase the accuracy of forecast models. While much of this research focuses on the balance between net primary production and heterotrophic respiration (e.g., Arora et al., 2013; Nemani et al., 2003; Running et al., 2004; Sitch et al., 2015), recent studies have highlighted the role of animals in ecosystem functioning, including elemental storage and cycling (Atwood et al., 2015; Forbes et al., 2019; Schmitz et al., 2018; Tanentzap & Coomes, 2012). Through their consumption of plant matter, herbivores directly impact the growth of primary producers, with the potential to alter the structure and composition of plant communities (Asner et al., 2009; Frerker et al., 2014; Kolstad, Austrheim, Solberg, De Vriendt, et al., 2018; Reed et al., 2022). Trampling also directly impacts vegetative cover and abiotic soil conditions, in turn, impacting the biomass and activity of soil communities (Heggenes et al., 2017; Schrama et al., 2013; Tuomi et al., 2021). Animals return elements to their environments through deposits of urine, feces, carcasses, and reproductive material, as well as through respiration (Barthelemy et al., 2018; Bump et al., 2009; Ferraro et al., 2023; Le Roux et al., 2020). Animals also play an important role in the movement of elements laterally across landscapes, as well as between terrestrial and aquatic ecosystems (Earl & Zollner, 2017; McInturf et al., 2019). For example, Clyde et al. (2021) noted increased productivity of Arctic islands with large colonies of common eiders (*Somateria mollissima*) compared to reference islands. This suggested that the seabirds played a key role in transporting marine-derived elements to their nesting sites.

The strength and direction of herbivore impacts on elemental storage and cycling may vary with primary productivity, intensity of herbivory, and body size and density of herbivores (Andriuzzi & Wall, 2017; Bardgett et al., 2001; Bernes et al., 2018; Daskin & Pringle, 2016; Le Roux et al., 2020; Ramirez et al., 2018). A lack of evolutionary history between herbivores and vegetation (i.e., introduced herbivores), may result in stronger impacts in novel environments (Forbes et al., 2019; Milchunas & Lauenroth, 1993; Wardle et al., 2001). For example, Chollet et al. (2021) found that browsing by invasive Sitka black-tailed deer (*Odocoileus hemionus sitkensi*) on the islands of Haida Gwaii, British Columbia, decreased litter quality and rate of decomposition through their selective browsing of high-quality plants (i.e., low C:N ratio). Herbivore impacts may also be stronger in early-successional forests (i.e., recently disturbed), due to herbivory on abundant and accessible vegetation (Kolstad, Austrheim, Solberg, De Vriendt, et al., 2018; Mason et al., 2010; Nuttle et al., 2013).

1.6. A case study in Newfoundland

The island of Newfoundland represents the easternmost portion of the North American boreal forest, with a climate heavily influenced by the surrounding ocean and forests dominated by balsam fir and black spruce (Arsenault et al., 2016; Brandt, 2009; Moroni & Harris, 2011). Insect outbreaks, particularly hemlock looper and spruce budworm, are the dominant forest disturbance agents in Newfoundland (Arsenault et al., 2016). On the island, both insects use balsam fir as their main host, with hemlock looper outbreaks recorded since 1912 and spruce budworm outbreaks recorded since 1942 (Carroll, 1956; Otvos & Moody, 1978). On Newfoundland, forest fires have typically been small and infrequent, particularly in balsam fir-dominated stands (Arsenault et al., 2016). However, fires have been an important disturbance agent within the Central Newfoundland Forest and Maritimes Barrens ecoregions, where black spruce is a common canopy-forming tree species (Arsenault et al., 2016; Damman, 1983).

Newfoundland has a history of species introductions; of the 26 mammals currently inhabiting the island, 12 were introduced or naturally expanded their range to the island (i.e., coyotes; Strong & Leroux, 2014). Moose were introduced to central Newfoundland in 1878, and again to western Newfoundland in 1904 (Pimlott, 1953). With wolves (*Canis lupus*) being extirpated in the 1930s (Pimlott, 1953), moose have few natural predators on the island. The lack of predators and abundance of suitable habitat allowed moose populations to grow, peaking at more than 150,000 individuals (> 1 individual/km^2) (McLaren et al., 2004). Moose populations reached especially high densities in Terra Nova and Gros Morne National Parks as hunting was prohibited within park boundaries until 2011, with Gosse et al. (2011) reporting respective average densities of 0.7 and 3 moose/km^2.

There is considerable evidence that selective browsing by ungulates can suppress forest regeneration, with negative impacts on the height and abundance of saplings (Allen et al., 2023; McInnes et al., 1992; Ramirez et al., 2018), number of adult trees (Swain et al., 2023), and overall reductions in tree biomass (Salisbury et al., 2023). Balsam fir is a dominant, canopy-forming tree in Newfoundland forests (Moroni & Harris, 2011), and is heavily browsed when moose densities are high (Connor et al., 2000; McLaren et al., 2004). Under high moose densities, intensive moose herbivory on balsam fir seedlings and saplings can slow or disrupt natural forest regeneration following forest disturbances (Leroux et al., 2021), with the potential to impact forest carbon storage (Leroux et al., 2020). For example, Salisbury et al. (2023), found that in the years following forest harvesting, moose browsing in Norway decreased carbon storage by reducing aboveground tree biomass. While many studies have reported effects on aboveground vegetation (see above), and some have focused on belowground elemental storage and cycling (Ellis & Leroux, 2017; Kolstad, Austrheim, Solberg, Venete, et al., 2018; Swain et al., 2023), further exploration of the net effects of moose browsing and forest disturbances will help to clarify moose impacts on overall (i.e., total, aboveground, and belowground) carbon storage.

1.7. Thesis Overview

The aim of my thesis is to explore the net effects of ungulate browsing and forest disturbances on carbon storage and plant-available nitrogen in boreal forests, using moose herbivory on Newfoundland, Canada as a case study. This work will inform boreal forest management, providing a link between disturbance and ungulate impacts on forest communities to their impacts on forest ecosystem functioning (i.e., carbon storage). In Chapter 2, we report results from a field study conducted in Gros Morne National Park and Terra Nova National Park, where we tested our hypothesis that forest disturbances and herbivory by non-native moose negatively impact carbon storage and plant-available nitrogen in soil. We measured stocks to estimate the amount of total, aboveground, and belowground carbon stored in disturbed (i.e., insect disturbances, burned areas) and undisturbed forests (i.e., mature forests) using both observational and experimental (i.e., paired moose exclosure-controls) data; we also collected data on the supply rates of ammonium in soil. Using our observational data, we found that forest disturbances were a key driver of carbon storage dynamics but did not find a relationship between moose densities and carbon storage. We also found that supply rate of ammonium was negatively correlated with soil temperature and positively correlated with moose density. Using our experimental data, we did not detect any effect of disturbance history or moose presence on carbon storage or ammonium supply rates after 24-27 years of moose exclusion, though this may have resulted from a high-level of site variability.

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1.9. Co-Authorship Statement

Chapter 2 is under preparation for submission to a peer-reviewed journal and is co-authored by Dr. Shawn Leroux, Dr. Yolanda Wiersma, and Dr. Darroch Whitaker. I led project design, field sampling, laboratory work, data management, analysis, and writing, with feedback and guidance from SL, YW, and DW throughout.

CHAPTER 2: Impacts of insect outbreaks, fire, and moose on carbon stocks and plant-available nitrogen in boreal forests of Newfoundland, Canada

2.1. Introduction

The conservation and management of ecosystems for carbon storage has been proposed as a key climate change mitigation tool (Drever et al., 2021; Griscom et al., 2017). Forests comprise 31 percent of global land area (FAO, 2020) and act as an important natural climate solution through their estimated uptake of 2.4 petagrams of carbon per year (Pan et al., 2011). However, both human (e.g., deforestation, anthropogenic fires) and natural (e.g., insect outbreaks, pathogens, forest fires) disturbances can alter the carbon storage capacity of forests (Anderegg et al., 2020; Bradshaw & Warkentin, 2015; IPCC, 2000). Humans have also altered forests and terrestrial elemental cycling through impacts on wildlife populations and food webs (Peltzer et al., 2010; Schmitz et al., 2018). While large herbivores are in decline in some biomes (Ceballos et al., 2015), they have also been introduced, are increasing in abundance, or are expanding their range in others (Leroux et al., 2020; Wardle et al., 2011). Empirical evidence has shown that these gains and losses of large herbivores can have important effects on forest structure and composition (e.g., Cardinal et al., 2012; Kolstad et al., 2018; Ramirez et al., 2021). Although there is much evidence for the ability of large herbivores to alter forests, the extent to which these species also affect net ecosystem carbon storage remains unclear, especially in recently disturbed forests (but see Allen et al., 2023; Salisbury et al., 2023).

In boreal forests, disturbances such as insect outbreaks and forest fires are primary drivers of forest renewal (Brandt et al., 2013), and can affect the ecosystem's capacity to serve as a carbon sink (Bond-Lamberty et al., 2007; Dymond et al., 2010; Kurz, Dymond, et al., 2008). Forest insect outbreaks can result in high levels of mortality of host tree species, altering forest structure and composition, leading to a decrease in carbon uptake through reduced growth (Hicke et al., 2012; Quirion et al., 2021). Forest fires can almost instantaneously release large amounts of carbon through the combustion of vegetation and soil organic matter, whereas insect outbreaks result in increased amounts of dead organic matter and higher levels of respiration from increased decomposition (Gray, 2008; Hicke et al., 2012; Kasischke, 2000). However, both types of disturbance also benefit ecosystems, creating a heterogeneous landscape with diverse habitats and food sources critical for many wildlife species (Kuuluvainen & Gauthier, 2018; Swanson et al., 2011). Under projected climate scenarios, forest disturbances in the boreal are expected to increase in frequency, distribution, and severity, with negative implications for carbon sequestration and storage (Anderegg et al., 2020; Gauthier et al., 2015; Kurz, Stinson, et al., 2008; Pureswaran et al., 2015).

Large ungulate herbivores play an important role in mediating elemental storage and cycling (Schmitz et al., 2018; Tanentzap & Coomes, 2012), with their preferential browsing of high-quality trees and shrubs (i.e., low C:N ratio) impacting the regeneration and species composition of forests (Ellis & Leroux, 2017; McInnes et al., 1992; Ramirez et al., 2018; Swain et al., 2023). This effect is suggested to be amplified in recently disturbed forests (Kolstad et al., 2018; Mason et al., 2010; Nuttle et al., 2013), with ungulates benefitting from increases in forage resources (Fisher & Wilkinson, 2005; Francis et al., 2021). A recent synthesis of 100 paired moose (*Alces alces*) exclosure-control sites demonstrated that the aboveground effects of moose are prominent across the circumboreal (Petersen et al., 2023). Aboveground effects can also impact belowground conditions and elemental storage, altering soil temperatures, the depth of soil layers, and the quality and quantity of litter being returned to soil (Ellis & Leroux, 2017; Kolstad et al., 2019; Pastor et al., 1993; Swain et al., 2023). However, the direction and strength of herbivore impacts on elemental storage and cycling are highly context-dependent, varying with ecosystem productivity, the intensity of herbivory, and the body size and density of herbivores (Andriuzzi & Wall, 2017; Bernes et al., 2018; Daskin & Pringle, 2016; Ramirez et al., 2018). The impact of herbivores on forests in novel environments (i.e., introduced herbivores) may be stronger due to a lack of evolutionary history between vegetation and the herbivore (Forbes et al., 2019; Milchunas & Lauenroth, 1993). Further, impacts of introduced species are often more extreme on islands because of simplified ecosystem structure (Russell & Kaiser-Bunbury, 2019); typical traits of endemic island species, such as small populations and reduced defensive traits and behavior, may also make them vulnerable to introductions (Fernández-Palacios et al., 2021). Though the net effects of herbivory following forest disturbances on carbon storage in boreal forests are not well understood, they are likely important to inform climate-smart boreal forest management (Leroux et al. 2020). This study aims to explore these net effects using moose herbivory on Newfoundland, Canada as a case study.

Newfoundland is the largest island in the circumpolar boreal biome (111,390 km^2), and represents the easternmost portion of the North American boreal forest (Arsenault et al., 2016; Damman, 1983). Moose were introduced to Newfoundland in 1878 and 1904 (Pimlott, 1953). The moose population peaked at more than 150,000 individuals (> 1 moose/km^2) in the 1990s, with extreme densities (> 5 moose/km^2) in some areas (McLaren et al., 2004). This population growth is attributed to an abundance of suitable habitat and a lack of predators, with wolves being extirpated in the 1930s (McLaren et al., 2004; Pimlott, 1953). Balsam fir (*Abies balsamea*) is a dominant, canopy-forming tree in Newfoundland forests (Moroni & Harris, 2011) and is heavily browsed by moose, particularly when other high quality browse species are depleted (Connor et al., 2000; McLaren et al., 2004). Under high moose densities, moose herbivory on balsam fir seedlings and saplings can slow or disrupt natural forest regeneration (Bergerud & Manuel, 1968; Thompson et al., 1992), especially following forest disturbances (Leroux et al., 2021). This has been particularly problematic in the national parks on Newfoundland (Connor et al., 2000; Gosse et al., 2011), where moose hunting was prohibited until 2011.

We use observational and experimental field studies in Gros Morne National Park and Terra Nova National Park to examine the impacts of insect outbreaks, forest fires, and moose herbivory on carbon storage in Newfoundland forests, as well as plant-available forms of nitrogen in soil. We hypothesize that the disruption of forest regeneration through over browsing by moose will decrease carbon stored in forested areas that have experienced these disturbances, through a decreased uptake of carbon from the atmosphere by vegetation. We also hypothesize the disruption of forest regeneration will decrease the amount of plant-available nitrogen available in the soil for microbial communities and plant growth, through decreased litter input. We predict that plots in disturbed areas will have i) less total, aboveground, and belowground carbon stored and ii) less plant-available nitrogen in soil than plots in mature forests. Similarly, plots having high moose densities will have iii) less total, aboveground, and belowground carbon and iv) less plant-available nitrogen than plots with low moose-densities or an absence of moose (i.e., fenced exclosures). Using both experimental and observational data will allow us to sample across a range of moose densities, as well as in areas where they have been excluded. This work will help clarify the net effects of herbivory and forest disturbances on forest ecosystem functioning (i.e., carbon storage).

2.2. Methods

2.2.1. Study Area

We conducted this study in the boreal forest on Newfoundland, with a total of 46 plots divided equally between Gros Morne National Park and Terra Nova National Park (GMNP & TNNP; Figure 2.1). Plots were established in the following ecoregions: 18 in the Northern Peninsula Forest; 5 in the Western Newfoundland Forest; 6 in the North Shore Forest; 17 in the Central Newfoundland Forest (see Table 2.1 for descriptions of ecoregions; Damman, 1983). The Northern Peninsula Forest, North Shore Forest, and Central Newfoundland Forest are part of the Middle Boreal Zone, while the Western Newfoundland Forest is part of the Southern Boreal Zone. In 2011, both GMNP and TNNP began managing their moose populations through hunting, to mitigate impacts of moose over browsing on their forests (Connor et al., 2000; Gosse et al., 2011). This has resulted in large decreases in moose densities (Gosse, 2019; Robineau-Charette et al., 2021).

We sampled long-term (24 to 27 years) paired moose exclosure-controls (n = 10 paired exclosure-controls; 20 plots total), as well as novel plots (n = 26 plots; i.e., plots not part of the exclosure-control experimental design), sampling a total of 46 plots. We established plots in mature forests that have not been recently disturbed (n = 14), as well as in areas that had been previously burned (n = 7) or had experienced insect outbreaks (n = 25; see Table 2.2 for plot details). We established the majority of our plots in forests dominated by balsam fir. Exclosures in TNNP measure 35 m x 35 m and were established in 1998, while exclosures in GMNP measure 15 m x 15 m and were established in 1995. Our sampling plots measured 25 m x 25 m and included 4 pairs of 5 m^2 (5 m x 1 m) and 9 m^2 (3 m x 3 m) subplots, with 0.25 m^2 quadrats nested within each 9 m^2 subplot (see Figure 2.2). The only exception was within the exclosures in GMNP where we could only fit 3 pairs of subplots inside the fenced area (Table 2.2). Subplots were oriented north-south and located in the southwest corner of each plot. We aimed to avoid sampling within 5 m of exclosure borders, but this was not always possible due to the orientation and size of exclosures. Exclosures were designed to allow access to small wildlife species (e.g., snowshoe hare (*Lepus americanus*)), but exclude access to moose and caribou (*Rangifer tarandus*). Caribou are the only other ungulate in Newfoundland, but they are rarely observed near our forest sites and do not appear to compete for resources with moose (McLaren et al., 2004). This is likely because caribou are less dependent on forests, occupying a variety of habitats, including barrens and wetlands, throughout the year (Weir et al., 2014). The design and location of the exclosures therefore allow us to isolate the effect that moose are having on Newfoundland forests. Control and novel plots allowed access to all animals.

We collected in-field measurements, as well as litter and soil samples from June 13 to July 14, 2022. We deployed Plant Root Simulator (PRS) probes and soil temperature loggers between June 20 and July 14, 2022, and collected them 22-35 days later.

2.2.3. Moose Density

To estimate moose density at each of our plots, we used data collected during winter aerial surveys in GMNP and TNNP. Both parks have delimited survey blocks (~ 4 km^2 in GMNP; ranging from ~ 3 – 7 km^2 in TNNP) for the purpose of continuous moose population monitoring. GMNP conducted aerial surveys of randomly selected survey blocks in 2007/2009, 2015, 2017 and 2019; they also surveyed a fixed subset of blocks (n = 24) each year from 2013 to present, apart from 2020. TNNP has conducted annual aerial surveys of randomly selected survey blocks from 2014 to present. Due to a change in the survey block layout used by TNNP in

2022, we only used aerial survey data collected up to 2021 for our estimates for both parks. Both parks use the approach of Gasaway et al. (1986) to estimate moose populations.

To estimate moose density at our plots, we averaged available density estimates across years for the survey blocks in which they were located. Note that due to the random design of the aerial surveys, some plots were located in survey blocks that lacked density estimates (n = 2 in TNNP; n = 3 in GMNP); additionally, three plots in TNNP were located outside of the park boundary. For these plots, we averaged density estimates from the nearest survey blocks having aerial survey data. Two GMNP plots were located in a survey block that was only surveyed in 2019, and no moose were detected in the block at that time. Based on expert knowledge, we averaged this with data from the nearest surveyed block, as an estimate of zero would not accurately reflect the previously high densities in that area (S. Gerrow, personal communication, May 1, 2023).

2.2.4. Stand Age

For plots located in previously disturbed forests (i.e., burned area or insect outbreak), stand age was calculated based on the number of years that had passed between the disturbance event and our field sampling. We determined disturbance history using a Geographic Information System (GIS) geospatial database for GMNP and relied on expert knowledge provided by TNNP ecologists. As insect outbreaks can span several years, a year in the middle of the range of outbreak years was used to calculate stand age (e.g., outbreak occurred between 1983-1989, year 1986 was selected). To assess stand age of mature forests in GMNP and TNNP, we used Forest Resource Inventory (FRI) GIS geospatial databases, developed from high resolution (sub 10 cm pixel) 3D aerial photography collected in 2010 (Parks Canada, Rocky Harbour & Glovertown, NL, Canada). In these databases, forest stands were classified according to 20-year age classes; a value was selected in the middle of the age class to calculate the stand age of our plots. The FRI databases were completed in 2010, however we conducted fieldwork in 2022; due to this time lapse, we added 12 years to the designated age classes.

2.2.5. Aboveground Carbon

To test predictions i) and iii), we quantified the carbon stored in trees, deadwood, woody shrubs, saplings, dominant herbaceous plants, ground vegetation, and litter. For all stocks, except litter, we collected in-field measurements and used published allometric equations to calculate biomass (Table 2.3); we then converted biomass to carbon content, with an assumed 50% carbon content of calculated dry biomass (Coomes et al., 2002; Latte et al., 2013). For litter, we collected in-field samples, which were processed and sent for carbon analysis. Although these stocks were measured and sampled in subplots and quadrats of varying sizes, the carbon quantity of each stock was calculated at the scale of the 9 m^2 subplot for the purpose of summing all aboveground carbon (Figure 2.2; Table A.1).

Tree Biomass

Within each 5 m^2 subplot, we measured the diameter-at-breast-height (DBH), estimated height, and recorded the species or genus of all live trees that were ≥ 3 m tall (Figure 2.2). Following Lambert et al. (2005), we input these data into allometric equations to calculate the biomass of various tree compartments (e.g., wood, bark, foliage, and branches; see Table 2.3). We then summed these compartments to calculate the biomass of each tree, and multiplied this value by 0.5 to estimate its carbon content. The carbon content of all measured trees within each 5 m^2 subplot was summed and then extrapolated to the scale of the 9 m^2 subplot.

Shrub, Sapling & Herbaceous Plant Biomass

We recorded the height, cross-sectional diameters at the top of the plant (i.e., area) or stem basal diameter, and species of each woody shrub and tree sapling, between 30 cm and 3 m tall within each 5 m^2 subplot. We also recorded the percent cover of dominant herbaceous plants (i.e., grasses and ferns). If many individuals of the same species were present within the subplot, they were sorted into groups of similar sizes; we then measured one individual within that class and counted the number of individuals within that group. We used allometric equations to calculate the biomass of all recorded species within each 5 m^2 subplot before extrapolating to the scale of the 9 m^2 subplot and converting to carbon content (Table 2.3).

Ground Vegetation

In each corner of the 9 m^2 subplot, we placed a 0.25 m^2 (0.5 m x 0.5 m) quadrat (Figure 2.2). We recorded the percent cover of vascular species under 30 cm tall (graminoids, forbs, brambles, and ferns), as well as lichens and mosses (bryoids) within these quadrats. We recorded the percent cover of bare soil, rock, leaf litter, and needle duff to provide insight into the data post-collection (i.e., an explanation for a lack of vegetative cover). We also recorded the species, height, and cross-sectional diameters (i.e., area) of woody shrubs less than 30 cm tall within each quadrat. We used allometric equations to calculate and sum the biomass of all ground vegetation and small woody shrubs within each quadrat (Table 2.3). We summed the biomass within all four 0.25 m^2 quadrats per 9 m^2 subplot (i.e., area of 1 m^2), then extrapolated this to the scale of the 9 m^2 subplot and converted to carbon content.

Deadwood

Within each 9 m^2 subplot (Figure 2.2), we measured all fallen logs, stumps, and standing deadwood having a diameter ≥ 10 cm, following protocols from Coomes et al. (2002) and

Richardson et al. (2009). We estimated or measured the height and DBH of standing deadwood. For fallen logs, we measured the length and cross-sectional diameters at both ends; for stumps, we measured the height and cross-sectional diameters of the top. If a log exited the subplot or tapered to below 10 cm in diameter, the length was only measured to that point and the second pair of diameters was assumed to be the same as the first; this same assumption was made for stumps. We recorded the decay class of all deadwood following the classes outlined in Harmon et al. (2011).

We calculated deadwood volume using equations listed in Richardson et al. (2009). We then used equations from Harmon et al. (2011) to convert volume to biomass using average densities based on the deadwood form (standing/stump or downed), recorded decay class, and hardwood/softwood classification. For stumps, the standing deadwood decay reduction factors were used. If the deadwood had not been classified as either hardwood or softwood, the average density for the recorded decay class and form was used (see Table 2.3). We multiplied the calculated biomass by 0.5 to estimate carbon content and summed the carbon content of all measured deadwood within each 9 m^2 subplot.

Litter

We collected litter samples from within the southwest and northwest 0.25 m^2 ground vegetation quadrats (n = 2 litter samples per 9 m^2 subplot). At most 9 m^2 subplots we were able to collect litter within both quadrats; however, due to a lack of litter we collected a sample from just one of these quadrats in some subplots (n = 5).

In the field, we placed litter samples in sealed bags, transported them in a cooler, and kept them frozen until lab processing. In the lab, we combined litter samples according to the subplots in which they were collected. We placed samples in aluminum tins, weighed them, and then dried them at 60° C until they reached a constant weight (~24-48 hours). We noted the final weight of the dried sample and then used a research-grade grinder to homogenize the sample.

After grinding, we sent approximately 10 mg of each sample to the Agriculture and Food Laboratory at the University of Guelph (Guelph, ON, Canada) to determine the percent of carbon per sample. We then extrapolated the results from these analyses to the dry weight of the sample; these data represented the amount of carbon in litter in 0.5 m^2 of each 9 m^2 subplot, which we then extrapolated to the scale of the 9 m^2 subplot (Figure 2.2). To summarize, the carbon content of litter was calculated using the following equation: Carbon in litter per subplot (g C/9-m^2) = [(percent carbon content/100) * final dry weight of litter samples] * (9 m^2/0.5 m^2) .

2.2.6. Belowground Carbon

To test predictions i) and iii), we quantified the carbon stored in organic soil and the roots of all trees, woody shrubs, saplings and herbaceous vegetation. We used published allometric equations to calculate root biomass (Table 2.3); we then converted biomass to carbon content, with an assumed 50% carbon content of calculated dry biomass (Coomes et al., 2002; Latte et al., 2013). For organic soil, we collected in-field samples, which were processed and sent for carbon analysis. All carbon stocks were calculated at the scale of the 9 m^2 subplot for the purpose of summing total belowground carbon content (Figure 2.2; Table A.1).

Root Biomass

For live trees ≥ 3 m tall, we calculated root biomass using equations based on aboveground-belowground biomass relationships. Following Li et al. (2003), we used equations to calculate the total root biomass of softwood and hardwood trees, using their calculated aboveground biomass (see above; Table 2.3). Following Coomes et al. (2002), we calculated the root biomass of all woody shrubs (i.e., shrubs less than 30 cm tall or between 30 cm and 3 m tall), saplings, and herbaceous vegetation roots as 25% of the calculated aboveground biomass. The biomass of roots was extrapolated to the scale of the 9 m^2 subplot and then converted to carbon content.

Carbon in Organic Soil

We collected a soil core from within the southwest and northwest 0.25 m^2 ground vegetation quadrats in each 9 m^2 subplot (n = 2 soil samples per 9 m^2 subplot). We collected samples of the organic soil layers (layers L, F, and H; Soil Classification Working Group, 1998). To do this, we used a mallet to insert a brass cylinder having a 1.90 cm (0.75 in) radius into the soil to the fixed depth of the cylinder (10.16 cm; 4 in). Once extracted, the soil was pushed out of the cylinder using the handle of the mallet. If the core included a layer of mineral soil, a knife was used to divide the core at the interface between the soil layers and the mineral layer was discarded. Organic soil samples were refrigerated at 4^o C until lab processing.

In the lab, we dried organic soil samples at 60^o C until they reached constant weight (~24-48 hours), then noted the final dry weight of the samples. We used a 2 mm-sieve to remove rocks from the sample and weighed all remaining material. We removed the rocks from the sieve and noted the weight of any organic material (i.e., small roots) before adding the organic material back into the soil sample. We combined samples according to the subplots in which they were collected and used a research-grade grinder to create a homogenous sample.

After grinding, we sent approximately 10 mg of each sample to the Agriculture and Food Laboratory at the University of Guelph (Guelph, Ontario, Canada) to determine the percent of carbon per sample. We then extrapolated the results from these analyses to the final dry weight of the organic soil and organic material and used the combined soil surface area of the two cores (i.e., 22.68 cm^2) to calculate the amount of carbon in the organic soil layers within each 9 m^2 subplot. To summarize, we calculated the carbon content of the organic soil layer using the following equation: Soil carbon per subplot (g C/9 m^2) = [(percent carbon content/100) * final dry weight of soil & organic material] * (9 m^2 / area of two soil cores).

2.2.7. Plant-Available Nitrogen

To test predictions ii) and iv), we used plant root simulator probes (PRS probes; Western Ag Innovations, Inc., Saskatoon, SK, Canada) to measure the supply rates of plant-available nitrogen at our plots. We placed a pair of PRS probes at each corner of every 9 m^2 subplot, for a total of four pairs per 9 m^2 subplot (four anion and four cation probes; Figure 2.2). Plots having three pairs of subplots had a total of 12 pairs of PRS probes deployed, while plots with four pairs of subplots had a total of 16 pairs of PRS probes deployed (Table 2.2). To place the probes, we used a knife to create an opening in the soil that would allow for the entirety of the membrane to be belowground. We then placed the probes vertically into the hole and pressed the soil down to ensure there was contact between the soil and the membrane on the probes. The pairs of PRS probes were left to adsorb positively- and negatively- charged soil ions for 22-35 days following burial (Table A.2). Following retrieval, probes were cleaned with deionized water and refrigerated at 4° C until shipped to Western Ag Innovations (Saskatoon, SK) for lab analysis; note that probes were analyzed according to subplot (i.e., four pairs of probes placed in the same subplot were analyzed together).

We also used data loggers (HOBO Pendant Temperature/ Light Data Logger) to record soil temperature measurements. We deployed one data logger at each plot, randomly selecting the 0.25 m^2 quadrat to place it in. We used a knife to create an opening in the soil and placed the logger within the organic soil layers. Temperature loggers were left for the same duration of the PRS probes within the same plot, collecting one temperature reading per hour.

2.2.8. Statistical Analysis

For the carbon analyses, we summed the various carbon stocks to calculate the total carbon, aboveground carbon, and belowground carbon stored within each 9 m^2 subplot. We then calculated the mean total, aboveground, and belowground carbon across all subplots within each plot and used these values as our response variables. For the plant-available nitrogen analyses, we focused on the supply rate of ammonium, as values for nitrate were frequently below detection limits. We calculated the supply rate to probes per day (i.e., result of analysis/the number of days deployed), and calculated the mean rate of supply (micrograms/10-cm^2/day) of all subplots within each plot and used that value as our response variable. We also calculated the mean soil temperature of the measurements recorded at each plot over the duration of their deployment.

We analyzed the data as two groups based on sampling design. First, we analyzed all novel plots (i.e., plots not part of the exclosure-control experimental design) as well as control plots (controls paired to exclosure plots) together. We refer to these plots as “open” plots throughout as these areas were accessible to moose; the minimum distance between open plots was ~ 230 m. This first analysis included moose density as a continuous explanatory variable. Second, we analyzed the paired exclosure-control plots where moose density was experimentally controlled (i.e., no moose in exclosures). We fit a suite of models (see details below) based on our a-priori predictions for each response variable (see introduction). We performed all statistical analyses using the lm function within the *stats* package (R Core Team, 2023), and the lmer, glm, and glmer functions within the *lme4* package (Bates et al., 2015) using R.v.4.2.3 statistical software (R Core Team, 2023). We used Akaike Information Criterion corrected for small sample size (AIC_c) to rank the models based on explanatory power (Burnham & Anderson, 2004; Symonds & Moussalli, 2011), using the *AICcmodavg* package (Mazerolle, 2023). To measure model fit, we used Nagelkerke's pseudo R^2, within the *rcompanion* package (Mangiafico, 2023), for generalized linear models (GLMs) and generalized linear mixed models (GLMMs); we used adjusted R^2 for linear models and marginal and conditional R^2 for linear mixed models. Following Leroux (2019), we removed models with uninformative variables from each model set.

Carbon Analyses

Open Plots

To test predictions i) and iii), we ran generalized linear models with a Gamma error distribution and log link function, and having either total carbon, aboveground carbon, or belowground carbon as the response variable. We included three fixed effects as explanatory variables: disturbance type (categorical having 3 classes; insect, fire, and mature forest [i.e., undisturbed]), moose density (continuous; moose/km^2), and stand age (continuous; time since last disturbance or estimated age of mature stand). We fit the same set of 8 a-priori models to each response variable (Table A.3), including a null model and all three univariate models. The model set also included additive and multiplicative (i.e., interaction) bi-variate models that included either stand age and moose density, or disturbance type and moose density. We did not include disturbance type and stand age as response variables in the same model, as both describe the disturbance history at our plots.

Paired Exclosure-Controls

To further test predictions i) and iii), we ran generalized linear mixed models having a Gamma error distribution and log link on the paired exclosure-control dataset, with total carbon, aboveground carbon, or belowground carbon as the response variable. We excluded deadwood from total and aboveground carbon for these analyses because deadwood may have been removed from the area during the construction of exclosures. We ran these models with three fixed effects as explanatory variables: disturbance type (as above), exclosure/control (categorical having 2 classes), and stand age (as above). We also included site (10 classes) as a random intercept to account for the paired design. We fit the same set of 8 a-priori models to each response variable (Table A.4), including a null model (site as sole explanatory variable). The model set also included additive and multiplicative (i.e., interaction) models that included either stand age and exclosure/control, or disturbance type and exclosure/control. We did not include disturbance type and stand age as response variables within the same models, as both describe the disturbance history at our plots.

Plant-Available Nitrogen Analyses

Open Plots

To test predictions ii) and iv), we ran linear models having a Gaussian error distribution on the open plot dataset, with the supply rate of ammonium to PRS probes as our response variable. We included three fixed effects as explanatory variables: disturbance type (categorical having 3 classes; insect, fire, and mature forest [i.e., undisturbed]), moose density (continuous; moose/km^2), and stand age (continuous; time since last disturbance or age of mature stand). We also included soil temperature (mean temperature recorded over the duration of deployment) as a control variable, as temperature can influence the supply rate of ammonium through its influence on soil microorganism activity (Dieleman et al., 2012; Knoepp & Swank, 2002). We fit 16 a-priori models, including a null model and four univariate models (Table A.5). The model set also included additive and multiplicative (i.e., interaction) models that included either stand age and moose density, or disturbance type and moose density, with temperature included as a control variable in 7 of the models and in a univariate model. We did not include disturbance type and stand age as response variables within the same models, as both describe the disturbance history at our plots.

Paired Exclosure-Controls

To further test predictions ii) and iv), we ran linear mixed models having a Gaussian error distribution on the ammonium supply rate data from the paired exclosure-control dataset. We included three fixed effects as explanatory variables: disturbance type (as above), exclosure/control (categorical having 2 classes) and stand age (as above); we also included soil temperature (the mean temperature over the period of probe deployment) as a control variable, and site (10 classes) as a random intercept to account for the paired design. We fit 16 a-priori models, including a null model (site as sole explanatory variable) and four models with just one fixed effect (Table A.6). The model set also included additive and multiplicative (i.e., interaction) models that included either stand age and exclosure/control, or disturbance type and exclosure/control, with temperature included as a variable in 8 of the models. We did not include disturbance type and stand age as response variables within the same models, as both describe the disturbance history at our plots.

2.3. Results

2.3.1. Carbon Analyses

Open Plots

On average organic soil accounted for 43.4 ± 28.9% of carbon measured at each plot, while live trees and deadwood accounted for 28.4 ± 28.6% and 9.4 ± 9.7%, respectively, of carbon measured at each plot (mean ± SD; Figure 2.3). Across all open plots, total carbon ranged from 13.03 – 926.78 kg C/9-m^2; aboveground carbon ranged from 2.32 – 766.88 kg C/9-m^2; belowground carbon ranged from 10.71 – 191.61 kg C/9-m^2 (Table A.1).

In open plots, the plot having the most total and aboveground carbon stored was a mature forest plot (stand age = 83 years) in GMNP, that had an estimated moose density of 1.31 moose/km^2 (GM-13-CTRL). The plot having the most belowground carbon stored was a mature forest plot (stand age = 83 years) in TNNP, that had an estimated moose density of 0.18 moose/km^2 (TN-32). The plot having the least total, aboveground, and belowground carbon stored was in a 20-year-old burned plot in TNNP, which had an estimated moose density of 1.71 moose/km^2 (TN-25-CTRL).

In open plots, total carbon storage increased with increasing stand age (Figure 2.4). Mature forest plots had the most total carbon stored (293.05 ± 311.56 kg C/9-m^2; mean ± SD), followed by insect outbreak plots (66.60 ± 44.08 kg C/9-m^2), and forest fire plots (42.81 ± 34.22 kg C/9-m^2; Figure 2.5). There was no clear relationship between moose density and carbon storage (Figure A.1)

Total Carbon Model

The univariate stand age model was the top model for explaining variation in total carbon ($R^2 = 0.59$). There were no competing models which demonstrates no relationship between moose density or disturbance type and total carbon (Table 2.4).

We observed evidence that stand age had a positive relationship with total carbon storage ($\beta = 0.03$; SE = 0.01; Figure 2.4). The top model indicates that with each one-year increase in stand age, total carbon storage increased by a multiplicative factor of 1.03 (e.g., 50 kg C/9-m^2 at 25 years; 219.20 kg C/9-m^2 at 75 years).

Aboveground Carbon Model

The univariate stand age model was the top model for explaining variation in aboveground carbon ($R^2 = 0.53$). The disturbance type model was a competing model (ΔAICc = 1.46; $R^2 = 0.55$). We observed no relationship between moose density and aboveground carbon (Table 2.4).

We observed evidence that stand age had a positive relationship with aboveground carbon storage ($\beta = 0.04$; SE = 0.01; Figure 2.4). The top model indicates that with each one-year increase in stand age, aboveground carbon storage increased by a multiplicative factor of 1.04 (e.g., 50 kg C/9-m^2 at 25 years; 355.33 kg C/9-m^2 at 75 years).

Belowground Carbon Model

The univariate stand age model was the top model for explaining variation in belowground carbon ($R^2 = 0.42$). The disturbance type model was a competing model (ΔAICc = 1.43; $R^2 = 0.44$) but as above, we observed no relationship between moose density and belowground carbon (Table 2.4).

We observed evidence that stand age had a positive relationship with belowground carbon storage (β = 0.02; SE = 0.00; Figure 2.4). The top model indicates that belowground carbon storage increased annually by a multiplicative factor of 1.02 (e.g., 50 kg C/9-m^2 at 25 years; 134.58 kg C/9-m^2 at 75 years).

Paired Exclosure-Controls

Of all exclosure and control plots, the plot having the most total, aboveground, and belowground carbon stored was a mature forest plot (stand age = 83 years) in GMNP, which had an estimated moose density of 1.31 moose/km^2 (GM-13-CTRL). The plot having the least total and belowground carbon stored was in a 20-year-old burned plot in TNNP, which had an estimated moose density of 1.71 moose/km^2 (TN-25-CTRL). The plot having the least aboveground carbon stored was in a 36-year-old insect disturbance in GMNP, which had an estimated moose density of 2.99 moose/km^2 (GM-05-CTRL).

On average, controls stored more total carbon (165.95 ± 270.25 kg C/9-m^2; mean ± SD), than their paired exclosures (143.29 ± 141.46 kg C/9-m^2); however, there was no consistent directional effect across sites (Figure 2.6). Total stored carbon increased with increases in stand age (Figure A.2); mature forest plots stored the most total carbon (331.38 ± 322.84 kg C/9-m^2), followed by insect-disturbed plots (86.88 ± 63.98 kg C/9-m^2) and plots in burned areas (30.84 ± 25.19 kg C/9-m^2; Figure A.2).

Total Carbon Model

The stand age model was the top model explaining variation in total carbon ($R^2 = 0.17$); however, it was within 2 ΔAICc of the null model (ΔAICc = 0.48), indicating weak to no evidence of a relationship with stand age (Table 2.5). The disturbance model was a competing model (ΔAICc = 0.19; $R^2 = 0.30$) but again was within 2 ΔAICc of the null model. We therefore did not find evidence that any of the explanatory variables (stand age, disturbance type, moose exclusion), explained variation in total carbon storage.

Aboveground Carbon Model

The disturbance model had the lowest AICc estimate; however, as it failed to converge, we are unable to interpret the output. Although the stand age model was a competing model (ΔAICc = 1.97; $R^2 = 0.21$) it was within 2 ΔAICc of the null model (ΔAICc = 3.61), indicating weak to no evidence of a relationship between stand age and aboveground carbon (Table 2.5).

Belowground Carbon Model

The null model was the top model for the belowground carbon set of models ($\beta = 3.71$; SE = 0.20; Table 2.5). Thus, we did not find evidence that any of the explanatory variables (stand age, disturbance type, moose exclusion), explained any variation in belowground carbon storage.

2.3.2. Plant-Available Nitrogen Analyses

Open Plots

Across open plots, the supply rate of ammonium in soil ranged from 0.12 to 1.53 μg/10-cm^2/day (0.53 ± 0.35 μg/10-cm^2/day; mean ± SD; Table A.2), and soil temperature ranged from 12.6 to 19.2° C (15.7 ± 1.54° C). The plot having the highest ammonium supply rate was a mature forest plot (stand age = 63 years) in GMNP, which had an estimated moose density of 2.67 moose/km^2 and a mean soil temperature of 13.9° C (GM-14). The plot with the lowest ammonium supply rate was in a 46-year-old burned area in TNNP, which had an estimated moose density of 0.2 moose/km^2 and a soil temperature of 17.7° C (TN-30).

Mature forest plots had the highest ammonium supply rate (0.63 ± 0.40 μg/10-cm^2/day), followed by insect-disturbed plots (0.58 ± 0.32 μg/10-cm^2/day) and burned plots (0.20 ± 0.07 μg/10-cm^2/day; Figure 2.7). Previously burned plots had the highest average soil temperatures (16.5 ± 1.2° C), followed by insect-disturbed plots (16.0 ± 1.5° C), and mature forest plots (14.6 ± 1.2° C; Figure 2.7).

In open plots, the additive model including moose density and soil temperature was the top model for explaining variation in the supply rate of ammonium in soil ($R^2 = 0.38$). There were no competing models (Table 2.6). We observed evidence that estimated moose density had a positive relationship with the ammonium supply rate ($\beta = 0.09$; SE = 0.03), while soil temperature was negatively related to ammonium supply rate ($\beta = -0.11$; SE = 0.03; Figure 2.8).

Paired Exclosure-Controls

In paired exclosure-control sites, mature forest plots had the highest ammonium supply rate (0.52 ± 0.24 μg/10-cm^2/day; mean ± SD), followed by insect-disturbed plots (0.43 ± 0.26 μg/10-cm^2/day) and burned plots (0.20 ± 0.05 μg/10-cm^2/day; Figure 2.7). Previously burned plots had the highest average soil temperatures (16.0 ± 1.8° C), followed by insect-disturbed plots (15.7 ± 1.6° C) and mature forest plots (14.3 ± 1.3° C; Figure 2.7). The supply rate of ammonium in soil was higher in exclosures (0.47 ± 0.26 μg/10-cm^2/day) than in controls (0.39 ± 0.25 μg/10-cm^2/day; Figure 2.8), whereas average soil temperature was higher in controls (16.2 ± 1.6° C) than in exclosures (14.4 ± 1.0° C; Figure A.3).

In paired exclosure-controls, the soil temperature model was the top model for explaining variation in the supply rate of ammonium in soil (marginal $R^2 = 0.17$; conditional $R^2 = 0.75$); there were no competing models (Table 2.7). We observed evidence that soil temperature had a negative relationship with the supply rate of ammonium ($\beta = -0.06$; SE = 0.02; Figure 2.8).

2.4. Discussion

We used observational and experimental data to measure the impacts of insect outbreaks, forest fires, and moose on carbon storage (i.e., total, aboveground, and belowground carbon) and plant-available nitrogen in forests in two national parks on Newfoundland. In our open plot data (i.e., novel and control plots; plots that were accessible to moose), we found that disturbed forests were associated with reduced carbon storage, while carbon storage increased as forest stands aged. However, we did not find evidence of a relationship between carbon storage and moose density. We also found that supply rate of ammonium was negatively correlated with soil temperature and positively correlated with moose density. Using our experimental data (i.e., moose exclosures and paired controls), we did not detect any effect of disturbance history or moose presence on carbon storage or ammonium supply rates after 24-27 years of moose exclusion.

2.4.1. Carbon Storage

In our open plots, we found evidence to support our prediction that forest disturbances were associated with reduced carbon storage. We observed that sites with older forest stands which did not experience forest disturbance in the past several decades stored more total, aboveground, and belowground carbon than forest stands disturbed in the past several decades (Table 2.4; Figure 2.4). Forest disturbances, such as insect outbreaks and fire, result in canopy tree mortality, but in doing so create canopy openings that allow for the rapid growth of understory and pioneer plants and regenerating trees (Franklin et al., 2000; Swanson et al., 2011). However, since live trees act as a large carbon store (Figure 2.3; Moroni et al., 2010), mature forests store more carbon than recently disturbed forests (Fu et al., 2017; Hicke et al., 2012; Kurz et al., 2013). Additionally, while forest disturbances result in the recycling of elements to the soil (Arango et al., 2019; Wan et al., 2001), disturbances may also lead to decreases in elemental inputs from litterfall. It is also important to note a loss of trees and shrubs aboveground also leads to a reduction in our calculations of belowground root biomass.

The amount of carbon that is lost during a disturbance and the length of time it will take to replace this carbon is largely dependent on the type and severity of the disturbance (Fu et al., 2017; Kurz et al., 2013). Our analysis demonstrates that previously burned areas have less aboveground and belowground carbon stored than those in insect-disturbed areas (Table 2.4; Figure 2.5). The difference in carbon stored between burned areas and insect outbreaks may have arisen because of the selective nature of insect outbreaks; with only host trees being targeted during the outbreak, non-host species may benefit from decreased competition post-outbreak (Hennigar et al., 2007). Areas that experience insect outbreaks also retain much of their stored carbon in the form of dead organic matter (e.g., dead wood, litter, and organic soils; Hansen, 2014; Hicke et al., 2012), whereas large amounts of carbon may be lost to the atmosphere during a forest fire through the combustion of dead organic matter (Kasischke, 2000).

The length of time required to recover carbon lost due to a disturbance may be exaggerated in our study system, as moose over browsing impedes natural forest regeneration (Leroux et al., 2020). Specifically, insect outbreaks and forest fires remove adult balsam fir and reduce seed sources, while moose browsing inhibits fir seedlings and saplings from growing, providing a significant delay in forest regeneration (Connor et al., 2000; Gosse et al., 2011; Leroux et al., 2021). However, counter to our prediction, we did not find evidence of a relationship between moose densities and carbon storage in our open plots (Table 2.4; Figure A.1). We also did not observe consistent impacts of forest disturbances or moose after 24-27 years of moose exclusion (Table 2.5). This result is supported by findings in Allen et al. (2023), who also reported no effect of ungulate herbivory on carbon storage in their long-term (>20 years) exclosure-control plots arrayed across New Zealand temperate forest sites. These results, however, run counter to other evidence of strong impacts of moose herbivory on boreal plant communities (De Vriendt et al., 2021; Ellis & Leroux, 2017; Kolstad et al., 2018; Rotter & Rebertus, 2015). Our results are also contrary to a recent synthesis of 100 paired moose (*Alces alces*) exclosure-control sites across the boreal forest biome which found that moose have consistent and strong negative effects on aboveground biomass (Petersen et al., 2023). We offer three potential explanations for our findings of no relationship between moose densities and carbon storage: i) heterogeneous effects, ii) active management of moose, and iii) poor resolution moose density data.

First, the effects of moose herbivory may be heterogenous across landscapes, as indicated by the high level of variability between sites within our paired exclosure-control dataset (Figure 2.6). For example, at site TN-22 the exclosure stored > 2x more total carbon than its paired control, in contrast to site TN-20, where the exclosure stored > 2x less total carbon than its paired control. Overall, in 6 paired exclosure-controls, the exclosure stored more total carbon than the control, in 3 the exclosure stored less total carbon than the control, and in 1 total carbon was approximately equal in the exclosure and control (Figure 2.6). Newfoundland forest canopies are dominated by balsam fir and black spruce trees (*Picea mariana*). Balsam fir can be heavily browsed when moose are abundant and this can lead a loss of forest cover (Connor et al., 2000; McLaren et al., 2004) which can contribute to lower carbon storage. However, in some cases, selective browsing of palatable species such as fir may result in reduced competition, facilitating the growth of some non-palatable trees, such as black spruce (Pastor & Cohen, 1997; Zonnevylle et al., 2023). The growth of non-palatable trees to the canopy may have compensated for lost carbon from the reduced presence of palatable species. Moose effects on carbon storage, therefore, may be mediated by plant palatability and future research could conduct more comprehensive plant surveys (e.g., sample all trees in a plot) to test this hypothesis.

Second, both GMNP and TNNP began managing their moose populations through hunting in 2011. Moose management is ongoing in the parks and has resulted in decreases in moose densities of 50% or more (Gosse, 2019; Robineau-Charette et al., 2021), particularly in areas near roads or trails that are accessible to hunters (Perry et al., 2020). Over a decade of hunting in the parks has begun to allow for the regeneration of many unfenced forested areas (i.e., open to moose; Parks Canada Agency, 2018), with regenerating areas being dominated by numerous fir saplings that have not yet self-thinned (McCarthy & Weetman, 2007; see Figure A.4). It may therefore have been difficult to detect the effect of moose on carbon storage, as the trajectory of these effects and spatial heterogeneity in these effects were altered following the initiation of moose management.

Finally, we did not have moose density data available for the years immediately following the occurrence of the disturbances and establishment of exclosures when the increase in foraging opportunity may have increased moose densities in those areas. We speculate that data on earlier moose densities may have been better predictors of present-day carbon storage than the more recent densities used in our study. Consequently, we recommend regular moose density surveys be maintained to better track population dynamics and understand moose impacts on forest ecosystems. Overall, this work provides evidence of strong moose effects on carbon storage at some sites but weak to no effects, on average. Given the challenges of measuring the long-term impact of animals on ecosystem processes, we propose that mathematical models may play an important role in forecasting animal impacts on carbon sequestration. This is common practice in the ecology and management of insect outbreaks (e.g., Dymond et al., 2010; Kurz et al., 2008; Liu et al., 2022).

2.4.2 Plant-Available Nitrogen

Similar to Bieser and Thomas (2019) and Shenoy et al. (2013), we used PRS probes to measure the supply rate of ammonium in soil. Overall, site (a random effect) accounted for a large proportion of variation in the supply rate of ammonium in soils across our paired exclosure-controls. In both our open plot and paired exclosure-control datasets, we found evidence that soil temperature had a negative relationship with the supply rate of ammonium (Table 2.6 & 2.7; Figure 2.8). While increases in soil temperatures are typically found to increase nitrogen mineralization rates (Guntiñas et al., 2012; Knoepp & Swank, 2002), we speculate that soil temperatures at our plots may have been linked to disturbance history, with higher temperatures at plots with less shading (i.e., disturbed plots, Siwek, 2021; Smith-Tripp et al., 2022). For example, mature forest plots had the lowest soil temperatures and the highest supply rate of ammonium, while burned plots had the highest soil temperatures and the lowest supply rate of ammonium (Figure 2.7). We offer three potential explanations for this finding: i) decreased litter quality and quantity, ii) loss of soil moisture, and iii) decreased diffusion in soils.

First, our plots with the highest soil temperatures (i.e., disturbed plots) may have experienced losses in aboveground biomass or changes in aboveground plant community composition, resulting in decreased quantity and/or quality of litter input (Ficken & Wright, 2017; Li et al., 2022). This could then impact nitrogen mineralization and immobilization. Second, while we did not measure the moisture content of soils at our plots, warmer soils in disturbed areas with decreased canopy cover may have been drier or more variable due to increased evaporation and convection. Previous research in our system has reported much greater variability in soil moisture in controls plots compared to moose exclosures plots (Swain et al. 2023). Periods of low moisture levels may have then inhibited microbial activity (Borken & Matzner, 2009; Evans et al., 2022), decreasing the amount of ammonium in soil. Finally, PRS probes are sensitive to soil moisture due to the decrease of elemental diffusion in dry soils (Qian & Schoenau, 2002). Consequently, it is possible that our results may not be indicative of an absolute reduction in ammonium in soil, but instead reflect a decreased supply rate to plant roots caused by a decrease in soil moisture. To test this, we suggest that future work pair the use of PRS probes with an in-situ method of measuring nitrogen mineralization rates, such as the use of soil cores, while also collecting soil moisture measurements.

In our open plots, we found evidence that moose density had a positive relationship with the supply rate of ammonium in soil (Table 2.6; Figure 2.8). Moose browsing may have stimulated nitrogen production by increasing rhizodeposition, as suggested by Dufresne et al. (2009) for whitetail deer (*Odocoileus virginianus*) browsing on Anticosti Island, Quebec. Localized inputs from moose feces and urine deposits may also have contributed to the elemental pool, although Pastor et al. (1993) did not find that this input was enough to compensate for the changes in plant communities in their boreal system. As suggested by Kolstad et al. (2018), aboveground changes in species composition and canopy cover associated with moose presence may have altered soil temperature and moisture, leading to increased elemental cycling and diffusion (although note a lack of relationship between moose density and soil temperature [Figure A.3]). Finally, as mentioned above, both GMNP and TNNP have experienced an increase in forest regeneration within the last decade due to their implementation of moose population reduction programs. Consequently, it is possible, that some of our plots associated with mid to high moose densities are now regenerating. Soil moisture can be higher in early-successional stands compared to mature forests, due to decreases in canopy interception of precipitation and water loss through evapotranspiration (Elliott et al., 1998). If regenerating stands were able to retain more moisture through partial shade, then this may have stimulated microbial activity, as well as increased elemental diffusion in soil. See Appendix B for further discussion of our paired exclosure-control results.

2.4.3. Conclusion

Our study has shown that forest disturbances can reduce total, aboveground, and belowground carbon storage in boreal forests, and that carbon storage increases as regenerating forests age. However, we found that moose effects on carbon storage were variable with no relationship emerging on average. Although we did not find evidence of impacts of disturbance or moose exclusion in our paired exclosures, we recommend that further research be conducted into the spatial variability of our results given that we observed considerable variation between sites. Promising future avenues may be to: a) expand local sampling; b) measure carbon stocks in the 100 moose exclosure-control plots sampled by Petersen et al. (2023); and/or c) conduct future work in areas with long-term ungulate population data, or where ungulate populations have been relatively stable. An additional consideration is how forest disturbances and moose may interact to impact carbon storage over longer time frames. While we have shown that plots in forest disturbances stored less carbon than mature forests, their role in creating a heterogeneous landscape and transferring carbon to the soil may still be important for long-term carbon persistence (Jactel et al., 2017; Kristensen et al., 2022; Kuuluvainen & Gauthier, 2018). Through our study, we have demonstrated that forest disturbances are a key driver of carbon storage dynamics, but that further research is necessary to understand the long-term impacts of moose herbivory on forest carbon stocks.

2.5. References

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Table 2.1: Descriptions of Newfoundland ecoregions where study plots were established. Information sourced from Damman (1983).

Ecoregion	Dominant Tree Species	Other Common Tree Species	Additional Notes	Number of Plots
Central Newfoundland	*Abies balsamea, Picea mariana*	*Betula papyrifera, Populus tremuloides*	Disturbance by fire is common, causing fir dominant forests to be replaced by spruce.	17
North Shore	*Abies balsamea, Picea mariana*	*Picea glauca*	Similar to Central Newfoundland, but *Picea glauca* is much more common; *Populus tremuloides* is rare and do not form stands.	6
Western Newfoundland	*Abies balsamea, Betula papyrifera, Betula alleghaniensis, Acer spp.*	*Picea mariana, Pinus strobus, Populus balsamifera, Populus tremuloides, Picea glauca, Larix Laricina*	Disturbance by fire is least common in this ecoregion. Has most favourable conditions for plant growth and many species are restricted to this ecoregion in Newfoundland.	5
Northern Peninsula	*Abies balsamea*	*Larix Laricina, Betula papyrifera, Picea mariana Picea glauca*	Similar to Western Newfoundland forests, with some characteristic species absent (e.g., *Acer rubrum, Populus tremuloides, Pinus strobus*)	18

Table 2.2: List of plots sampled in Newfoundland, Canada. The two letters at the beginning of each plot ID indicates which national park the plot was in (i.e., GM = Gros Morne National Park, TN = Terra Nova National Park). The two letters at the end of paired exclosure-control plot IDs indicate plot type (i.e., EX = exclosure, CTRL = control).

Plot ID	Plot size (m x m)	Number of subplots	Disturbance type	Moose exclosure	Moose density (moose/km$^{2)}$	Stand age
GM-01-EX	15 x 15	3	Insect Outbreak	St. Paul's	0	42
GM-01-CTRL	25 x 25	4	Insect Outbreak	St. Paul's	7.76	42
GM-02	25 x 25	4	Insect Outbreak	NA	2.10	36
GM-03	25 x 25	4	Insect Outbreak	NA	4.17	22
GM-04	25 x 25	4	Insect Outbreak	NA	1.70	22
GM-05-EX	15 x 15	3	Insect Outbreak	Millbrook	0	36
GM-05-CTRL	25 x 25	4	Insect Outbreak	Millbrook	2.99	36
GM-06	25 x 25	4	Insect Outbreak	NA	1.09	22
GM-07	25 x 25	4	Insect Outbreak	NA	4.20	36
GM-08	25 x 25	4	Insect Outbreak	NA	2.32	36
GM-09	25 x 25	4	Insect Outbreak	NA	3.71	36
GM-10	25 x 25	4	Insect Outbreak	NA	3.71	36
GM-11	25 x 25	4	Insect Outbreak	NA	2.10	36
GM-12	25 x 25	4	Insect Outbreak	NA	2.89	36
GM-13-EX	15 x 15	3	Mature Forest	Norris Point	0	83
GM-13-CTRL	25 x 25	4	Mature Forest	Norris Point	1.31	83
GM-14	25 x 25	4	Mature Forest	NA	2.67	63
GM-15	25 x 25	4	Mature Forest	NA	1.09	83
GM-16	25 x 25	4	Mature Forest	NA	2.32	63
GM-17	25 x 25	4	Mature Forest	NA	4.05	63
GM-18	25 x 25	4	Mature Forest	NA	4.92	83
GM-35	25 x 25	4	Mature Forest	NA	1.82	63
GM-36	25 x 25	4	Insect Outbreak	NA	2.89	36
TN-19-EX	25 x 25	4	Insect Outbreak	Ochre Hill	0	47
TN-19-CTRL	25 x 25	4	Insect Outbreak	Ochre Hill	0.43	47
TN-20-EX	25 x 25	4	Insect Outbreak	Platters Cove	0	47
TN-20-CTRL	25 x 25	4	Insect Outbreak	Platters Cove	1.96	47
TN-21-EX	25 x 25	4	Insect Outbreak	Blue Hill Centre	0	47
TN-21-CTRL	25 x 25	4	Insect Outbreak	Blue Hill Centre	0.90	47
TN-22-EX	25 x 25	4	Insect Outbreak	Minchin Cove	0	27
TN-22-CTRL	25 x 25	4	Insect Outbreak	Minchin Cove	1.20	27
TN-23	25 x 25	4	Insect Outbreak	NA	0.54	47
TN-24	25 x 25	4	Insect Outbreak	NA	1.96	42
TN-25-EX	25 x 25	4	Fire	Rocky Pond	0	20
TN-25-CTRL	25 x 25	4	Fire	Rocky Pond	1.71	20
TN-26	25 x 25	4	Fire	NA	0.13	4
TN-27	25 x 25	4	Fire	NA	0.26	16
TN-28	25 x 25	4	Fire	NA	0.35	26
TN-29	25 x 25	4	Fire	NA	0.57	40
TN-30	25 x 25	4	Fire	NA	0.20	46
TN-31-EX	25 x 25	4	Mature Forest	Hall's Beach	0	103
TN-31-CTRL	25 x 25	4	Mature Forest	Hall's Beach	0.97	103
TN-32	25 x 25	4	Mature Forest	NA	0.18	83
TN-33	25 x 25	4	Mature Forest	NA	0.61	103
TN-34-EX	25 x 25	4	Mature Forest	Outport Trail	0	103

TN-34-CTRL	25 x 25	4	Mature Forest	Outport Trail	1.20	103

Table 2.3: Published allometric equations used to calculate the biomass of each carbon stock.

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	

Table 2.4: Results of generalized linear models examining the impact of moose density, forest disturbances, and stand age on total, aboveground, and belowground carbon storage in plots open to moose in Newfoundland, Canada. Only those models having a ΔAICc < 4 are listed (see Table A.3 for full list of model results). Models having one or more uninformative variables are italicized. K: number of parameters; ΔAICc: difference in AICc score relative to the top model in the set; LL: measure of model fit; R^2: relative proportion of variation in the data explained by the model (Nagelkerke's pseudo R^2). Listed coefficients and standard errors are on the log scale; for coefficients, we report the estimate with standard error in brackets.

				Coefficients				
K	ΔAICc	LL	R^2	Intercept	Density	Insect	Fire	Age
Total Carbon								
3	0	-196.00	0.59	3.11				0.03
				(0.28)				(0.01)
4	*1.66*	*-195.56*	*0.60*	*3.24*	*-0.06*			*0.03*
				(0.32)	*(0.08)*			*(0.01)*
4	2.73	-196.10	0.59	5.68		-1.48	-1.92	
				(0.25)		(0.31)	(0.42)	
5	*3.80*	*-195.28*	*0.60*	*5.82*	*-0.09*	*-1.38*	*-2.02*	
				(0.30)	*(0.09)*	*(0.31)*	*(0.43)*	
Aboveground Carbon								
3	0	-180.46	0.53	2.10				0.04
				(0.39)				(0.01)
4	1.46	-179.92	0.55	5.40		-1.78	-2.83	
				(0.35)		(0.44)	(0.59)	
4	*2.14*	*-180.26*	*0.54*	*2.22*	*-0.06*			*0.04*
				(0.45)	*(0.11)*			*(0.01)*
5	*2.92*	*-179.30*	*0.56*	*5.56*	*-0.11*	*-1.66*	*-2.95*	
				(0.43)	*(0.13)*	*(0.44)*	*(0.61)*	
Belowground Carbon								
3	0	-153.96	0.42	2.87				0.02
				(0.20)				(0.00)
4	1.43	-153.41	0.44	4.26		-0.89	-0.87	
				(0.17)		(0.21)	(0.28)	
4	*1.46*	*-153.42*	*0.44*	*2.98*	*-0.05*			*0.02*
				(0.23)	*(0.06)*			*(0.00)*
5	*3.04*	*-152.86*	*0.46*	*4.35*	*-0.06*	*-0.83*	*-0.94*	
				(0.20)	*(0.06)*	*(0.21)*	*(0.29)*	

Table 2.5: Results of the generalized linear mixed models examining the impact of moose exclusion, forest disturbances, and stand age on total, aboveground, and belowground carbon storage in paired exclosure-controls in Newfoundland, Canada. Only those models having a ΔAICc < 4 are listed (see Table A.4 for full list of model results). Models having one or more uninformative variables are italicized. K: number of parameters; ΔAICc: difference in AICc score relative to the top model in the set; LL: measure of model fit; R^2: relative proportion of variation in the data explained by the model (Nagelkerke's pseudo R^2). Listed coefficients and standard errors are on the log scale; for cofficients, we report the estimate and standard error in brackets.

				Coefficients				
K	ΔAICc	LL	R^2	Intercept	Exclosure	Insect	Fire	Age
Total Carbon								
4	0	-113.93	0.17	3.57 (0.55)				0.02 (0.01)
5	0.19	-112.22	0.30	5.62 (0.37)		-1.25 (0.44)	-2.19 (0.71)	
3	0.48	-115.75	0	4.62 (0.32)				
5	*2.85*	*-113.55*	*0.20*	*3.42* *(0.58)*	*0.22* *(0.25)*			*0.02* *(0.01)*
4	*2.98*	*-115.42*	*0.03*	*4.50* *(0.35)*	*0.21* *(0.25)*			
6	*3.51*	*-111.79*	*0.33*	*5.51* *(0.38)*	*0.24* *(0.25)*	*-1.27* *(0.44)*	*-2.27* *(0.72)*	
***Aboveground Carbon**								
4	1.97	-106.49	0.21	2.25 (0.76)				0.03 (0.01)
6	*3.29*	*-103.26*	*0.43*	*5.20* *(0.50)*	*0.36* *(0.37)*	*-1.71* *(0.58)*	*-4.03* *(0.94)*	
3	3.61	-108.90	0	3.92 (0.45)				
Belowground Carbon								
3	0	-89.05	0	3.71 (0.20)				
4	1.20	-88.06	0.09	3.21 (0.37)				0.01 (0.01)
4	*2.29*	*-88.61*	*0.04*	*3.62* *(0.22)*	*0.16* *(0.17)*			
5	2.83	-87.07	0.18	4.24 (0.27)		-0.70 (0.32)	-0.96 (0.52)	
5	*3.89*	*-87.60*	*0.13*	*3.11* *(0.39)*	*0.17* *(0.17)*			*0.01* *(0.01)*

*The disturbance model was removed from the list of aboveground carbon models as it failed to converge.

Table 2.6: Results of linear models examining the impact of moose density, forest disturbances, stand age, and soil temperature on the supply rate of ammonium in soil in plots open to moose presence in Newfoundland, Canada. Only those models having a ΔAICc < 4 are listed (see Table A.5 for full list of model results). Models having one or more uninformative variables are italicized. K: number of parameters; ΔAICc: difference in AICc score relative to the top model in the set; LL: measure of model fit; R^2: proportion of variation in the data explained by the model (Adjusted R^2). Listed coefficients and standard errors are on the log scale; for cofficients, we report the estimate and standard error in brackets.

				Coefficients					
K	ΔAICc	LL	Adjusted R^2	Intercept	Density	Insect	Fire	Age	Soil temp.
NH4 adsorbed in soil									
4	0	-3.25	0.38	2.09 (0.48)	0.09 (0.03)				-0.11 (0.03)
5	*2.20*	*-2.99*	*0.37*	*2.26* *(0.55)*	*0.09* *(0.03)*			*-0.00* *(0.00)*	*-0.12* *(0.03)*
6	3.75	-2.32	0.38	2.08 (0.52)	0.07 (0.03)	0.06 (0.12)	-0.13 (0.16)		-0.11 (0.04)

Table 2.7: Results of linear mixed models examining the impact of moose exclusion, forest disturbances, stand age, and soil temperature on the supply rate of ammonium in soil in paired exclosure-controls in Newfoundland, Canada, with site included as a random intercept. Only those models having a ΔAICc < 4 are listed (see Table A.6 for full list of model results). Models having one or more uninformative variables are italicized. K: number of parameters; ΔAICc: difference in AICc score relative to the top model in the set; LL: measure of model fit; R^2: proportion of variation in the data explained by the model (Marginal R^2, Conditional R^2). Listed coefficients and standard errors are on the log scale; for cofficients, we report the estimate and standard error in brackets.

				Coefficients					
K	ΔAICc	LL	R^2	Intercept	Exclosure	Insect	Fire	Age	Soil temp.
NH4 adsorbed in soil									
4	0	4.96	0.17, 0.75	1.38 (0.39)					-0.06 (0.02)
3	2.03	2.37	0, 0.62	0.43 (0.07)					
5	*2.79*	*5.38*	*0.26, 0.80*	*1.93* *(0.68)*	*-0.09* *(0.09)*				*-0.10* *(0.04)*
4	3.55	3.19	0.03, 0.68	0.39 (0.08)	0.08 (0.06)				
5	*3.56*	*4.99*	*0.18, 0.75*	*1.33* *(0.44)*				*0.00* *(0.00)*	*-0.06* *(0.03)*

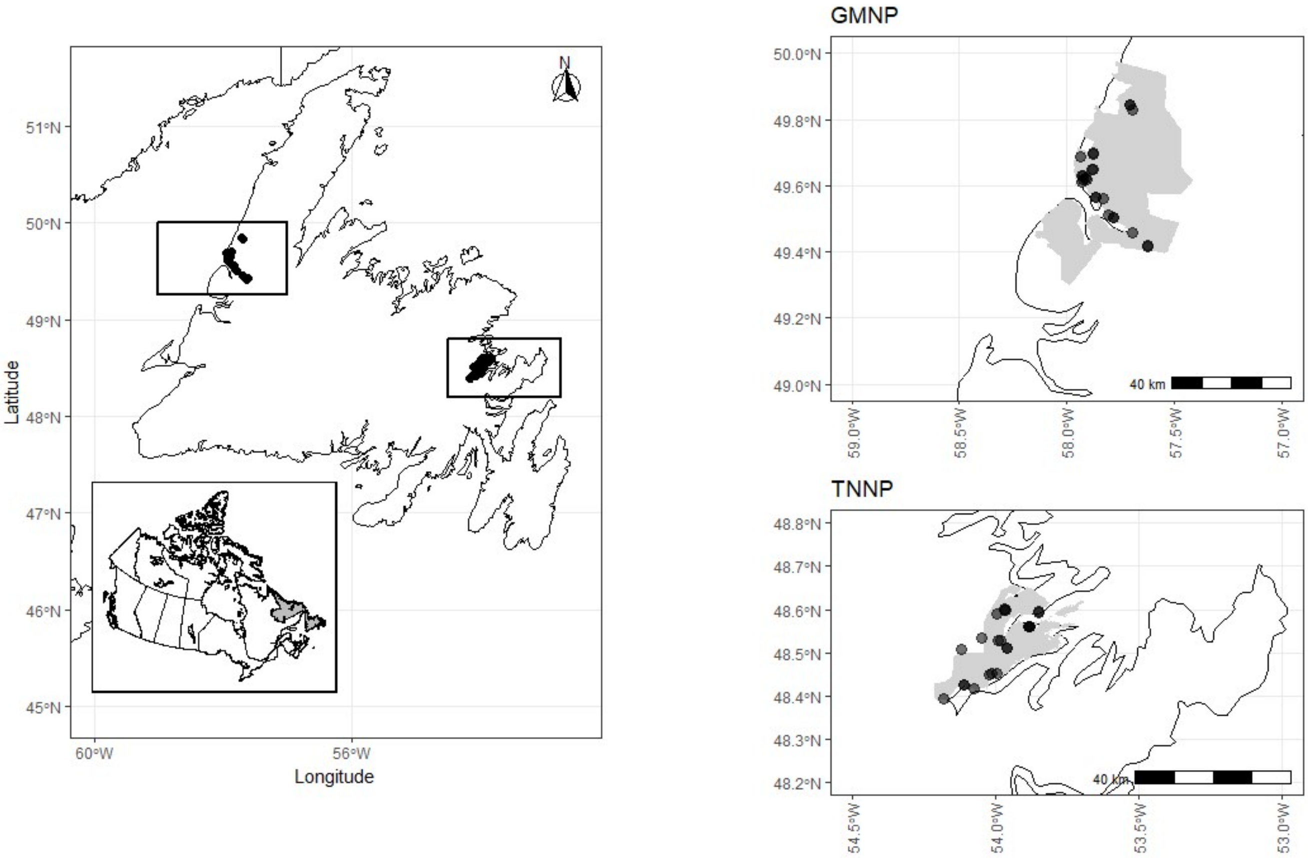

Figure 2.1: Locations of the 46 plots used in our study in Newfoundland, Canada (n = 10 paired exclosure-controls; n = 26 novel plots); 23 plots were established in Gros Morne National Park (GMNP) and 23 in Terra Nova National Park (TNNP).

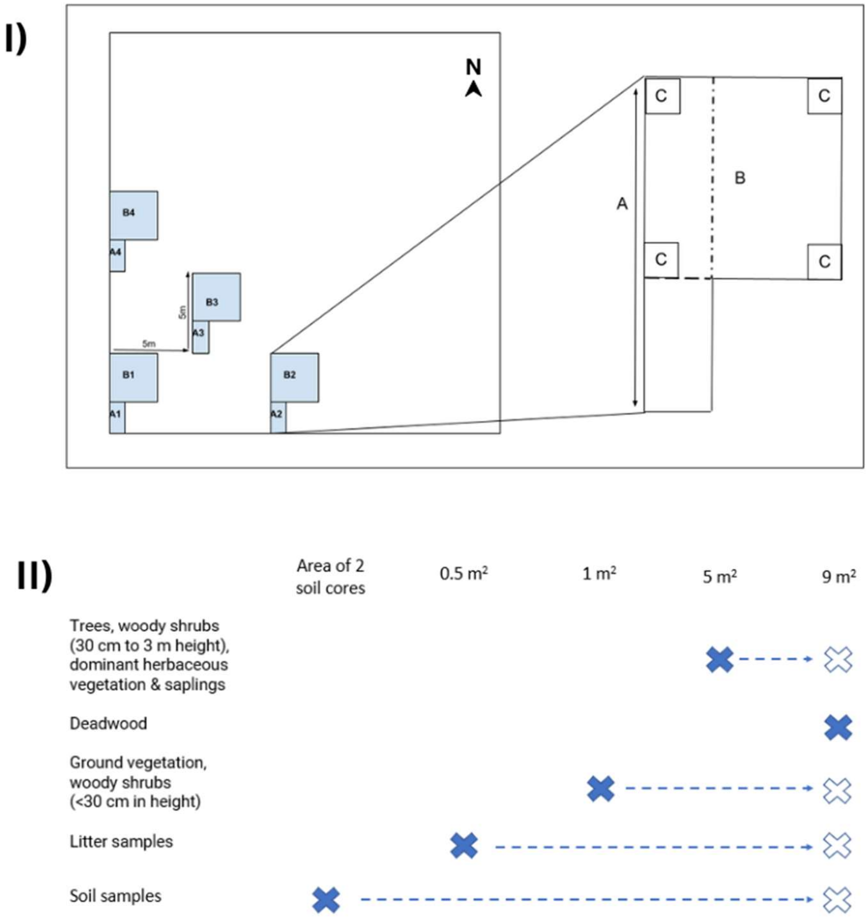

Figure 2.2: I) The layout of subplots and quadrats at each plot. At all plots, except exclosures located in GMNP (n = 3), A) four 5 m^2 (5 m x 1 m) subplots and B) four 9 m^2 (3 m x 3 m) subplots were established; within each 9 m^2 subplot, C) four 0.25 m^2 (0.5 m x 0.5 m) quadrats were placed. Dashed lines indicate where 5 m^2 and 9 m^2 subplots overlapped. II) Vegetation measurements and sample collections occurred in areas of various sizes (represented by the solid 'X'); however, all carbon estimates were scaled to the 9 m^2 subplot.

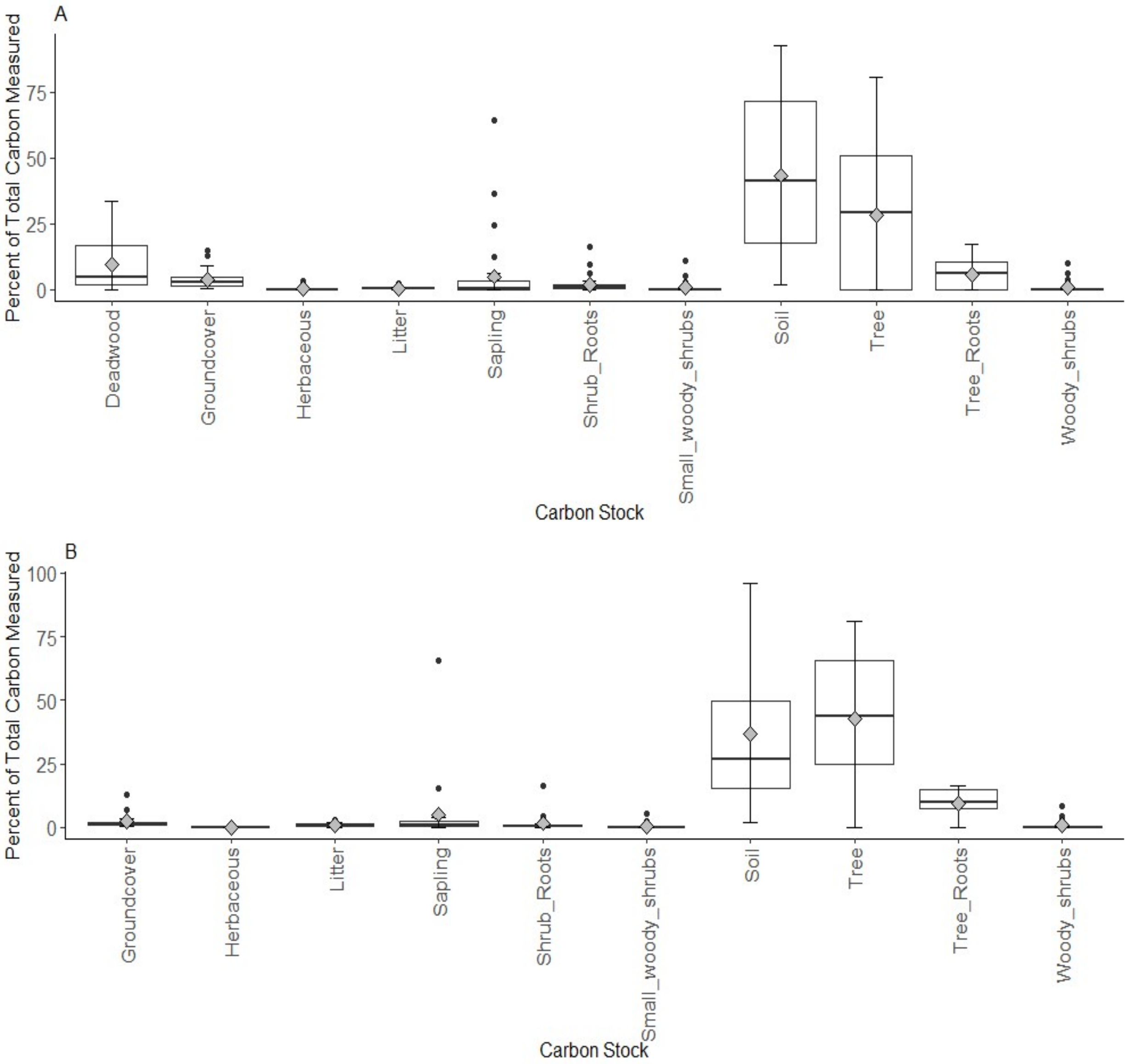

Figure 2.3: Percent of total carbon measured per plot that each carbon stock represented in A) the open plot dataset, and B) in the paired exclosure-control dataset. Note that deadwood was excluded from paired exclosure-control analyses because deadwood may have been removed during construction of the exclosures.

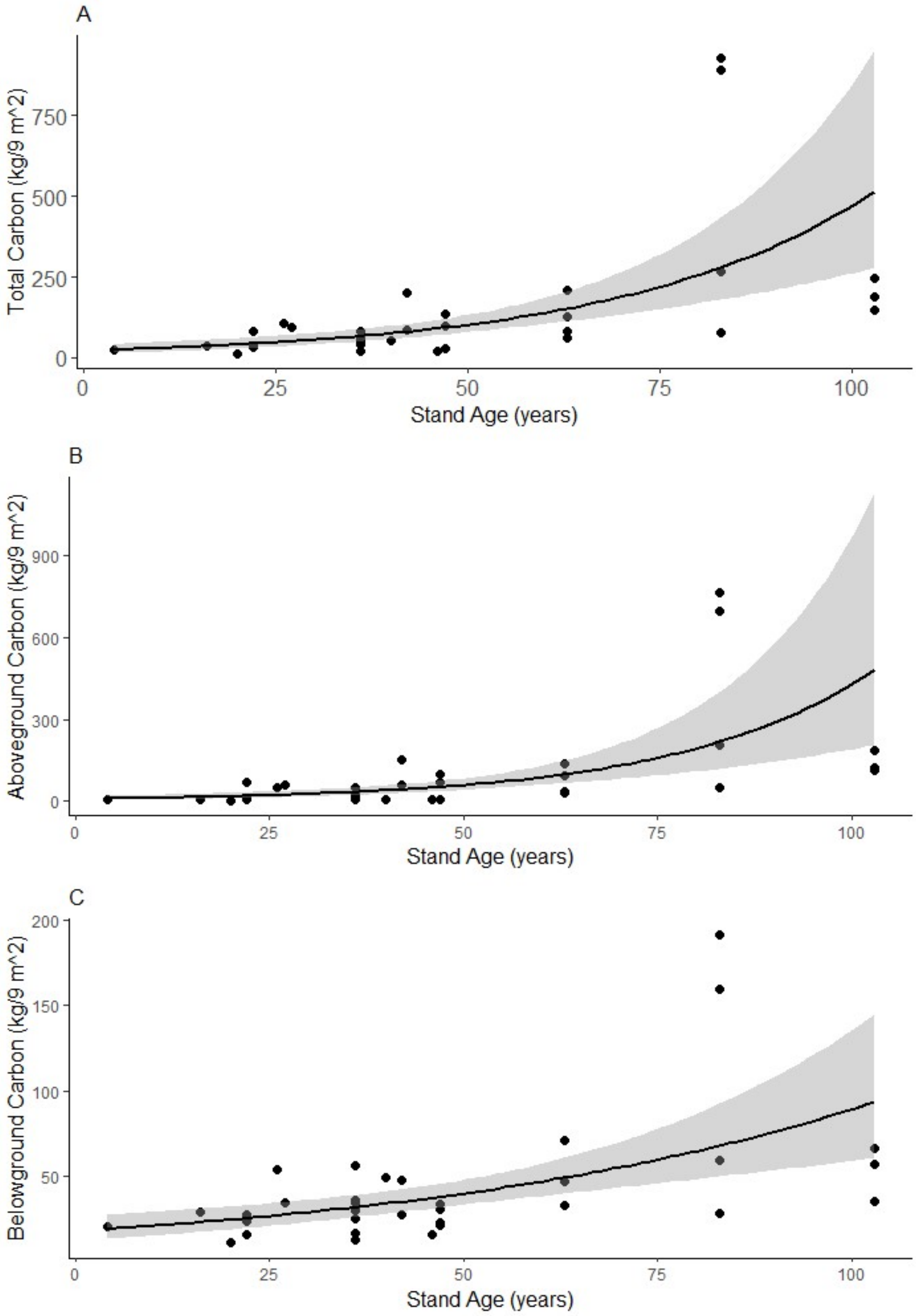

Figure 2.4: A) Total, B) aboveground, and C) belowground carbon content (kg C/9-m2) in open plots (n = 36) compared to the stand age (years; i.e., age since disturbance or age of forest stand). The fitted lines represent y ~ x and were modelled using a Gamma error structure and log link.

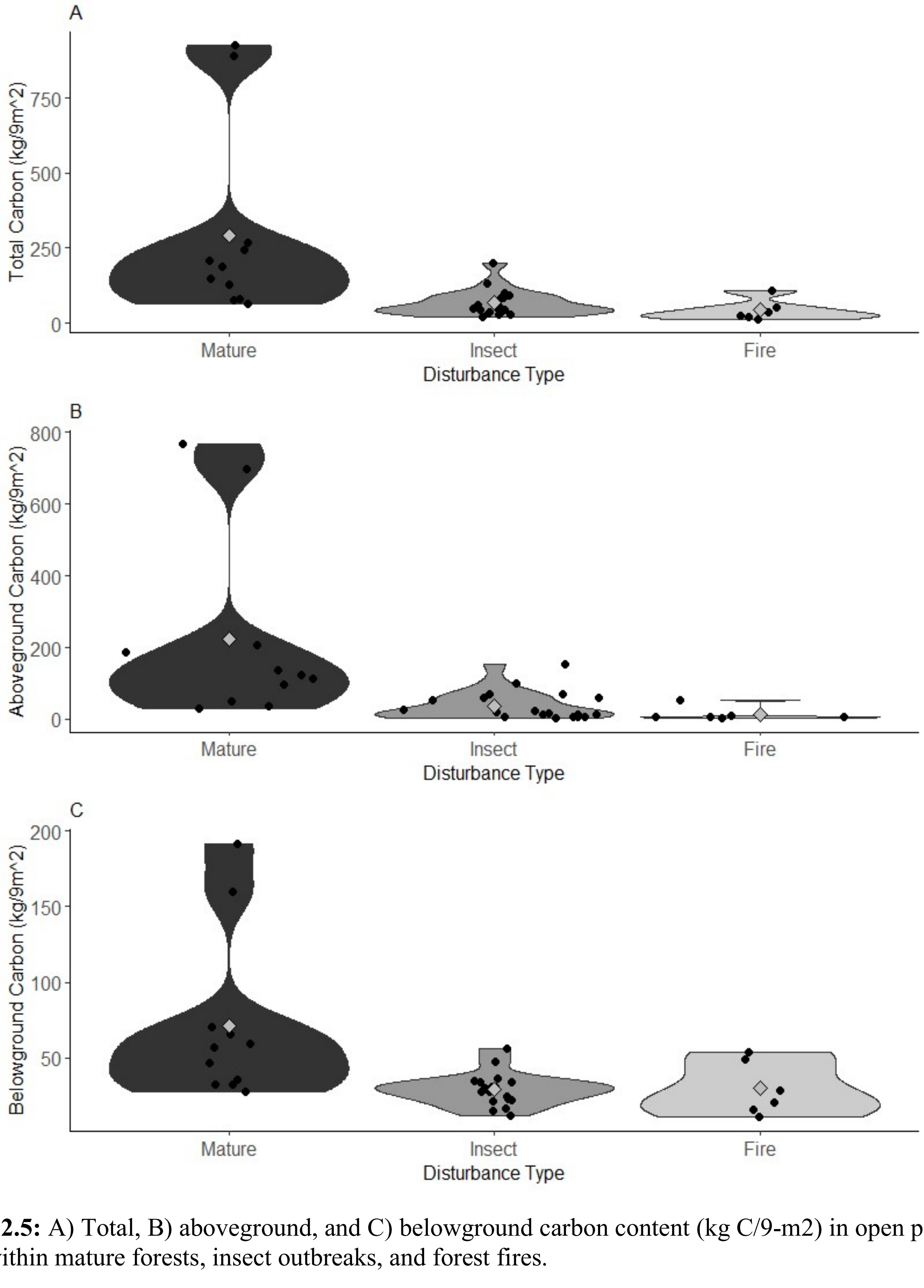

Figure 2.5: A) Total, B) aboveground, and C) belowground carbon content (kg C/9-m2) in open plots (n = 36) within mature forests, insect outbreaks, and forest fires.

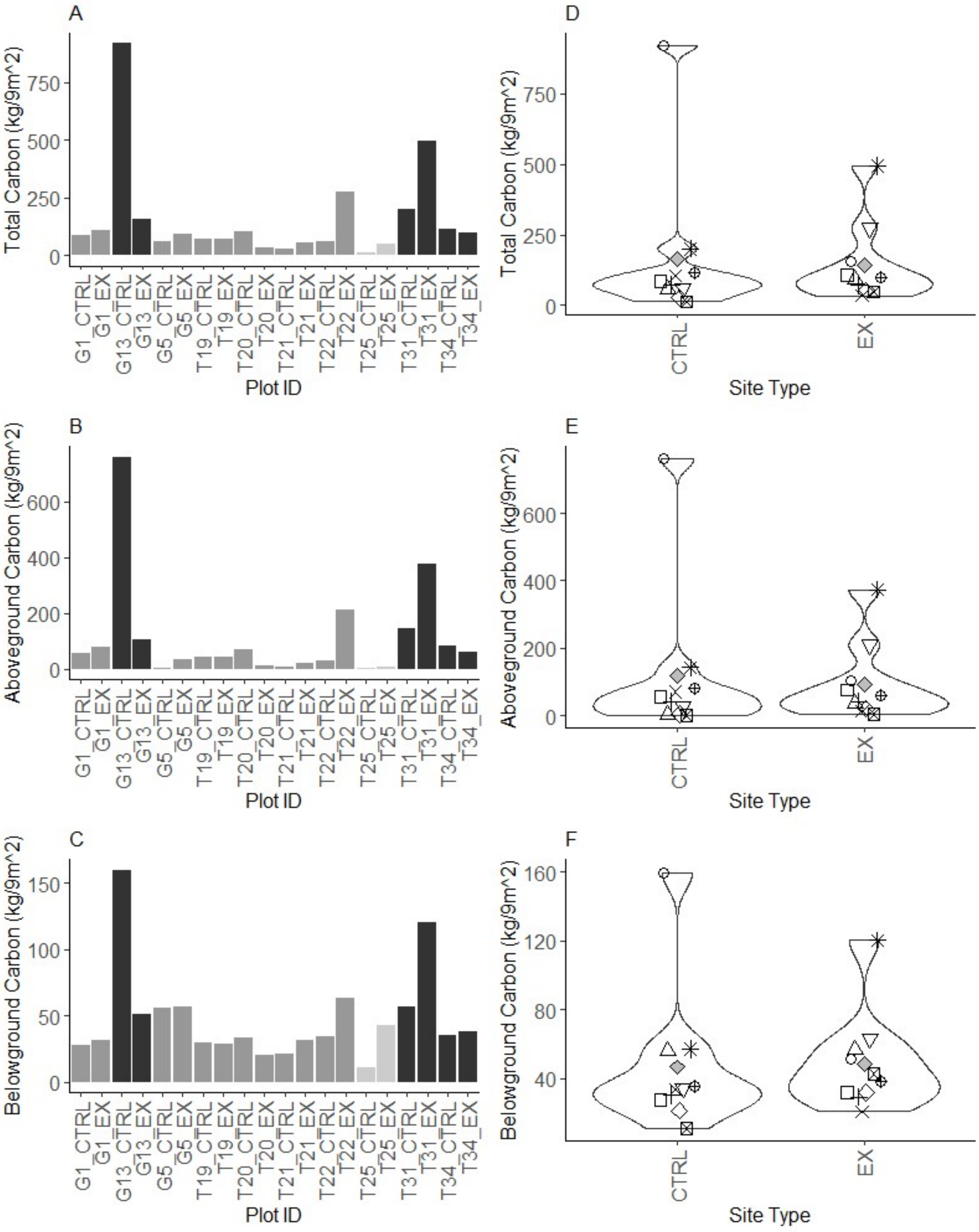

Figure 2.6: A) Total, B) aboveground, and C) belowground carbon content (kg C/9-m2) in paired exclosure-control plots (n = 10 exclosures, 10 controls); light grey = burned, medium grey = insect outbreak, dark grey = mature forest. D) Total, E) aboveground, and F) belowground carbon content in exclosures compared to controls. There was a high level of site variability in the paired exclosure-control dataset; for example, moose exclusion did not consistently positively or negatively impact carbon storage across sites. Symbols are defined as follows: □=GM-01, △=GM-05, ○=GM-13, +=TN-19, ×=TN-20, ◇=TN-21, ▽=TN-22, ⊠=TN-25, ✳=TN-31, ⊕=TN-34.

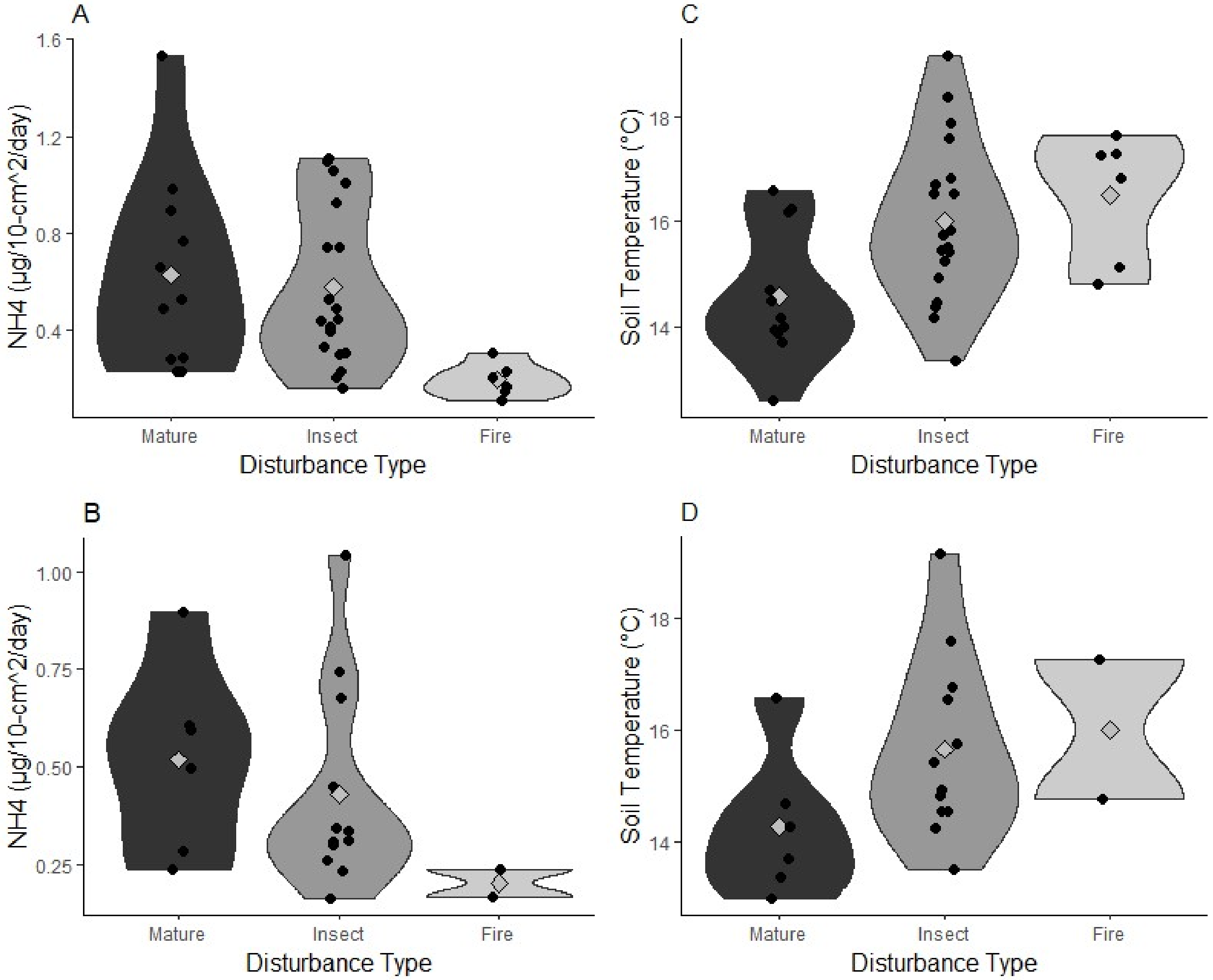

Figure 2.7: Supply rate of ammonium (µg/10-cm^2/day) in A) open plots (n = 36) and B) paired exclosure-control plots (n = 10 exclosures, 10 controls) and soil temperature (° C) in C) open plots and D) paired exclosure-control plots within mature forests, insect outbreaks, and burned sites.

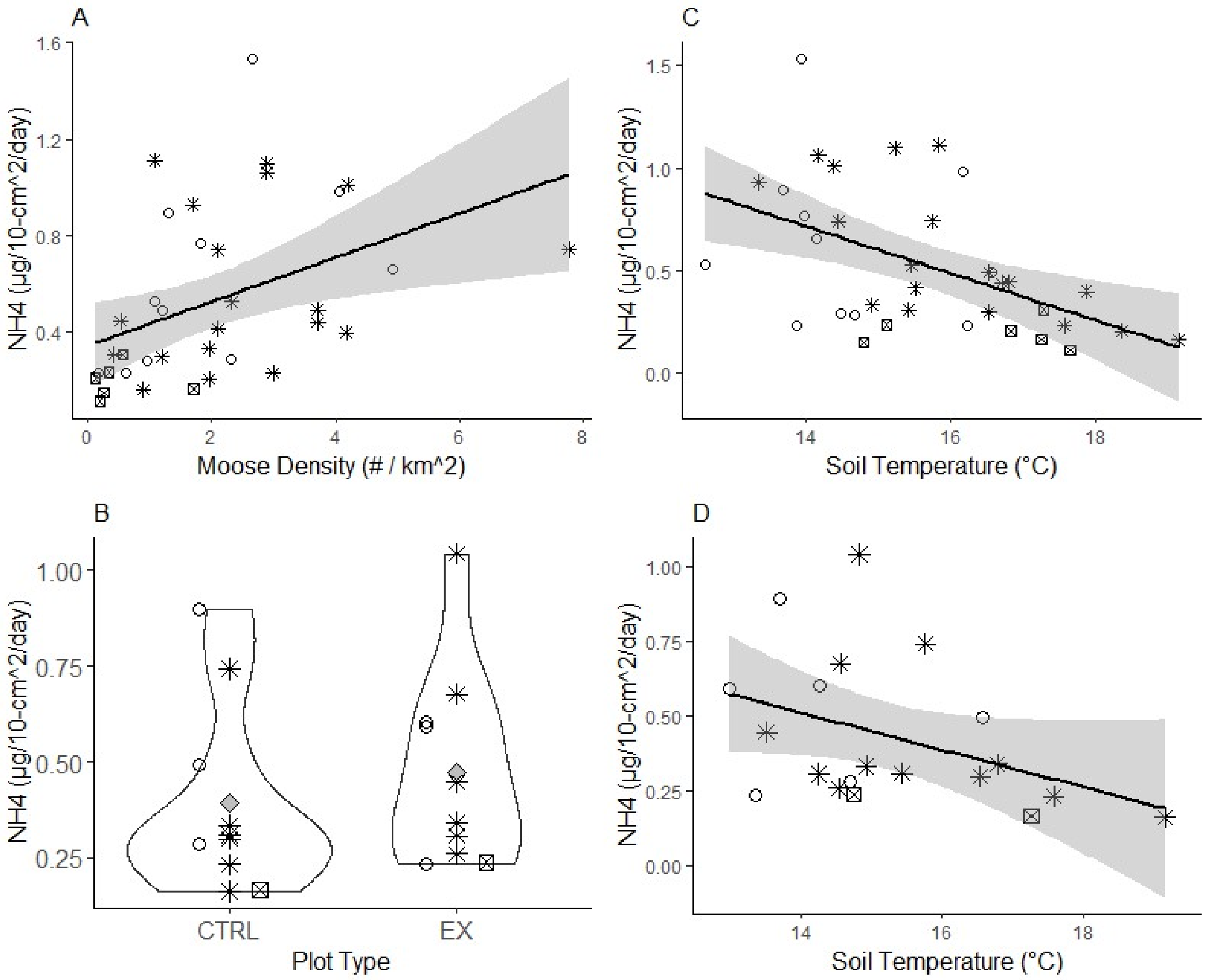

Figure 2.8: Supply rate of ammonium (µg/10-cm^2/day) in A) open plots (n = 36) compared to moose density (moose/km^2) and C) soil temperature (° C) and in B) paired exclosure-control plots (n = 10 exclosures, 10 controls) compared to fencing treatment and D) soil temperature. Symbols represent disturbance type and are defined as follows: ○= mature forest, ✳ = insect outbreak, ☒== burned.

CHAPTER 3: Summary and Conclusions

3.1. Impacts of forest disturbances and moose on elemental storage and cycling

The boreal forest is a key global carbon store but its capacity to act as a carbon sink may be weakening (Bradshaw & Warkentin, 2015). While disturbances such as forest fires and insect outbreaks are primary drivers of boreal forest renewal (Brandt et al., 2013), the severity and frequency of these disturbances may increase due to anthropogenic climate change (Dymond et al., 2010; Krawchuk et al., 2009; Price et al., 2013). Additionally, human impacts are increasing in the boreal forest due to activities such as land-clearing, oil and gas exploration, species introductions and exploitation, and industrial forestry (Brandt et al., 2013; Langor et al., 2014; Wells et al., 2020). The cumulative impacts of these human activities and climate change are directly affecting the ecological integrity of the boreal forest (Gauthier et al., 2015) and may lead to large losses of carbon (Kurz et al., 2013).

Natural disturbances are critical for creating a heterogeneous forest landscape composed of different seral stages and mixed vertical and age structures (Swanson et al., 2011; Thom & Seidl, 2016). With many species of boreal plants and animals adapted to use specific seral stages as habitat, ensuring that both mature and early-successional forest stands are present across a landscape is essential for maintaining biodiversity (Kuuluvainen & Gauthier, 2018). Additionally, many boreal tree species co-evolved with natural disturbances, and so benefit from conditions created by disturbances for regeneration (e.g., semi-serotinous cones of black spruce (Reid et al., 2023); recruitment of balsam fir in canopy gaps (Collier et al., 2022)). Many ungulates also benefit from the abundance of new growth following a disturbance (Fisher & Wilkinson, 2005). However, it has been found that the selective browsing of ungulates can suppress forest regeneration and diversity (Allen et al., 2023; McInnes et al., 1992; Ramirez et al., 2018), particularly in early-successional forests (Kolstad et al., 2019; Leroux et al., 2021; Mason et al., 2010; Nuttle et al., 2013). The selective consumption of high-quality plant material may reduce the quality and quantity of litter inputs to soil, impacting belowground elemental storage and cycling (Ellis & Leroux, 2017; Pastor et al., 1993).

Although there is much evidence demonstrating that large ungulates can impact forest structure and composition, the implications of these changes for overall carbon storage remain unclear. We studied the effects of insect outbreaks, forest fires, and moose on carbon storage and plant-available nitrogen in the boreal forests of Newfoundland. We measured stocks to estimate the amount of total, aboveground, and belowground carbon stored in disturbed (i.e., insect disturbances, burned areas) and undisturbed forests (i.e., mature forests) using both observational and experimental (i.e., paired moose exclosure-controls) data. We also collected data on the supply rate of ammonium in soils. The following results were in support of our predictions:

1) In open plots, we found that forest disturbances led to reduced aboveground and belowground carbon storage, with forest fire plots storing the least, followed by insect outbreak plots and then mature forest plots.
2) In open plots, we found a positive relationship between stand age and total, aboveground, and belowground carbon storage.

These results are consistent with previous research on forest disturbances. Both insect outbreaks and forest fires can lead to large losses of carbon (Kurz et al., 2008; Quirion et al., 2021; Van Der Werf et al., 2017). Insect outbreaks reduce carbon sequestration by reducing tree growth, and release carbon by increasing amounts of dead organic matter, thereby increasing decomposition rates (Gray, 2008; Hicke et al., 2012). Forest fires also release carbon by increasing amounts of dead organic matter, as well as through the combustion of organic material (Kasischke, 2000). However, because disturbances are typically followed by a rapid flush of growth by regenerating and released vegetation, forests can quickly return to being a carbon sink post-disturbance, with recovery time depending on the type and severity of the disturbance (Amiro et al., 2010; Fu et al., 2017; Kurz et al., 2013).

The following results did not support our predictions:

1) In open plots, we found the supply rate of ammonium increased with increasing moose densities but decreased with temperature.
2) In paired exclosure-controls, we found the supply rate of ammonium did not differ between moose exclosures and their paired controls, or between disturbance types, but decreased with temperature.
3) In open plots, we did not find a relationship between moose density and carbon storage.
4) In paired exclosure-controls, we found that total, aboveground, and belowground carbon did not differ between exclosures and controls, or between disturbance types.

These results are inconsistent with previous studies focused on ungulate impacts on soil elements. For example, Pastor et al. (1993), found that moose presence negatively impacted nitrogen in soil, in contrast to our findings of a positive relationship in our open plots and no effect in our paired exclosure-controls. Several previous studies have also reported no difference in nitrogen mineralization rates or nitrogen content between paired exclosure-controls (Ellis & Leroux, 2017; Kolstad et al., 2018; Swain et al., 2023). Our results are also inconsistent with previous work studying soil temperature, as microbial activity is generally positively associated with temperature increases (Dieleman et al., 2012; Knoepp & Swank, 2002).

The lack of evidence found to support a relationship between moose density and carbon storage in our paired exclosure-controls and open plots is consistent with findings in Allen et al. (2023). Specifically, Allen et al. (2023) reported that although browsing by ungulates altered forest structure, this did not impact total carbon storage in their temperate forest study area in New Zealand. However, this result differs from other recent studies. For example, Petersen et al. (2023) found that, on average across 100 paired exclosure-control sites, moose presence decreased aboveground plant biomass, in turn reducing carbon sequestration (Salisbury et al., 2023). Similar to our study (e.g., Figure 2.6), however, Petersen et al. (2023)'s meta-analysis, also reports lots of variation in moose effects on aboveground biomass – with sites with neutral, negative and positive relationships between moose presence and aboveground plant biomass. Further, several studies have found that moose browsing decreased the height and abundance of palatable saplings, both in other regions of the boreal forest (Kolstad et al., 2018; McInnes et al., 1992), as well as in the boreal forests of Newfoundland (Ellis & Leroux, 2017; Leroux et al., 2021; Swain et al., 2023). We suggest that the effects of moose browsing are heterogenous across landscapes and that the growth of non-palatable trees may have compensated for the reduced growth of palatable species in our system.

While ungulate impacts on vegetation have been highly studied, and some studies have also investigated belowground impacts, comparatively fewer studies have focused on how the biotic impacts of ungulates affect the overall storage and cycling of important elements, such as carbon (Schmitz et al., 2018). We report evidence from our open plot data that disturbance from insect outbreaks and forest fires negatively impacted overall carbon storage in the boreal forests of Newfoundland. However, we found no evidence to support a relationship between moose over browsing and carbon storage. Many studies of herbivore impacts use experimental exclosure-controls, studying impacts after total herbivore exclusion; however, our combined use of experimental and observational data allowed us to sample across a range of moose densities and stand ages. This work demonstrates the impacts of forest disturbances and herbivory on forest ecosystem functions, such as carbon sequestration. We recommend further research be conducted to understand the long-term impacts of moose herbivory on forest carbon stocks.

3.2. Limitations and future directions

Site history is often key to understanding the present state of an ecosystem (Bürgi et al., 2017; Cuddington, 2011; Rhemtulla & Mladenoff, 2007). Factors such as past climate, as well as land-use and disturbance history, can have long-lasting impacts on biodiversity and ecosystem functions (Delgado-Baquerizo et al., 2017; Dupouey et al., 2002; Freschet et al., 2014). The effects of browsing by large ungulates can also persist through time (Tanentzap et al., 2011; White, 2012). Ungulate browsing of saplings can impact forest structure and composition, especially under high densities, by altering the abundance and diversity of species in the understory available to be recruited to the forest canopy (Allen et al., 2023; Ellis & Leroux, 2017; Leroux et al., 2021; Ramirez et al., 2018; White, 2012). Moose also benefit from the growth of understory vegetation following natural disturbances due to the abundance of accessible browse (Bjørneraas et al., 2011; Francis et al., 2021). Unfortunately, we did not have moose density data available for the years immediately following the occurrence of the disturbances when the increase in foraging opportunity may have increased moose densities in those areas. The trajectory of moose impacts on our study sites was also complicated by the initiation of moose management in the national parks in 2011, as the moose populations in the parks had been reduced by more than 50% after 11 years of hunting. Consequently, we speculate that earlier densities may have been better predictors of present-day carbon storage than the more recent densities used in our study. We suggest that future empirical work be conducted in areas with long-term ungulate population data, or where ungulate populations have been relatively stable, to better understand how the interaction between disturbance and ungulates impacts ecosystems.

Large ungulates preferentially browse high-quality plant material in forest understories and early successional stands; impacts of herbivory may therefore depend on forest type (Kupferschmid, 2018), with a potential for stronger impacts in forest types dominated by palatable species. In Newfoundland, balsam fir is a dominant canopy-forming species (Moroni & Harris, 2011) and is heavily browsed by moose (Gosse et al., 2011; McLaren et al., 2004). Canopy gaps created by disturbances allow for the growth of advanced regeneration of balsam fir (i.e., competitive release of seedlings and saplings that were established in closed canopy mature stands ; MacLean, 1984); however, forest disturbances also result in adult tree mortality, removing seed sources (especially stand-replacing disturbances; Collier et al., 2022). Removal of mature seed trees in combination with moose herbivory can result in delayed or suppressed forest regeneration (Leroux et al., 2021). We established the majority of our plots in balsam fir dominant forests to capture this impact on the most widespread canopy-forming plant communities on the island of Newfoundland. We recommend that future studies focus on sampling an array of forest types to capture the variation in their response to forest disturbances and moose herbivory. This will also help to predict these impacts across the landscape, informing forest management decisions at a larger scale.

The carbon budget of a terrestrial ecosystem can be estimated by measuring how much carbon is fixed from the atmosphere and stored in biomass and soil or is returned through respiration (Baldocchi et al., 2018; Landsberg & Gower, 1997). The strength and direction of herbivore impacts on carbon storage and fluxes (e.g., respiration) can be highly variable. For example, Cahoon et al. (2012), found that herbivore exclusion in the Arctic tundra increased carbon uptake through an increase in shrub cover. In contrast, Falk et al. (2015), found that herbivore exclusion in an Arctic mire decreased carbon uptake, due to a shift in plant composition. Additionally, neither study found a difference in soil respiration between controls and exclosures. To fully capture the impacts of insect outbreaks, fires, and moose herbivory on the boreal forest carbon cycle, we recommend that future studies incorporate measurements of carbon fluxes (e.g., heterotrophic respiration from soil), through remote sensing (Xiao et al., 2019) or direct measurements (Forbes et al., 2023), in addition to measuring carbon stocks.

3.3. Management Implications

Under global climate change, natural resource managers are being challenged to deliver natural climate solutions through land management, protection, and restoration (Cook-Patton et al., 2021; Drever et al., 2021; Sharma et al., 2023). Understanding the net effects of herbivory following forest disturbances on carbon storage in boreal forests may help to inform climate-smart boreal forest management. Although we found that forest disturbances negatively impacted carbon storage, they are also crucial for a healthy, heterogenous forest. Their role in creating a diverse landscape provides important habitat for native species and increases the resilience of forests to future disturbances, as well as climate change and other ecosystem stressors. These disturbances may therefore be critical for long-term carbon persistence. Despite our finding that they result in a short-term loss of carbon, we do not recommend suppressing insect outbreaks and forest fires. However, long-term shifts in the carbon storage capacity of forests may be triggered by ungulate herbivory (Allen et al., 2023), with previous findings in our boreal study system indicating that moose browsing suppressed forest regeneration by reducing the height and density of palatable saplings (Ellis & Leroux, 2017; Leroux et al., 2021; Swain et al., 2023). Thus, management of moose populations may be an important consideration in developing nature-based solutions to climate change in boreal forests, particularly in areas where they have been introduced or lack natural predators.

Due to the potential for long-term implications for carbon storage we recommend that both Gros Morne National Park and Terra Nova National Park continue to manage their moose populations through hunting. Further, with the ongoing spruce budworm outbreak in Gros Morne National Park, there will be an increase in browse availability once newly disturbed stands begin to regenerate. Increasing hunting quotas in heavily disturbed areas may be important to allow saplings to escape the browse zone, mitigating future negative impacts of heavy moose browsing following a spruce budworm outbreak on carbon storage. As mentioned, we suspect that moose densities in the years closely following a disturbance may be useful for predicting future carbon storage. We, therefore, recommend that both parks conduct widespread aerial moose surveys following large forest disturbances or prescribed burns. Finally, we suggest that it would be useful to establish additional moose exclosures in a range of forest types, as well as in recently disturbed areas within each park to capture the variation in their responses to forest disturbances and moose herbivory. This experimental approach over long periods is essential to learn from management decisions and adapt as needed.

Our findings suggest forest disturbances are a key driver in carbon storage dynamics, but the effects of moose browsing may only appear on a longer time scale. We suggest that management of introduced herbivores in other systems may also be an important consideration when managing for long-term carbon storage.

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APPENDIX A

Table A.1: Average carbon content per plot (kg C/9-m^2). We established four subplots and transects with nested sampling in each plot, except within moose exclosures in GMNP, which were only large enough for three subplots. All carbon calculations were extrapolated to the scale of the subplot. The mean carbon content of all subplots in each plot is presented with standard deviation in parentheses. In total carbon and aboveground carbon columns, unbolded values were used in open plot carbon analyses, while bolded values were used in paired exclosure-control carbon analyses. Deadwood was excluded from paired exclosure-control carbon analyses as it may have been removed from the area during the construction of exclosures.

Plot ID	Total carbon	Aboveground carbon	Belowground carbon	Disturbance type
GM-01-EX	**108.01 (± 56.32)**	**76.30 (± 46.57)**	31.71 (± 10.73)	Insect Outbreak
GM-01-CTRL	86.18 (± 69.70)/ **84.70 (± 69.91)**	58.63 (± 56.06)/ **57.15 (± 56.26)**	27.55 (± 13.73)	Insect Outbreak
GM-02	46.26 (± 32.39)	21.73 (± 24.64)	24.53 (± 10.98)	Insect Outbreak
GM-03	36.34 (±13.55)	13.17 (± 11.01)	23.18 (± 8.37)	Insect Outbreak
GM-04	32.22 (± 15.91)	4.65 (± 1.51)	27.57 (± 16.30)	Insect Outbreak
GM-05-EX	**92.36 (± 25.25)**	**35.68 (± 17.18)**	56.68 (± 10.43)	Insect Outbreak
GM-05-CTRL	60.48 (± 14.16)/ **58.45 (± 13.84)**	4.35 (± 3.13)/ **2.32 (± 0.46)**	56.14 (± 13.85)	Insect Outbreak
GM-06	84.10 (± 82.62)	68.93 (± 70.78)	15.18 (± 12.35)	Insect Outbreak
GM-07	42.04 (± 8.07)	11.41 (± 3.84)	30.62 (± 8.04)	Insect Outbreak
GM-08	43.65 (± 34.85)	27.22 (± 29.75)	16.42 (± 6.40)	Insect Outbreak
GM-09	19.10 (± 8.33)	6.84 (± 4.78)	12.26 (± 4.45)	Insect Outbreak
GM-10	51.85 (± 12.53)	17.40 (± 11.52)	34.45 (± 10.86)	Insect Outbreak
GM-11	48.65 (± 21.68)	12.49 (± 14.17)	36.16 (± 9.38)	Insect Outbreak
GM-12	49.52 (± 24.00)	19.90 (± 17.28)	29.62 (± 7.38)	Insect Outbreak
GM-13-EX	**156.23 (± 125.34)**	**104. 84 (± 100.12)**	51.39 (± 25.33)	Mature Forest
GM-13-CTRL	926.78 (± 519.35)/ **920.56 (± 528.39)**	766.88 (± 429.96)/ **760.66 (± 439.14)**	159.91 (± 99.95)	Mature Forest
GM-14	128.01 (± 47.35)	95.61 (± 39.26)	32.41 (± 8.62)	Mature Forest
GM-15	76.33 (± 63.57)	48.28 (± 49.87)	28.05 (± 14.07)	Mature Forest
GM-16	207.63 (± 15.54)	137.10 (± 16.81)	70.53 (± 5.68)	Mature Forest
GM-17	81.71 (± 48.32)	34.92 (± 31.43)	46.79 (± 17.10)	Mature Forest
GM-18	267.23 (± 182.83)	207.90 (± 171.32)	59.33 (± 15.43)	Mature Forest
GM-35	62.89 (± 53.36)	30.09 (± 43.13)	32.80 (± 13.03)	Mature Forest
GM-36	83.09 (± 52.83)	52.56 (± 39.56)	30.53 (± 14.40)	Insect Outbreak
TN-19-EX	**72.25 (± 1.94)**	**43.05 (± 2.12)**	29.19 (± 2.81)	Insect Outbreak
TN-19-CTRL	98.55 (± 72.25)/ **72.39 (± 77.11)**	68.28 (± 60.70)/ **42.13 (± 64.10)**	30.26 (± 13.20)	Insect Outbreak
TN-20-EX	**34.22 (± 13.56)**	**13.52 (± 8.36)**	20.70 (± 5.98)	Insect Outbreak
TN-20-CTRL	133.83 (± 129.83)/ **104.39 (± 144.85)**	100.19 (± 122.44)/ **70.75 (± 137.37)**	33.64 (± 10.05)	Insect Outbreak
TN-21-EX	**53.19 (± 19.19)**	**21.42 (± 11.16)**	31.77 (± 9.35)	Insect Outbreak
TN-21-CTRL	28.10 (± 10.78)/ **26.70 (± 9.18)**	6.85 (± 3.78)/ **5.46 (± 2.19)**	21.24 (± 7.88)	Insect Outbreak
TN-22-EX	**273.61 (± 252.98)**	**210.29 (± 203.58)**	63.32 (± 49.59)	Insect Outbreak
TN-22-CTRL	93.75 (± 45.68)/ **62.23 (± 63.53)**	59.69 (± 39.09)/ **28.17 (± 47.87)**	34.06 (± 17.56)	Insect Outbreak

TN-23	27.22 (± 3.95)	5.05 (± 3.90)	22.17 (± 7.20)	Insect Outbreak
TN-24	200.55 (± 357.55)	153.21 (± 292.18)	47.34 (± 65.39)	Insect Outbreak
TN-25-EX	**48.65 (± 16.01)**	**5.91 (± 0.79)**	42.74 (± 15.85)	Fire
TN-25-CTRL	13.03 (± 8.64)/ **13.03 (± 8.64)**	2.32 (± 0.54)/ **2.32 (± 0.54)**	10.71 (± 8.55)	Fire
TN-26	26.17 (± 13.70)	5.80 (± 2.14)	20.37 (± 12.14)	Fire
TN-27	37.21 (± 17.94)	8.33 (± 3.59)	28.88 (± 14.63)	Fire
TN-28	106.41 (± 94.53)	52.59 (± 80.17)	53.81 (± 19.25)	Fire
TN-29	53.58 (± 10.64)	4.70 (± 1.50)	48.89 (± 10.11)	Fire
TN-30	20.45 (± 2.04)	4.70 (± 2.46)	15.76 (± 3.96)	Fire
TN-31-EX	**494.32 (± 119.67)**	**374.05 (± 95.99)**	120.27 (± 24.68)	Mature Forest
TN-31-CTRL	244.68 (± 202.09)/ **200.59 (± 205.78)**	187.62 (± 160.05)/ **143.53 (± 163.24)**	57.06 (± 42.58)	Mature Forest
TN-32	889.34 (± 650.75)	697.73 (± 548.26)	191.61 (± 102.87)	Mature Forest
TN-33	189.55 (± 135.46)	123.60 (± 114.19)	65.95 (± 21.36)	Mature Forest
TN-34-EX	**100.09 (± 140.57)**	**61.70 (± 119.39)**	38.39 (± 21.55)	Mature Forest
TN-34-CTRL	149.40 (± 172.33)/ **116.50 (± 176.12)**	114.17 (± 151.72)/ **81.27 (± 155.81)**	35.23 (± 21.27)	Mature Forest

Table A.2: Average supply rate of ammonium in soil (µg/10-cm^2/day). Pairs of PRS probes were placed in each corner of each of the four subplots (see Figure 2.2). The mean supply rate of ammonium and soil temperature (° C) of the four subplots is presented with standard deviation in parentheses.

Plot ID	Number of days deployed	Supply rate of ammonium	Temperature	Disturbance type
GM-01-EX	23	1.04 (± 0.27)	14.82 (± 2.01)	Insect Outbreak
GM-01-CTRL	23	0.74 (± 0.25)	15.76 (± 2.47)	Insect Outbreak
GM-02	24	0.74 (± 0.13)	14.46 (± 1.38)	Insect Outbreak
GM-03	22	0.40 (± 0.11)	17.88 (± 4.35)	Insect Outbreak
GM-04	24	0.93 (± 0.52)	13.36 (± 1.00)	Insect Outbreak
GM-05-EX	23	0.68 (± 0.39)	14.55 (± 1.97)	Insect Outbreak
GM-05-CTRL	24	0.23 (± 0.03)	17.58 (± 2.48)	Insect Outbreak
GM-06	24	1.11 (± 0.84)	15.85 (± 3.58)	Insect Outbreak
GM-07	24	1.01 (± 0.36)	14.39 (± 1.43)	Insect Outbreak
GM-08	28	0.53 (± 0.34)	15.47 (± 1.50)	Insect Outbreak
GM-09	28	0.49 (± 0.10)	16.53 (± 1.48)	Insect Outbreak
GM-10	28	0.44 (± 0.18)	16.72 (± 1.71)	Insect Outbreak
GM-11	24	0.42 (± 0.08)	15.53 (± 1.55)	Insect Outbreak
GM-12	24	1.10 (± 0.46)	15.24 (± 1.23)	Insect Outbreak
GM-13-EX	24	0.59 (± 0.15)	12.99 (± 1.05)	Mature Forest
GM-13-CTRL	22	0.90 (± 0.46)	13.70 (± 1.24)	Mature Forest
GM-14	24	1.53 (± 2.26)	13.93 (± 1.30)	Mature Forest
GM-15	23	0.53 (± 0.12)	12.62 (± 1.43)	Mature Forest
GM-16	28	0.29 (± 0.07)	14.49 (± 1.41)	Mature Forest
GM-17	23	0.98 (± 0.25)	16.18 (± 2.65)	Mature Forest
GM-18	24	0.66 (± 0.11)	14.16 (± 1.25)	Mature Forest
GM-35	25	0.77 (± 0.18)	13.99 (± 1.54)	Mature Forest
GM-36	25	1.06 (± 0.24)	14.17 (± 1.81)	Insect Outbreak
TN-19-EX	33	0.26 (± 0.14)	14.53 (± 1.67)	Insect Outbreak
TN-19-CTRL	33	0.31 (± 0.27)	15.42 (± 1.44)	Insect Outbreak
TN-20-EX	34	0.45 (± 0.33)	13.51 (± 1.22)	Insect Outbreak
TN-20-CTRL	34	0.33 (± 0.08)	14.92 (± 1.46)	Insect Outbreak
TN-21-EX	32	0.34 (± 0.14)	16.78 (± 2.53)	Insect Outbreak
TN-21-CTRL	32	0.16 (± 0.05)	19.16 (± 3.46)	Insect Outbreak
TN-22-EX	35	0.31 (± 0.05)	14.25 (± 1.94)	Insect Outbreak
TN-22-CTRL	35	0.30 (± 0.07)	16.53 (± 3.03)	Insect Outbreak
TN-23	34	0.45 (± 0.52)	16.81 (± 2.76)	Insect Outbreak
TN-24	35	0.21 (± 0.14)	18.38 (± 2.68)	Insect Outbreak
TN-25-EX	32	0.24 (± 0.08)	14.75 (± 1.51)	Fire
TN-25-CTRL	32	0.17 (± 0.05)	17.27 (± 1.68)	Fire
TN-26	35	0.21 (± 0.10)	16.84 (± 2.64)	Fire
TN-27	33	0.15 (± 0.04)	14.81 (± 2.17)	Fire
TN-28	32	0.24 (± 0.04)	15.12 (± 2.02)	Fire
TN-29	34	0.31 (± 0.11)	17.29 (± 3.20)	Fire
TN-30	32	0.12 (± 0.04)	17.66 (± 2.08)	Fire
TN-31-EX	34	0.23 (± 0.07)	13.36 (± 1.43)	Mature Forest
TN-31-CTRL	34	0.28 (± 0.08)	14.69 (± 1.81)	Mature Forest
TN-32	35	0.23 (± 0.05)	13.87 (± 1.52)	Mature Forest
TN-33	33	0.23 (± 0.04)	16.24 (± 2.89)	Mature Forest
TN-34-EX	35	0.60 (± 0.58)	14.27 (± 1.97)	Mature Forest

TN-34-CTRL	35	0.49 (± 0.51)	16.58 (± 2.92)	Mature Forest

Table A.3: Results of all generalized linear models examining the impact of moose density, forest disturbances, and stand age on total, aboveground, and belowground carbon storage in plots open to moose in Newfoundland, Canada (see Table 2.4 for parameter estimates for the top and competing models only). Models having one or more uninformative variables are italicized. K: number of parameters; ΔAICc: difference in AICc score relative to the top model in the set; LL: goodness of fit estimate; Pseudo R^2: relative proportion of variability in the data attributed to the explanatory variables (Nagelkerke's pseudo R^2).

Response variable	Explanatory model	K	ΔAICc	LL	Pseudo R^2
Total Carbon	1) Stand Age	3	0	-196.00	0.59
	2) Stand Age + Moose Density	*4*	*1.66*	*-195.56*	*0.60*
	3) Disturbance Type	4	2.73	-196.10	0.59
	4) Disturbance Type + Moose Density	*5*	*3.80*	*-195.28*	*0.60*
	*5) Stand Age * Moose Density*	*5*	*4.36*	*-195.56*	*0.60*
	*6) Disturbance Type * Moose Density*	*7*	*6.99*	*-193.87*	*0.63*
	7) Null	2	29.49	-211.94	0
	8) Moose Density	*3*	*29.74*	*-210.87*	*0.06*
Aboveground Carbon	1) Stand Age	3	0	-180.46	0.53
	2) Disturbance Type	4	1.46	-179.92	0.55
	3) Stand Age + Moose Density	*4*	*2.14*	*-180.26*	*0.54*
	4) Disturbance Type + Moose Density	*5*	*2.92*	*-179.30*	*0.56*
	*5) Stand Age * Moose Density*	*5*	*4.82*	*-180.25*	*0.54*
	*6) Disturbance Type * Moose Density*	*7*	*6.58*	*-178.13*	*0.59*
	7) Null	2	25.15	-194.23	0
	8) Moose Density	*3*	*25.83*	*-193.38*	*0.05*
Belowground Carbon	1) Stand Age	3	0	-153.96	0.42
	2) Disturbance Type	4	1.43	-153.41	0.44
	3) Stand Age + Moose Density	*4*	*1.46*	*-153.42*	*0.44*
	4) Disturbance Type + Moose Density	*5*	*3.04*	*-152.86*	*0.46*
	*5) Stand Age * Moose Density*	*5*	*4.15*	*-153.41*	*0.44*
	6) Disturbance Type * Moose Density	7	5.10	-150.89	0.51
	7) Null	2	17.46	-163.89	0
	8) Moose Density	3	17.88	-162.91	0.05

Table A.4: Results of all generalized linear mixed models examining the impact of moose exclusion, forest disturbances, and stand age on total, aboveground, and belowground carbon storage in paired exclosure-control plots in Newfoundland, Canada. (see Table 2.5 for results for the top and competing models only). Models having one or more uninformative variables are italicized. K: number of parameters; ΔAICc: difference in AICc score relative to the top model in the set; LL: goodness of fit estimate; Pseudo R^2: relative proportion of variability in the data attributed to the explanatory variables (Nagelkerke's pseudo R^2).

Response variable	**Explanatory model**	**K**	**ΔAICc**	**LL**	**Pseudo R^2**
Total Carbon	1) Stand Age	4	0	-113.93	0.17
	2) Disturbance Type	5	0.19	-112.22	0.30
	3) Null	3	0.48	-115.75	0
	4) Stand Age + Ex/ Ctrl	*5*	*2.85*	*-113.55*	*0.20*
	5) Ex/ Ctrl	4	2.98	-115.42	*0.03*
	6) Disturbance + Ex/ Ctrl	*6*	*3.51*	*-111.79*	*0.33*
	7) Stand Age * Ex/ Ctrl	6	4.09	-112.08	0.31
	*8) Disturbance * Ex/ Ctrl*	*8*	*9.91*	*-109.67*	*0.46*
Aboveground Carbon	*1) Disturbance Type	5	0	-103.70	0.41
	2) Stand Age	4	1.97	-106.49	0.21
	3) Disturbance + Ex/ Ctrl	*6*	*3.29*	*-103.26*	*0.43*
	4) Null	3	3.61	-108.90	0
	5) Stand Age + Ex/ Ctrl	5	4.37	-105.88	0.26
	6) Stand Age * Ex/ Ctrl	6	5.27	-104.25	0.37
	7) Ex/ Ctrl	4	5.71	-108.37	0.05
	*8) Disturbance * Ex/ Ctrl*	*8*	*11.42*	*-102.01*	*0.50*
Belowground Carbon	1) Null	3	0	-89.05	0
	2) Stand Age	4	1.20	-88.06	0.09
	3) Ex/ Ctrl	*4*	*2.29*	*-88.61*	*0.04*
	4) Disturbance Type	5	2.83	-87.07	0.18
	5) Stand Age + Ex/ Ctrl	*5*	*3.89*	*-87.60*	*0.13*
	6) Disturbance Type + Ex/ Ctrl	6	6.03	-86.58	0.22
	7) Stand Age * Ex/ Ctrl	6	6.50	-86.81	0.20
	*8) Disturbance Type * Ex/ Ctrl*	*8*	*8.90*	*-82.70*	*0.47*

*The disturbance type model for the aboveground carbon analysis failed to converge.

Table A.5: Results of all linear models examining the impact of moose density, forest disturbances, and stand age on the supply rate of ammonium in soil in plots open to moose in Newfoundland, Canada (see Table 2.6 for results of top-ranked models only). Average soil temperature was included as a controlling variable. Models having one or more uninformative variables are italicized. K: number of parameters; ΔAICc: difference in AICc score relative to the top model in the set; LL: goodness of fit estimate; Adjusted R^2: proportion of variability in the data attributed to the explanatory variables.

Response variable	Explanatory model	K	ΔAICc	LL	Adjusted R^2
Supply Rate of Ammonium	1) Moose Density + Temperature	4	0	-3.25	0.38
	2) Stand Age + Moose Density + Temperature	*5*	*2.20*	*-2.99*	*0.37*
	3) Disturbance Type + Moose Density + Temperature	6	3.75	-2.32	0.38
	*4) Stand Age * Moose Density + Temperature*	*6*	*5.08*	*-2.99*	*0.35*
	5) Disturbance Type + Temperature	5	5.93	-4.86	0.30
	6) Temperature	3	6.51	-7.78	0.23
	7) Disturbance Type * Moose Density + Temperature	8	7.59	-1.02	0.38
	8) Stand Age + Temperature	*4*	*8.30*	*-7.40*	*0.22*
	9) Moose Density	3	9.67	-9.35	0.16
	10) Disturbance Type + Moose Density	5	10.74	-7.26	0.20
	11) Stand Age + Moose Density	*4*	*12.02*	*-9.26*	*0.14*
	12) Disturbance Type	4	12.06	-9.28	0.14
	*13) Stand Age * Moose Density*	*5*	*14.35*	*-9.07*	*0.12*
	14) Intercept	2	14.54	-12.98	0
	*15) Disturbance Type * Moose Density*	*7*	*15.16*	*-6.48*	*0.19*
	16) Stand Age	*3*	*16.88*	*-12.96*	*-0.03*

Table A.6: Results of all linear mixed models examining the impact of moose exclusion, forest disturbances, and stand age on the supply rate of ammonium in soil in paired exclosure-control plots in Newfoundland, Canada. (see Table 2.7 for results of top ranked models only). Average soil temperature was included as a controlling variable and site was included to account for the paired design. Models having one or more uninformative variables are italicized. K: number of parameters; ΔAICc: difference in AICc score relative to the top model in the set; LL: goodness of fit estimate; R^2: proportion of variability in the data attributed to the explanatory variables (Marginal R^2, Conditional R^2).

Response variable	**Explanatory model**	**K**	**ΔAICc**	**LL**	**R^2**
Supply Rate of Ammonium	1) Temperature	4	0	4.96	0.17, 0.75
	2) Intercept	3	2.03	2.37	0, 0.62
	3) Ex/ Ctrl + Temperature	*5*	*2.79*	*5.38*	*0.26, 0.80*
	4) Ex/ Ctrl	4	3.55	3.19	0.03, 0.68
	5) Stand Age + Temperature	*5*	*3.56*	*4.99*	*0.18, 0.75*
	6) Stand Age	*4*	*4.66*	*2.64*	*0.04, 0.62*
	7) Stand Age + Ex/ Ctrl	*5*	*6.63*	*3.46*	*0.07, 0.68*
	8) Disturbance Type + Temperature	*6*	*6.84*	*5.44*	*0.25, 0.75*
	9) Stand Age + Ex/ Ctrl + Temperature	*6*	*6.96*	*5.38*	*0.25, 0.80*
	10) Disturbance Type	5	7.12	3.22	0.13, 0.63
	11) Stand Age * Ex/ Ctrl	6	8.93	4.40	0.10, 0.74
	12) Disturbance Type + Ex/ Ctrl	6	9.65	4.04	0.16, 0.68
	13) Stand Age * Ex/ Ctrl + Temperature	7	10.54	6.03	0.25, 0.82
	14) Disturbance Type + Ex/ Ctrl + Temperature	*7*	*11.06*	*5.77*	*0.30, 0.80*
	15) Disturbance Type * Ex/ Ctrl	8	16.40	5.98	0.21, 0.79
	16) Disturbance Type * Ex/ Ctrl + Temperature	9	19.23	8.01	0.35, 0.88

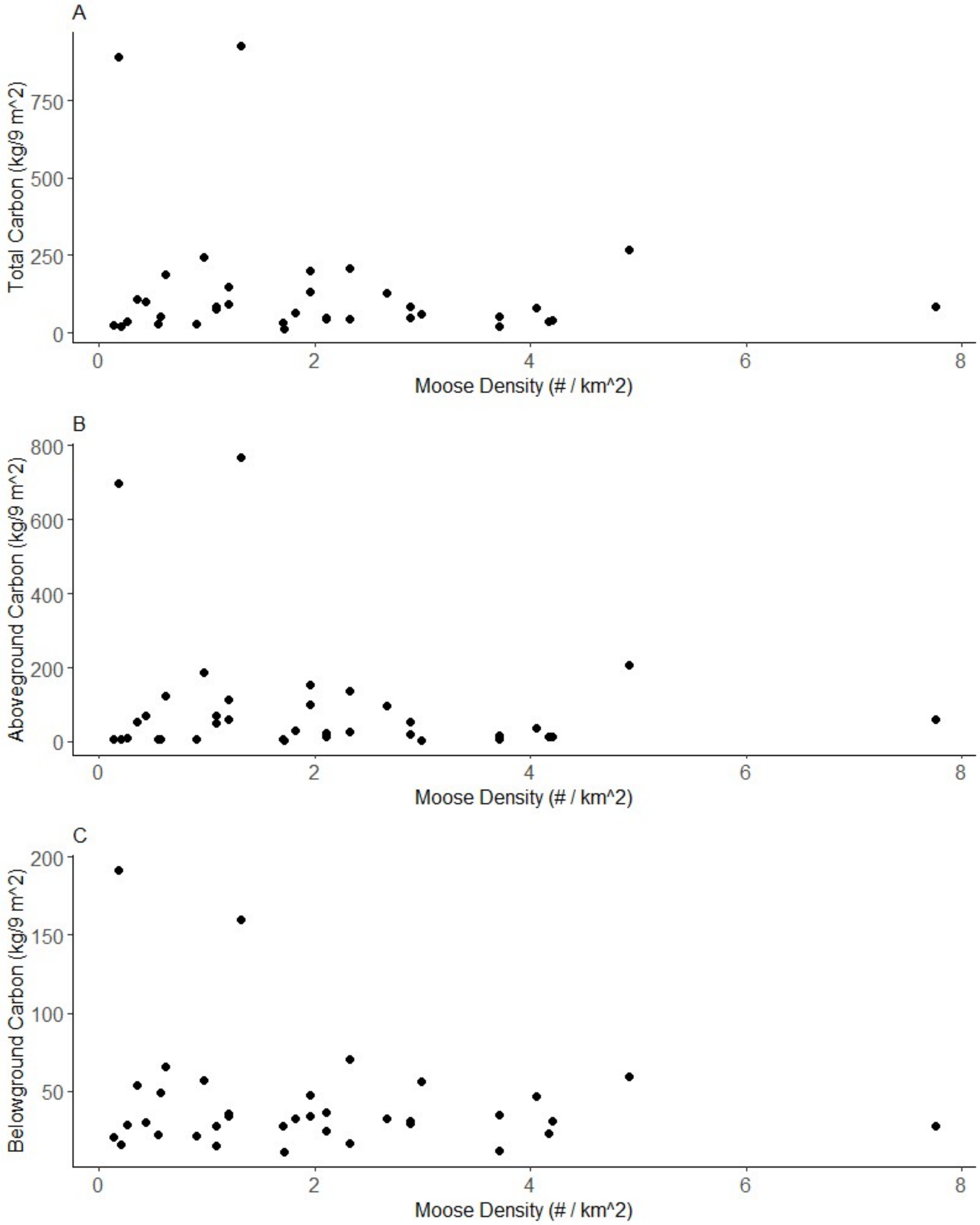

Figure A.1: A) Total, B) aboveground, and C) belowground carbon content in open plots (n = 36) compared to estimated moose density (moose/km^2).

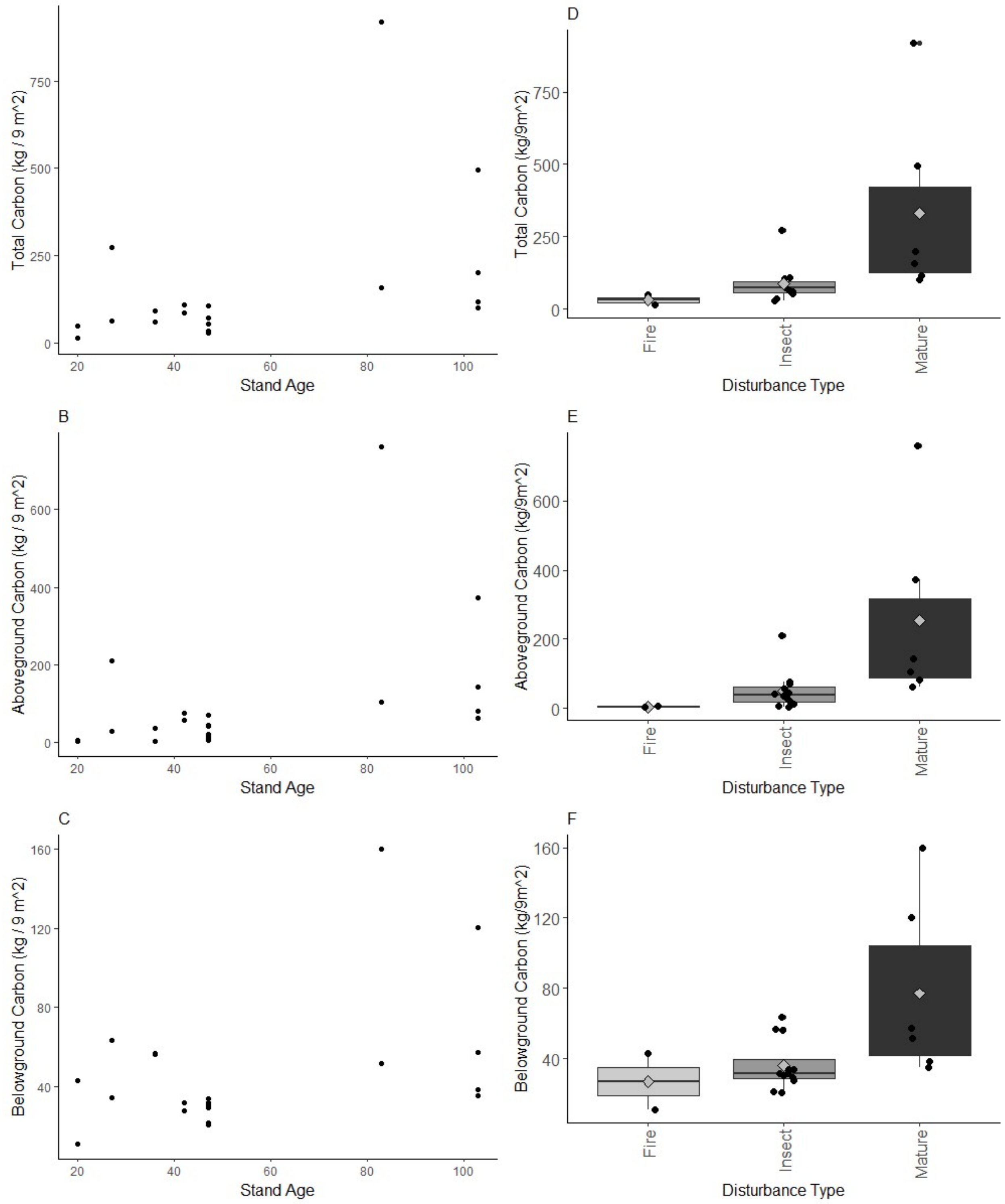

Figure A.2: A) Total, B) aboveground, and C) belowground carbon content (kg C/9-m2) compared to stand age (years; i.e., age since disturbance or age of forest stand) in paired exclosure-control plots (n = 10 ex, 10 ctrl). D) Total, E) aboveground, and F) belowground carbon content (kg C/9-m^2) in mature forests, insect outbreaks, and forest fires in paired exclosure-control plots.

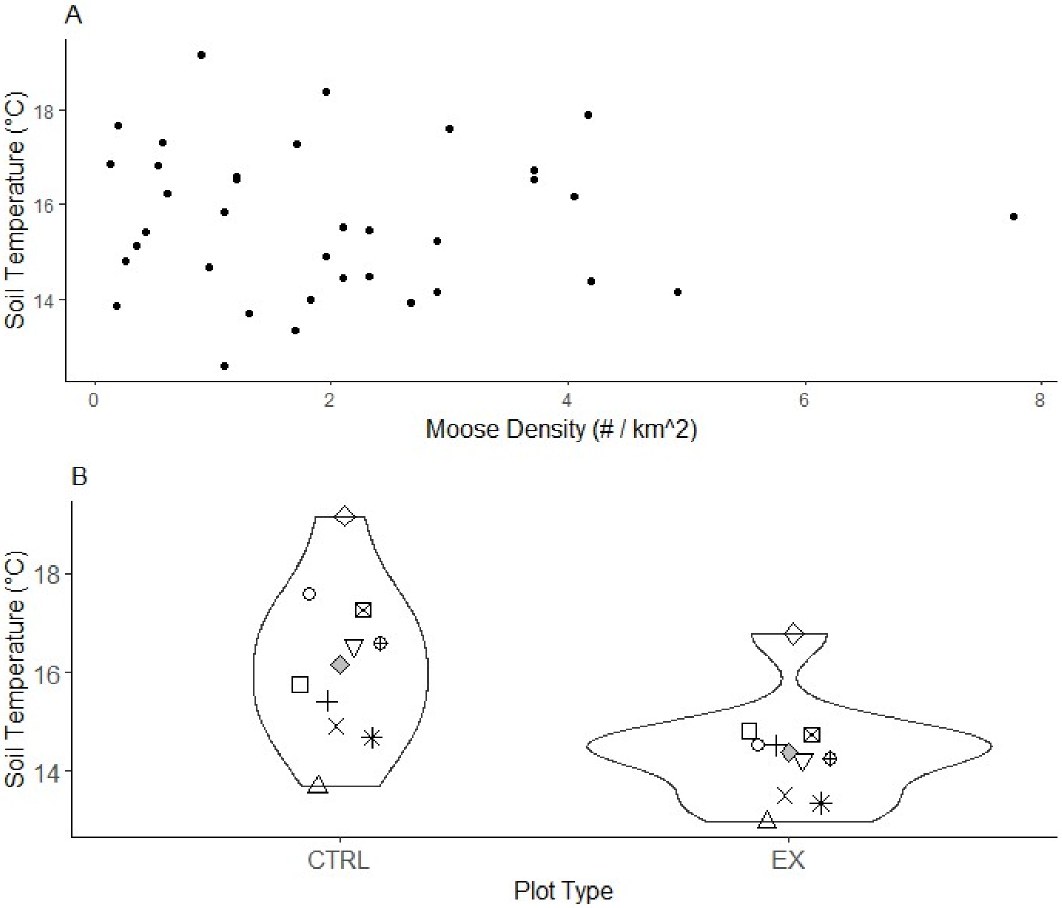

Figure A.3: A) In open plots, there was no apparent relationship between average soil temperature and moose density. B) In paired exclosure-control plots (n = 10 exclosures, 10 controls), controls had higher average soil temperatures ($\bar{x}$ = 16.2° C) than exclosures ($\bar{x}$ = 14.4° C). Symbols are defined as follows: □=GM-01, ○=GM-05, △=GM-13, +=TN-19, ×=TN-20, ◇=TN-21, ▽=TN-22, ⊠=TN-25, ✳=TN-31, ⊕=TN-34.

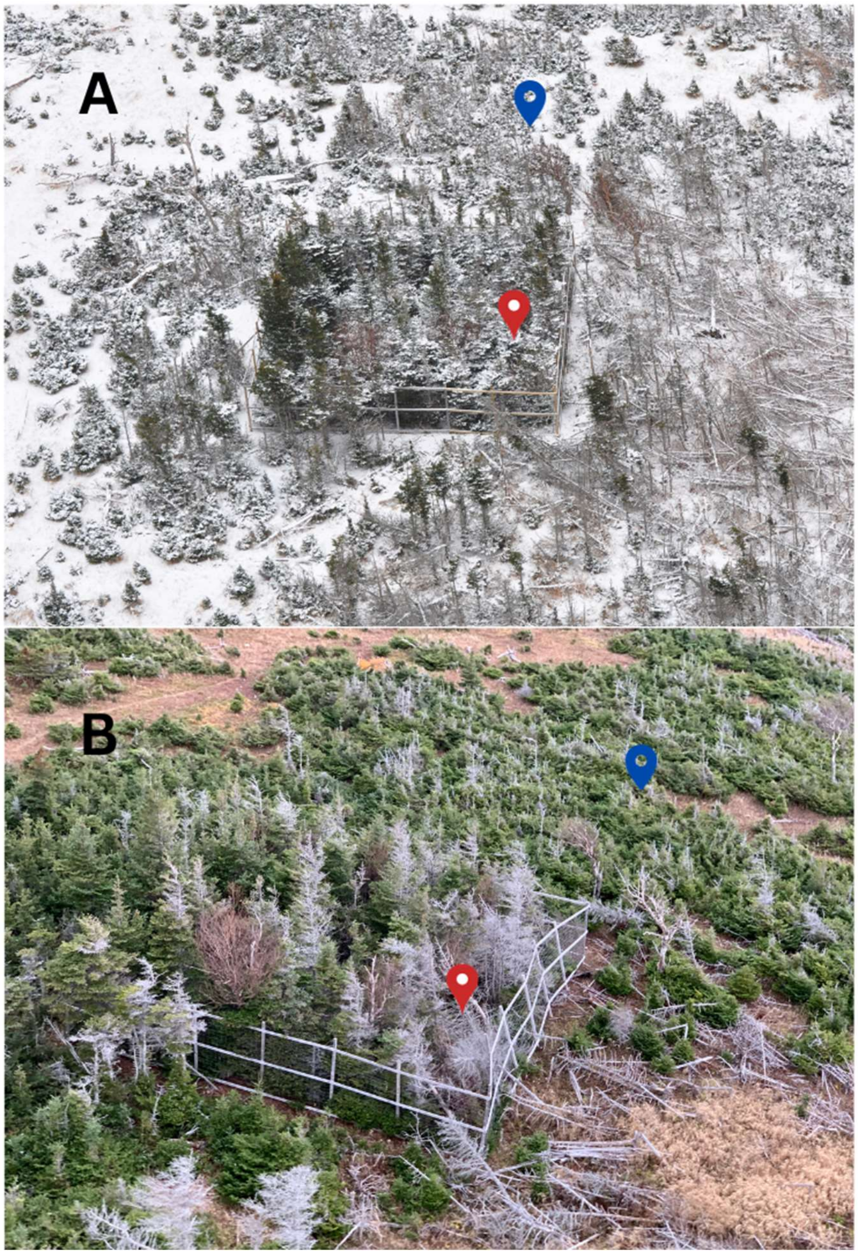

Figure A.4: Moose management has been occurring in both GMNP and TNNP since 2011. Moose management programs in each park have successfully decreased moose populations allowing for regeneration to occur in unfenced areas; see A for a 2013 aerial oblique photo (photo by Darroch Whitaker, Parks Canada) of a GMNP exclosure (15 m x 15 m; red pin) and control (blue pin), compared to B for a 2023 aerial photo (retrieved from Google Earth) of the same exclosure-control pair (GM-01).

APPENDIX B

The small sample size of our paired-exclosure data, may have excluded the hypothesized regenerating stands from our open plot data. This may explain why, unlike in our open plot data, we did not observe an effect of moose on the supply rate of ammonium. In recently clear-cut forests, Kolstad et al. (2018) found a similar result, with moose exclusion having no impact on the availability of important ions in soil, including ammonium. Additionally, within our own study system, Ellis & Leroux (2017) and Swain et al. (2023) reported no change in the percentage of nitrogen in soil or the amount of nitrogen mineralized, respectively. The shorter and cooler growing season in Newfoundland, compared to other boreal regions, may be leading to the lack of an overall impact of moose on belowground elemental cycling. As suggested by Kolstad et al. (2018), aboveground changes in species composition and canopy cover associated with moose presence may alter soil properties, such as temperature and moisture, to increase cycling and diffusion of elements outside fencing, resulting in no net change (Figure A.3; note that Swain et al. (2023) found little evidence of moose impacts on temperature). Additional changes, such as browsing-stimulated increases in rhizodeposition and inputs from moose feces and urine may have also contributed to the elemental pool in soil outside fencing (Dufresne et al., 2009; Pastor et al., 1993).