RESTORING FORESTS DEGRADED BY OVERABUNDANT MOOSE ON THE ISLAND OF NEWFOUNDLAND

by

© Louis Charron

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ABSTRACT

Global forests are being degraded at an alarming rate; hence ecological restoration becomes an integral component ensuring future forest health. Beneficial effects of restoration will arise from scientifically based practices that are efficient and effective. On the island of Newfoundland, moose (*Alces alces)* have become overabundant since their introduction in early 1900's. Intensive selective browsing by moose on foundation species such as balsam fir (*Abies balsamea*) interacts with natural insect disturbance and limits advanced regeneration, creating moose meadows. In this thesis, I focused on *where* and *how* active restoration should be implemented in Terra Nova National Park (Newfoundland, Canada) balsam fir forests within the context of the natural disturbance regime under conditions of overbrowsing. Environmental surveys and experimental seedling planting were carried out along a disturbance gradient from closed canopy forest to large insect-disturbed stands. To develop cost-effective and science-based planting protocols, several ground treatments were tested to enhance seedlings success: (1) control, field planting, (2) removal of the aboveground vegetation and (3) ground scarification. Results indicate that (1) priority for restoration should be given to insect-disturbed areas > 5 ha rather than smaller gaps, and (2) that active restoration should be implemented following scientifically determined field planting protocols, as no substantial benefit was detected following ground treatment. The recommendations arising for this thesis allow for the development of efficient and effective protocols towards the reestablishment of multi-aged balsam fir forests in Newfoundland.

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Deep thank you

And "*Merci pour tout*"

From the tinniest, to the most monstrous contribution

Helping in the achievement of this educational foundation

> *Comme une liane,*
>
> *J'ai pu compter sur le support de vos troncs*
>
> *Pour atteindre la chaude lumière de la canopée.*
>
> > And, as a moose
> >
> > You suppressed the growth
> >
> > Of unproductive and darker moment.

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CHAPTER 1

1 GENERAL INTRODUCTION

Global forests are being degraded at an increasing rate, with a documented net loss of 1.5 million km^2 over a period of 12 years (Hansen *et al.*, 2013): hence ecological restoration becomes an integral component, ensuring future forest health, biodiversity and community livelihood (Lamb *et al.*, 2005; Chazdon, 2008; Lamb, 2015). The Society of Ecological Restoration (SER) defines “ecological restoration” as “the process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed” (SER, 2004). In spite of the simple definition, beneficial long-term effects of restoration will result from efficient and effective practices, based on scientifically-sound protocols.

Efficient restoration practices are achieved when efforts are balanced as a function of needs (Holl and Aide, 2011). In some instances, natural regeneration or “passive” restoration may allow the recovery of the ecosystem (Prach and Hobbs, 2008). However, if an ecosystem has passed an ecological threshold that has fundamentally changed its environmental conditions, “active” restoration becomes necessary (Hobbs and Harris, 2001). Passive restoration occurs in areas where disturbance is removed (e.g. removal of herbivores to reduce browsing pressure), allowing natural unassisted recovery, compared with active restoration where, in addition to herbivore reduction, land could be managed by burning, thinning and/or planting vegetation to achieve a desired state (Benayas *et al.*, 2008). A threshold is defined as a point where a small change in environmental conditions following natural or anthropogenic disturbance leads to a large change in the ecosystem state (Suding and Hobbs, 2009). In the field of ecological restoration, an ecological threshold can be defined in a step-wise manner, where both as biotic and abiotic components can reach a tipping point; a biotic threshold being crossed when plant community is modified beyond its natural ability to regenerate to a former state, while an abiotic threshold is modified beyond some baseline set of physical factors that change physical environment (Whisenant, 1999; Hobbs and Harris, 2001). For instance, along the Bongil Peninsula, Australia, Cummings *et al.* (2005) show that substrate degradation following mineral sands mining resulted in the crossing of an abiotic threshold, making vegetation restoration practices insufficient to return to its prior state, unless combined with active soil improvement. As well, on Anticosti Island a critical density below 15 deer/km^2 allows for the natural regeneration of the native balsam fir forest (Tremblay *et al.*, 2007). Efficient active restoration would then target heavily altered forest stands that have undergone significant community change, and allow natural regeneration to occur in the least degraded ones that have not yet reached this tipping point.

To be effective, restoration projects must address ecological, financial and social context of the particular situation. A successful restoration case is related by Poffenberger (2006) in North-western Vietnam, where the degradation of limestone forests following fuelwood and timber extraction in the Phuc Sen communities between 1960's and 1970's has led to protection and planting of indigenous trees, recovering lost biodiversity and spring water flow following this community initiative. On the other hand, Palmer *et al.* (2014) note that out of 644 river restoration projects studied, a large proportion failed to reach their restoration goals, mainly because of techniques focusing on channel design, which did not consider broader ecological processes, such as productivity or nutrient dynamics. Both examples show the importance of having adaptive management; adjusting practices, following inherent project limitations, to reach restoration goals (Hobbs and Harris, 2001). Validated restoration protocols developed by experimentation are a robust way to ensure effective and successful restoration (Cummings *et al.*, 2005).

Forests around the world are home to high diversity and abundance of herbivores, often creating a disturbance by selective browsing of preferred species, which can impede natural regeneration if densities are above a natural density (McInnes *et al.*, 1992; Vourc'h *et al.*, 2001; Wardle *et al.*, 2001; Côté *et al.*, 2014). It is especially severe on islands where ungulates were introduced (e.g., Anticosti Island, Côté *et al.* (2014); Haida Gwaii, Vourc'h *et al.* (2001); Isle Royale, McInnes *et al.* (1992); Newfoundland, McLaren *et al.* (2004); New Zealand archipelago, Wardle *et al.* (2001)). On the island of Newfoundland, the introduction of moose (*Alces alces*) in the early 1900s (Pimlott, 1953) and the absence of natural predators have led to an overabundant moose population (McLaren *et al.*, 2004). Selective browsing on foundation species, such as balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) affects advanced regeneration, weakening ecosystem resilience after natural disturbance impeding the ecosystem's ability to regenerate to its former state (Pimlott, 1953; McLaren *et al.*, 2004).

Overabundant populations of moose and associated overbrowsing results from the high number of individuals, considering the size of Newfoundland, with >10% of total continental moose population present on the island, which only comprised <2% of its range (McLaren *et al.*, 2004). The high number of moose is explained by the eradication of the wolf (*Canis lupus*) population around 1930s (Pimlott, 1959) and the absence of disease in Newfoundland (McLaren *et al.*, 2004). Predator reintroduction has proven to be an effective passive restoration option for forest regeneration (Ripple and Beschta, 2003, 2007, 2012); however, in Newfoundland, the precarious caribou (*Rangifer tarandus*) population would potentially be harmed by apparent competition, preventing the option of reintroducing wolf (Fortin *et al.*, 2015). In some areas of the island, widespread impacts on forest composition are observed after an initial moose population "boom" triggered by the productive forest; but the subsequent population "crash" suggest that carrying capacity was exceeded (McLaren *et al.*, 2004). It was notably documented in Terra Nova National Park (~400 km^2), where after an initial population peak of ~650 individuals in the 1990s, the current population has decrease to ~180 moose in 2015 (J. Feltham, ecologist, Parks Canada, *pers. comm.*). However, even with a low moose population, regeneration failure is observed in the park and various areas across the island of Newfoundland due to legacy effects (McLaren *et al.*, 2004; Gosse *et al.*, 2011).

Balsam fir regeneration is adapted to the natural disturbance of spruce budworm (*Choristoneura fumiferana*) – hemlock looper (*Lambdina fiscellaria*) insect disturbance and windfall events (Baskerville, 1975; Morin, 1994; Engelmark, 1999). Insects preferentially attack mature individuals > 70 years of age (Morin, 1994), with wind felling compromised trees (Morin, 1990). Following canopy opening, the balsam fir seedling bank is released from light suppression and grows to reach the canopy, allowing forest regeneration (Morin and Laprise, 1997; Greene *et al.*, 1999). Balsam fir seeds are viable for < 9 months, preventing the creation of a persistent seed bank (Greene *et al.*, 1999). Seed production and germination is therefore critical to create the seedling bank and is affected by seedbed quality. Previous studies found that seedling survivorship was reduced on broadleaf litter seedbed when compared to needle litter or moss seedbed, explained by a decrease in moisture retention capacity and extreme temperature (Plamondon and Grandtner, 1975; Côté and Bélanger, 1991). When established, seedlings and saplings are shade-tolerant and can be suppressed many years before growing to reach the canopy (Messier *et al.*, 1999); this is a critical period where seedlings and saplings are sensitive to browsing by herbivores (McInnes *et al.*, 1992; Gosse *et al.*, 2011; Côté *et al.*, 2014).

Intensive browsing by moose in Newfoundland reduces the seedling bank and disrupts the natural regeneration cycle (Gosse *et al.*, 2011). For example, in Terra Nova National Park, disturbance by insects in the 1970s led to canopy breakdown and opening, which was not replaced by seedlings and saplings, creating "spruce-moose meadows" dominated by grass and white spruce due to heavy browsing of the understory vegetation and foundation tree species. Previous studies have shown that a tipping point has been reached and that even with the removal of moose, the forest would not return to the former balsam fir-dominated forest (McLaren *et al.*, 2009), hence the consideration given to active restoration. Seeding is often a solution used in restoration to assist natural regeneration (Whisenant, 1999); however in Newfoundland, the predation by various non-native species and the deep shift in environmental conditions impedes balsam fir emergence, hence seedling stock is preferred (Noel, 2004; Gosse *et al.*, 2011).

The negative effects of moose are widespread on large forest tracts in Newfoundland, making restoration planning difficult (Gosse *et al.*, 2011). The current thesis examined efficient and effective options of forest restoration, with the objective of re-establishing a future multi-aged balsam fir forest in Newfoundland. The objective was investigated by:

(1) exploring where active restoration practices should be implemented, while passive restoration via natural recovery could operate in the other areas (Chapter 2); and (2) experimentally testing how active forest restoration protocols such as ground treatment and seedling planting density should be implemented to assess the most successful method of restoring closed canopy balsam fir forests (Chapter 3). I hypothesized that: (1) active restoration is not needed for the entire park; focusing on active restoration efforts on highly degraded areas allowing for efficient restoration and creating a heterogeneous landscape of restored and naturally regenerated stands; and (2) restoration treatments (ground and planting density) have the potential to enhance the ecosystem (decrease plant-light competition, ameliorate seedbed conditions, etc.) ensuring effective restoration efforts.

Currently, no protocols have been developed to restore non-regenerating areas of the boreal balsam fir forest. Balsam fir forests are widespread across North America (Frank, 1990) and they are one of the dominant forest types on the Island of Newfoundland (Damman, 1964), highlighting the importance of this project. Recommendations towards the rehabilitation of those forests will ensure that vital habitats for species at risk, such as the Newfoundland marten (*Martes americana atrata*; (Gosse *et al.*, 2005; Hearn *et al.*, 2010)), the red crossbill (*Loxia curvirostra percna*; (COSEWIC, 2004)) and the boreal felt lichen (*Erioderma pedicellatum*; (Scheidegger, 2003; Goudie *et al.*, 2011)) are present on the landscape, underscoring the importance of this research project. The experiments were carried out in Terra Nova National Park, eastern Newfoundland (Canada) and will assist Parks Canada in managing their forests and to contribute to achieving their mandate of preserving the park's ecological integrity (Parks Canada, 2008).

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CO-AUTHORSHIP STATEMENT

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In all instances, I was the principal contributor to project design and proposal, implementation of the field research component, gathering and analysis of the data, and manuscript preparation. Dr. Hermanutz contributed to the project design, seedling planting, results interpretation and editing of the thesis and these manuscripts.

CHAPTER 2

2 PRIORITIZING BOREAL FOREST RESTORATION SITES BASED ON DISTURBANCE REGIME

2.1 Abstract

Selection of high priority sites for ecological restoration becomes essential with globally decreasing forest cover following natural and anthropogenic disturbances. A disturbance gradient resulting from native insect (*Choristoneura fumiferana*) outbreaks and non-native moose (*Alces alces*) browsing was studied in balsam fir forest stands in Newfoundland (Canada) to inform land managers where active *vs.* passive restoration would be most appropriate. The disturbance gradient ranged from small gaps (area < 5 ha) to medium and large gaps created by insects, in addition to a control (i.e., "no gap") closed canopy mature balsam fir forest. In all areas, seedlings and saplings (< 2 m) were browsed by moose causing failed forest regeneration. Differences in the plant community, environmental conditions and species functional groups were quantified across the disturbance regime using non-metric multidimensional analysis and nested analysis of variance. In this study, the closed canopy stand retained the optimal conditions for balsam fir forest regeneration and does not need active restoration to regenerate if moose densities are low. Insect-disturbed areas < 5 ha retained conditions that would allow them to regenerate naturally under conditions of low herbivory (i.e., they would not need active restoration); they were dominated by late succession forbs, retained low densities of balsam fir adults and optimal abiotic conditions for seedlings, with an increase in sunlight and decline in the quality of feathermoss seedbed. In contrast, a complete shift was observed in open areas > 5 ha, which were dominated by grasses, early succession forbs and had abiotic conditions closer to early succession boreal forest, indicating an ecological threshold had been crossed, confirming

the need for active restoration. To allow regeneration regardless of gap size, reduction of moose numbers must be continued. Threshold identification in the boreal forest should be based on disturbance regime and used to inform critical areas for future forest restoration strategies. Based on our study, insect outbreak areas > 5 ha should be prioritized for active restoration, as the crossing of a biotic threshold indicates that such sites cannot naturally return to pre-disturbance balsam fir forests.

2.2 Introduction

The degradation and loss of forest globally has led to an urgent call for restoration protocols (Hobbs and Harris, 2001; Lamb *et al.*, 2005). Forests are declining due to multiple synergistic causes, resulting in the alteration of important ecosystem function and services (Hansen *et al.*, 2013). For example, on Santa Cruz Island (California, USA) an increase of 97% of the carbon sequestration followed the removal of grazing ungulates and recovery of the native woody vegetation on the island (Beltran *et al.*, 2014). Prioritization of restoration sites has become a pressing issue given limited resources (i.e. financial, technical and social) faced by land managers (Hobbs *et al.*, 2014). Priority sites can be determined by identifying the state at which assisted or active regeneration becomes crucial along the gradient of forest degradation (McIntyre and Hobbs, 1999; Chazdon, 2008; Hobbs *et al.*, 2014). The highest priority will be assigned to the most heavily altered forest stands that have undergone significant community-level change, while allowing natural regeneration (passive recovery) to occur in the least degraded stands. This approach would be especially helpful to support ecological integrity targets within protected areas (Parks Canada, 2008; Keenleyside *et al.*, 2012). Traditional restoration projects are sometimes carried out in areas so degraded that establishing novel ecosystems is seen as the best solution (Hobbs *et al.*, 2009); however, since protected areas are usually less degraded (Wiens and Hobbs, 2015) limiting efforts to areas that actively require restoration would be most efficient (Holl and Aide, 2011).

Depending upon the stand regeneration trajectory, spontaneous succession might occur naturally when stressors are removed, reducing the need for active management efforts (Prach and Hobbs, 2008; Holl and Aide, 2011); however, when ecological thresholds are crossed, active management becomes necessary (Whisenant, 1999; Hobbs and Harris, 2001). Passive restoration occurs in areas where disturbance is removed (e.g. removal of herbivores to reduce browsing pressure), allowing natural unassisted recovery, compared to active restoration where, in addition to herbivore reduction, land is managed by burning, thinning and/or planting vegetation to achieve a desired state (Benayas *et al.*, 2008). A threshold is defined as a point where a small change in environmental conditions following natural or anthropogenic disturbance leads to a large change in the ecosystem state (Suding and Hobbs, 2009). In Tasmania, a shift from forest to an alternative grassland state was observed, originating from fire and stabilized by eco-hydrological feedbacks during the last 7,000 years (Fletcher *et al.*, 2014). Because of the potential hysteretic behavior of ecological thresholds, restoration leading to ecosystem recovery might take a different trajectory than the trajectory that led to the degraded state, and may involve complex and costly intervention (Suding *et al.*, 2004; Suding and Hobbs, 2009). Therefore, identification of such ecological thresholds is important for effective and efficient management and restoration of ecosystems.

Detecting ecological thresholds usually involves large-scale and long-term data collection for modeling purposes (Scheffer and Carpenter, 2003; Scheffer *et al.*, 2012); hence, identifying thresholds is difficult for land managers and often leads to restoration decisions based on qualitative expert knowledge. Suding *et al.* (2004) suggested more manageable, and scientifically sound, proxy lines of evidence. For instance, determining abiotic and biotic interactions helps to predict ecosystem resilience, as strong ecosystem interactions indicate a self-organized structure more prone to thresholds behavior due to biotic feedbacks (Suding and Hobbs, 2009). Heffernan (2008) found positive feedbacks between soil stability and plant growth on some soil substrates, causing a bimodal response in plant communities to floods in Arizona. Species functional groupings also provide a mechanistic understanding of important ecosystems capacity that might have been lost or gained in a community and gives a more general response than is provided by individual species (McGill *et al.*, 2006; Suding and Hobbs, 2009; Standish *et al.*, 2014).

Globally, negative impacts of herbivores on ecological thresholds of forest ecosystems have been widely documented (Dublin *et al.*, 1990; Augustine *et al.*, 1998; Tremblay *et al.*, 2007; Hidding *et al.*, 2013). In Kenya, Dublin *et al.* (1990) report a shift from woodlands to grasslands caused and perpetuated by a combination of fire and elephant browsing. Browsing pressure by overabundant herbivores has created a new disturbance regime in many forested ecosystems (Persson *et al.*, 2000; Wardle *et al.*, 2001; Côté *et al.*, 2004; Hobbs, 2006) that is especially severe on islands where ungulates were introduced (e.g. Anticosti Island, Côté *et al.* (2014); Haida Gwaii, Vourc'h *et al.* (2001); Isle Royale, McInnes *et al.* (1992); Newfoundland, McLaren *et al.* (2004); New Zealand archipelago, Wardle *et al.* (2001)). On the island of Newfoundland, the introduction of moose (*Alces alces*) in the early 1900's (Pimlott, 1953) and the absence of natural predators led to an overabundant population (McLaren *et al.*, 2004). Selective browsing on foundation species, such as balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*) affects advanced regeneration, weakening ecosystem resilience after natural disturbance (Pimlott, 1953; McLaren *et al.*, 2004). The negative effects of moose are widespread on large forest tracts in Newfoundland, making restoration planning difficult (Gosse *et al.*, 2011). Moreover, to date, there has been no protocol to inform if active restoration is needed, and if so which sites should be prioritized.

In the eastern Canadian boreal forest dominated by balsam fir, the primary natural disturbance is insect outbreak (spruce budworm [*Choristoneura fumiferana*] and hemlock looper [*Lambdina fiscellaria*]), which target adult trees opening the mature canopy cover and releasing the young latent regeneration to reach the canopy (Morin and Laprise, 1997). As pointed out by Pureswaran *et al.* (2015) insect disturbance regimes are currently undergoing rapid changes toward more frequent, extensive and severe outbreaks, caused by climate change and human practices. Other disturbances originate from wind events and forestry activities (Engelmark, 1999). The synergistic effect of natural disturbance and browsing by overabundant moose has shifted the balsam fir forest ecosystem towards the creation of "spruce-moose meadows" in highly browsed areas (McLaren *et al.*, 2004; Gosse *et al.*, 2011). While insect outbreaks trigger early succession by removing the canopy trees, moose herbivory modifies vegetation assemblages by selective browsing, decreasing the resilience of the ecosystem. Indirectly, the impact of canopy opening has led to shifts in environmental conditions and degradation of optimal seedbed for foundation species (McLaren and Janke, 1996; Rooney and Waller, 2003). Previous studies noted that seedling survivorship was reduced on broadleaf litter seedbed when compared to needle litter or moss seedbed, explained by a decrease in moisture retention capacity and extreme temperature (Plamondon and Grandtner, 1975; Côté and Bélanger, 1991). Negative impacts are also amplified by balsam fir's short seed dispersal (< 75 m) and seed bank viability of < 9 months (Greene *et al.*, 1999).

Lack of regeneration of balsam fir forest communities, even when moose pressure is eliminated, suggests that ecological thresholds have been crossed in Newfoundland (McLaren *et al.*, 2009; Gosse *et al.*, 2011) and active management through restoration is necessary to reclaim ecological integrity of the forest. However, research to disentangle the effects of insect outbreak extent and severity, and moose browsing is lacking, and hence selection of high priority restoration site is hampered. Our objectives were (1) to use scientific lines of evidence to: (i) evaluate abiotic factors associated with ecological thresholds in balsam fir forests; (ii) assess plant community shifts in balsam fir stands; and (iii) determine if there has been a shift in functional groups by comparing forests across a natural disturbance gradient; (2) to identify ecological thresholds across the insect disturbance gradient (from closed canopy with no gaps to large gaps) for the purpose of restoration site selection and prioritization. We hypothesized that (1) the cumulative moose-insect effects have created negative ecosystem changes that block natural forest regeneration; and (2) thresholds have only been crossed for a small proportion of forest stands across the disturbance spectrum, underscoring that active restoration is needed only in most the degraded areas. This study will outline possible thresholds and inform guiding principles for scientifically and cost-effective decision-making toward restoration sites selection.

2.3 Methods

2.3.1 Study Site

Terra Nova National Park (TNNP; 48°30’N, 54°00’W) is a protected area of ~400 km^2, located in eastern Newfoundland, Canada. The climate is maritime with a mean temperature of -6.8°C and 16.1°C in January and July, respectively, and mean annual precipitation of 311.0 cm and 872.7 mm of snow and rain, respectively (Environment Canada, 1971-2000). TNNP boreal forest is dominated by black spruce (*Picea mariana*) inland and balsam fir along the coast. Balsam fir forest covers 15% of the park and is restricted to richer soil, predominantly humo-ferric podzols (Deichmann and Bradshaw, 1984). Historically, natural disturbances such as insect outbreaks and severe wind events, triggered balsam fir stand regeneration. Depending on the severity of the insect outbreak, and subsequent wind events, stand openings of various sizes are created within the forest matrix. The majority of the gap openings within balsam fir dominated forests are less than 5 hectares (ha), with rare occurrence of large gaps (Blais, 1983; Leblanc and Bélanger, 2000). Between the late 1970’s to early 1980’s, 1300 ha of TNNP forest experienced insect outbreaks, with 23 ha affected in the 1990’s (Power, 2000). Subsequent wind events further open the canopy by felling dead trees. The present study takes advantage of the natural gradient of disturbance ranging in magnitude from small to large gaps (0.06 – 66.62 ha; Parks Canada *unpubl.*), which encompasses the majority of variation in balsam fir forest within the park. In TNNP, gap size was skewed toward smaller open areas (75% of gaps are < 5 ha; Parks Canada *unpubl.*), limiting replication.

Since its introduction in 1904, TNNP moose population peaked at ~650 individuals in 1997; as of 2015 the population has decreased to 180 individuals (J. Feltham, ecologist, Parks Canada, *pers. comm.*). In an effort to lower browsing impacts by overabundant moose and restore ecological integrity within TNNP, Parks Canada implemented a recreational moose hunt in the fall of 2011, an activity prohibited since park establishment in 1957. The "Hyperabundant Species Management Plan for TNNP" was developed with stakeholders from local communities and provincial NGOs that included the participation of local hunters (Parks Canada, 2010). Hunting pressure was concentrated around access roads as the use of motorized vehicles is prohibited; recent incentives have included access to coastal areas, through the availability of a free boat service (J. Feltham, ecologist, Parks Canada, *pers. comm.*). The park issued 20, 35, 85 and 90 moose tags from 2011 to 2014. The licence quota for the park is designed to decrease the moose density by mimicking wolf (*Canis lupus*) predation levels; wolves were extirpated from the island in the early 1930's (Pimlott, 1959). TNNP's target density is 0.5-0.25 moose/km^2, with a removal of ~20 moose/year that is projected to allow balsam fir and hardwood regeneration, improving ecosystem structure and function (Parks Canada, 2010). Since 2011, a decrease in browsing intensity has resulted in increased balsam fir height growth, and hardwood regeneration in the hunted areas (J. Feltham, ecologist, Parks Canada, *pers. comm.*).

2.3.2 Sampling design

Four representative sites across the disturbance gradient were selected within the park boundaries (Fig. 2.1). The gradient of disturbance ranged from small gaps (area less than 5 ha) to medium and large gap created by insects, all sites from the late 1970's outbreak, in addition to a control (i.e., “no gap”) closed canopy mature balsam fir forest. In all selected sites, there was a lack of regeneration due to over browsing by moose on seedlings and saplings of balsam fir and broadleaf species (e.g. white birch, red maple [*Acer rubrum*]; Table 5.1, Fig. 5.1). To ensure equal sampling effort by area, between two and ten randomly distributed plots (24 m x 24 m) were selected in each of the four disturbance sites (Blue Hill Closed Canopy, Bread Cove Brook, Platter’s Cove and Blue Hill). Within each plot, five 1 m^2 quadrats were equally separated on a diagonal transect running between two opposite corners and when indicated, more than one measurement was done per quadrat. Vegetation and abiotic factors (ground: temperature, moisture, pH, resistance and decomposition rate; light: photosynthetically active radiation) were surveyed in each plot.

2.3.2.1 Vegetation survey

Percentage cover of all species < 2 m was visually estimated to the nearest 5% for each of the quadrats (4 sites, 24 plots × 5 quadrats; n=120). All grass species were grouped to the family level (*Poaceae*) because of low cover values in most of the sites (Table 5.2). Rare (making up < 5% per plot), or unidentifiable species at time of survey (e.g. non-flowering) were identified to genus (Table 5.3). The number of young trees (< 2 m) and canopy trees (> 2 m) were counted within each quadrat and plot, respectively. To evaluate the diversity in functional groups across the disturbance gradient, all species were subsequently assigned to 11 functional groups (Table 2.1), combining growth form, height, leaf and regeneration traits (Cornelissen *et al.*, 2003).

2.3.2.2 Soil survey

Monthly temperature and moisture measurements were taken the same day in each of the quadrats (4 sites, 24 plots × 5 quadrats; n=120) and averaged over the summer growing season (June – August) using a WET-sensor probe (Delta-T Devices Ltd. Burwell, Cambridge, UK). One soil core per quadrat (n=120) was taken to measure soil pH, following Hendershot *et al.* (2007). We estimated decomposition rate of the humus layer by burying six birch decomposition sticks (3 sticks in 2 groups) in two corners of each plot for a year (July 2013-2014; 4 sites, 24 plots × 2 quadrats × 3 measurements; n=144) and determined the percentage mass difference between the beginning and the end of the burial period. Soil resistance was measured as a proxy for seedbed quality, accounting for ground compaction and root system density. It was measured in each quadrat (n=120) in May, using a dynamic penetrometer, following Herrick and Jones (2002). Hammer mass and hammer fall was fixed at 2.02kg and 30cm, respectively.

2.3.2.3 Light availability survey

Four photosynthetically active radiation (PAR) measurements were taken with a LI-190 quantum sensor (LI-COR Inc. Lincoln, Nebraska, USA) in each quadrat at mid-understory height (25cm) and four at over-understory height (1m) (4 sites, 24 plots × 5 quadrat × 4 measurements; n=480, for each height level). Each measurement was associated with a full sunlight measurement (over the canopy) to estimate the %PAR. Light measurements were taken during cloudless days, between 10h and 15h in early July during full leaf stage (Jobidon, 1992).

2.3.2.4 Moose habitat use

To estimate moose density across the disturbance gradient, moose habitat use was evaluated for each plot by counting the number of pellet piles (> 20 pellets) accumulated during winter, since pellet pile density correlates positively with moose browsing intensity (Neff, 1968; Härkönen and Heikkilä, 1999). Pellets were cleared from the area the fall prior to the spring pellet pile count, following standard protocol (Neff, 1968).

2.3.3 Statistical Analysis

2.3.3.1 Plant communities

We used a non-metric multidimensional scaling analysis (NMDS) to determine differences in species composition across the disturbance gradient. NMDS was chosen because of non-linearity condition and a zero-rich dataset (Zuur *et al.*, 2007). The analysis was done using the “metaMDS” function of the Vegan package in R (Oksanen *et al.*, 2015). To ensure a global minimum was reached and not a local minimum, a loop with 1000 iterations was run using the “previous.best” function in the “metaMDS” wrapper. Analysis was performed on the mean understory vegetation cover for each plot. To ensure adequate data redundancy (Peck, 2010), moss species were combined to genus for analysis, which should not affect results as the dominant mosses were monospecific (Table 5.4). To illustrate the difference along the disturbance gradient, convex hull were drawn around each site. Pearson's Product-Moment correlation (r-value) was computed to evaluate the strength of relation between species and each NMDS axis. Significance of the r-value was met at $|r| > 0.404$ ($n=24$, $p<0.05$; Upton and Cook (2008)). A second matrix containing explanatory environmental variables was fit to the species ordination using Vegan's "envfit" function. The length and the direction of the arrows in the resulting graphical representation show the strength and the direction of the environmental gradient in species distribution.

2.3.3.2 Environmental variables

Differences in environmental conditions among gap sizes were evaluated using a nested analysis of variance; plot was nested within site (and quadrat within plot for the multiples measurements of %PAR and soil decomposition rate per quadrat) and F-values were computed using the nested mean square (Sokal and Rohlf, 2012). When needed, the response variable was ln-transformed to meet assumptions of residual homogeneity and normality. For both PAR variables, assumptions were not met with the transformation, and a restricted permutation test for nested design was performed (N=4,999) with plot kept together as a unit, to test the effect of site, following Anderson and Braak (2003). To determine trends of the environmental variables across the disturbance regime, *a priori* comparisons were performed between (1) no gap and small gap, (2) small and medium gaps, and (3) medium and large gaps, following the expected change with disturbance size increase. When the results showed a more complex behavior, subsequent *a posteriori* comparisons (no/medium, no/large or small/large gaps) were performed and a Bonferroni correction was applied to compensate for over-testing (Sokal and Rohlf, 2012).

2.3.3.3 Vegetation functional groups

To determine how species functional groupings respond to disturbance, we performed nested ANOVAs, similar to the one used for the environmental variables. Plot was nested within site and F-values were computed following the procedure of Sokal and Rohlf (2012). The response variable was the percentage cover of nine of the functional groups in each plot. For deciduous and coniferous trees, the response variable was the sum of young trees (< 2 m) per quadrat and canopy trees (> 2 m) per plot, computed for each plot. As the analysis is at the plot scale, a one-way ANOVA was performed for these two functional groups, instead of the nested analysis.

All analyses were performed using the R statistical environment version 3.1.2 and significance level was set at 0.05 (Bonferroni α: 0.0085 - 0.0127).

2.4 Results

2.4.1 Plant communities

The NMDS analysis indicates that the plant assemblage shifted with increased disturbance (Fig. 2.2). The majority of variation (82.2%) is explained by the first axis, which is highly correlated with soil moisture, soil decomposition rate, number of hardwood trees per plot and %PAR at 100cm (r-value $>|0.90|$; Table 5.5). Feathermoss and shade-tolerant herbaceous species characteristic of balsam fir forest stands (e.g. *Hylocomium splendens, Dicranum sp., Clintonia borealis, Linnaea borealis*; Frank (1990)) are positively correlated with "no gap" closed canopy stands (r-value > 0.404; Table 5.6), which contrasts with open gaps that are characterized by *Poaceae* sp., grass litter, early succession herbaceous, and light-tolerant plants (r-value < -0.404; Table 5.6). The increase in degraded seedbed conditions with forest opening suggests that these are the sites that should be restored. The second axis (10.3%) explained the within-, rather than across-sites variations. Broadleaf litter, *Ptilium crista-castrensis, Cornus canadensis*, *Ilex mucronata*, *Lycopodium annotinum*, *Populus tremuloides* (r-value $> |0.404|$; Table 5.6) and moose density based on pellet counts (r-value $>|0.90|$; Table 5.5) are highly correlated with the second axis. The strong correlation between abiotic factors and the species ordination indicate biotic-abiotic interactions and thresholds prevalence in the system (Suding and Hobbs, 2009). The hull containing plots of a same gap size shows no overlap among sites, confirming that vegetation is changing in response to disturbance regime, a consequence of the opening of the canopy, resulting in a dry, warm and compact substrate, as disturbance increases.

2.4.2 Environmental variables

2.4.2.1 Light availability

Light availability follows the gradient of disturbance size, increasing as disturbance size increases (Table 2.2). Light is at first intercepted by the canopy layer (%PAR at 1 m) and shows a clear difference between closed (24%) and open areas (79%, 82%, 96%; for small, medium and large gaps, respectively). Further light penetration (%PAR at 25cm) is intercepted by the understory vegetation, which is shown to be denser in open areas than closed areas. Therefore, canopy light limitation is experienced in the closed mature forests, but understory competition predominates in open areas.

2.4.2.2 Soil characteristics

Physical and chemical soil characteristics broadly follow the disturbance gap size, with an increase in soil pH (from 4.2 to 4.7), temperature (14.7 – 17.1 ^{o}C), resistance (281 – 755 N) and decomposition rate (13 – 35%), and a decrease in soil moisture (23 – 15 %V/V) as the gap size increases (Table 2.2). Except for soil temperature, there was no statistical difference between the different gap sizes. The largest difference is between closed and the open gaps. However compared to medium and large gaps, which are different in all aspects to the closed canopy forest site, there were no significant differences in soil moisture and decomposition rate for the small gap and the closed canopy stands (Table 2.2). Lower ground temperature measured at the large open area could be explained by the higher elevation of this site compare to the other opened ones (~118m *versus* 78m).

2.4.2.3 Moose habitat use

No statistically significant difference was observed in moose habitat use among gap sizes, with a higher variance observed among plots at the same site. This is consistent with the typical large home range of moose and its food selection at the plant level (Table 2.2).

2.4.3 Vegetation functional groups

Closed canopy stands are characterized by high cover of bryophyte and coniferous trees with low cover of graminoides and early succession forbs, which are significantly different from the medium and large openings ($F_{3,4}$ = 34.7, p = 0.003; $F_{3,20}$= 173, p = 1.8 e^{-14}; $F_{3,4}$ = 92.5, p = 0.0004; $F_{3,4}$ = 88.4, p = 0.0004; respectively; Fig. 2.3, Table 5.7). Both medium and large gaps have a similar distribution of functional groups. Small gap area has a minimal cover of graminoides and early succession forbs functional group, which is similar to the closed area. Results show a loss of the bryophyte cover in all gaps relative to closed area. Coniferous tree cover drastically decreases with disturbance, but the small gap area still retains a minimal cover of canopy trees. Balsam fir is the dominant tree in the closed canopy and the small gap areas, while black spruce dominates the few trees seen in the medium and large gaps. Pteridophytes, shrubs (all heights) and deciduous trees had a minimal mean cover (<25%) per site and show no significant difference across the disturbance gradient ($F_{3,4} = 0.1$, $p = 0.9$; $F_{3,4} = 3.7$, $p = 0.1$; $F_{3,4} = 1.3$, $p = 0.4$; $F_{3,4} = 2$, $p = 0.3$; $F_{3,20} = 0.6$, $p = 0.6$; respectively; Fig. 5.2, Table 5.7). Late succession forbs such as *Clintonia borealis, Cornus canadensis* and *Maianthemum canadense* do not follow the predicted trajectory with the highest abundance observed in the small gap, and differences were only statistically significant between the small and medium gaps ($F_{1,4} = 24.9$, $p = 0.008$). The lichen functional group was not analyzed statistically as it accounted for <1% at each site.

2.5 Discussion

As recommended by McIntyre and Hobbs (1999), our study showed that disturbance regime is a good framework with which to prioritize forest restoration, with some sites requiring active restoration while other can be left to naturally regenerate. Our objectives were to develop a method based on scientific evidence to determine if restoration thresholds have been crossed using multi-site comparisons across a boreal disturbance gradient. As scientific lines of evidences are not widely used in site selection, this approach is important for future restoration projects. Following recommendations made by Suding and Hobbs (2009) and Standish *et al.* (2014), multivariate analysis was used to study the plant community shift and its link with environmental change along an insect disturbance gradient of varying gap sizes in boreal forest stands within Terra Nova National Park, Newfoundland, Canada. We observed that closed canopy and small gaps have the potential to regenerate naturally following disturbance removal (moose), while medium and large insect disturbed areas (gaps > 5 ha) have crossed a biotic threshold, indicating that active restoration should be considered.

Our results suggest that there is a gradient in response to disturbance that reflects natural regeneration trajectories. First, areas undisturbed by insect outbreaks show that even with a lack of young balsam fir regeneration following moose browsing, environmental conditions reflect a natural intact system. For example, orchids (*Cypripedium acaule* and *Platanthera orbiculata*) were observed in the closed canopy area, indicative of a low disturbance mature forest (Bratton, 1985). Second, small openings generated by insect disturbance (< 5 ha) show that there are environmental impacts, but these gaps are still resilient to disturbance, indicated by the absence of early succession species, partial retention of optimal abiotic conditions and presence of sexually mature balsam fir trees. For the 2003-2012 period, a seed rain of 87 ± 202 (SD) seeds/m^2 was recorded at this location (Parks Canada *unpubl.*) suggesting there are sufficient seed for natural regeneration (Houle and Payette, 1991). Third, large areas disturbed by insect outbreaks (> 5 ha) result in degraded environments where resilience seems constrained by the canopy and seed tree loss, causing vegetation shift and affecting the abiotic conditions. Moreover, since the last large insect outbreak in the 1970's, the areas have remained in a degraded state without showing signs of returning to the pre-disturbance forested stands, similar to what has been observed in other systems around the world (Côté *et al.*, 2014; Nagel *et al.*, 2015). It indicates that the larger gaps (> 5 ha) have crossed an ecological threshold to an alternate stable state that may only return to natural state with active restoration (Hobbs and Harris, 2001).

The legacy effect of the high moose population from 1990's in TNNP (Parks Canada *unpubl.*) combined with variable severity insect outbreak led to an ecological threshold that has tipped the balance away from the pre-disturbance forest regeneration. Plant community (Fig. 2.2), abiotic conditions (Table 2.2) and species functional groups (Fig. 2.3) exhibit non-linear response to increasing disturbance size. As well, other cases have documented that addition of chronic browsing disturbance to an already disturbed forest could cause ecological "surprises" (Dublin *et al.*, 1990; Nagel *et al.*, 2015). On Anticosti Island, Tremblay *et al.* (2007) reported an exponentially increasing response of balsam fir survival and growth with decreasing deer density in clear-cut forest, and retention of the native forest with a density < 15 deer/km^2. The generation of alternative stable states resulting from disturbance interactions is not uncommon (Paine *et al.*, 1998; Darling and Cote, 2008). In the Southern Rocky Mountain (Colorado, USA), the forest naturally experienced a combination of disturbance (wind, salvage logging and fire). While fire "reset the landscape", when combined with severe blowdown (>20% down trees), seedling regeneration is impeded, a consequence of warmer fire temperature and larger burnt areas (Buma and Wessman, 2011). Since the link between disturbance regime and ecological thresholds is well established, the severity of disturbance can inform the selection and prioritization of restoration sites.

Scheffer and Carpenter (2003) suggested the use of experimentation to detect thresholds (Suding and Hobbs, 2009; Standish *et al.*, 2014), as has been used in other studies (Tremblay *et al.*, 2007; Buma and Wessman, 2011; Hidding *et al.*, 2013). Site selection in this study was based on a disturbance gradient, provided by a natural experimentation generated by insect, windfall and moose herbivory. We identified an ecological threshold based on measurements of (1) plant community, (2) environmental conditions and (3) species functional groups. Collectively these biotic and abiotic factors have been essential to define loss of native species, shift in species dominance, seed limitation, trophic interactions and functional groups loss or gain; all predictive tools for thresholds identification (Suding *et al.*, 2004; Suding and Hobbs, 2009). In TNNP forested ecosystem, grass dominance in larger gaps (> 5 ha) replaced the late succession plant community, modifying the environmental conditions to create a positive feedback loop that severely limited the regeneration of the foundation species, balsam fir by producing unfavorable seedbeds and reducing seed availability (Gosse *et al.*, 2011). In addition to a major change in native species, a suite of non-native species were observed, including *Cerastium fontanum* subsp. *vulgare*, *Pilosella aurantiaca*, *Rumex acetosella* and *Taraxacum officinale;* these were largely limited to the medium and large openings (only 2 occurrences in the no and small opening). Subsequent establishment failure of balsam fir is exacerbated by its short dispersal and the barrier created by dense grass vegetation (Davies, 1987; Greene *et al.*, 1999).

Insect disturbance generates unequal gap sizes that are highly biased toward very small sizes (Leblanc and Bélanger, 2000), hence we were unable to replicate this study. Considering the lack of availability of the larger gap sizes and accessibility limitation of disturbed areas in TNNP, our case study of possible regeneration approaches along a disturbance gradient is based on replicated plots at singles sites across the disturbance regime. The use of only one site per disturbance regime might have resulted in non-independence of plots; nonetheless, plots were large (24m x 24m), spanned across large portions of the outbreak areas and our results concur with additional observations from Newfoundland, reinforcing our outcomes (McLaren *et al.*, 2009; Gosse *et al.*, 2011).

Preserving ecosystem services are increasingly the goal of restoration projects (Hobbs *et al.*, 2014); however for protected areas globally, describing ecosystems in term of function, structure and composition is crucial in preserving ecological integrity. Parks Canada defines “ecological integrity” as: “condition that is determined to be characteristic of its natural region and is likely to persist, including abiotic components and the composition and abundance of native species and biological communities, rates of changes and supporting processes” (Parks Canada, 2008). Therefore, conservation agencies should ensure ecological integrity of their protected areas through restoration practices that are effective, efficient and engage society (Parks Canada, 2008). In TNNP, passive recovery would involve conservation of the native vegetation, minimizing invasion of non-native species and reduction of moose disturbance through recreational hunting. For the management of the more degraded areas, active restoration should be developed, and may include a suite of techniques such as planting balsam fir seedlings to compensate for the lack of seed bearing trees and to regenerate the conditions of the forest ecosystem (Gosse *et al.*, 2011).

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Table 2.1 – Classification of the functional species groups for the vegetation of Terra Nova National Park, Newfoundland, Canada. Non-native species are indicated in bold, following the VASCAN database. Functional groups after Cornelissen *et al.* (2003).

Table 2.2 – Environmental variables mean (± SE) for a disturbance gradient in Terra Nova National Park, Newfoundland, Canada. Letters indicated the significant difference (p<0.05[1]) between sites indicated by nested ANOVAs (F and p-value in Table E2). See Fig 1 for study site locations and descriptions.

Figure 2.1 – Map of study sites in Terra Nova National Park, Newfoundland, Canada. Distribution of balsam fir dominated forest is outlined in light gray and insect outbreak disturbed area in dark gray. Roads are shown as dark lines on the map.

Figure 2.2 – Ordination scatterplot (NMDS with Bray-Curtis distance) of the plant communities found along an insect disturbance gradient studied in Terra Nova National Park, Newfoundland, Canada in relation to environmental conditions and seedbed. Each site is represented by a different symbol and enclosed in a convex hull by solid lines. Species are represented by the "+" symbol and those with significant correlation coefficient are labeled (codes are provided in the Table C2). Environmental variables are represented by arrows, with length and direction indicating the correlation with the axes (codes are provided in the Table C1). %PAR at 25cm and resistance vectors are similar to the pH vector, and are not shown for visual clarity. The NMDS ordination resulted in a 2-dimensional solution (Stress = 0.105) with cumulative explained variance of 0.925.

Figure 2.3 – Distribution of functional group cover across the disturbance gradient in Terra Nova National Park, Newfoundland, Canada. Panels A-D show percentage cover of

the various functional groups and panel E shows the number of trees per plot. The box and whiskers show the extent of the data, with indication of the upper and lower quartile, and median (bold line). Letters indicated the significant difference (p<0.05) between sites using nested ANOVAs. Functional groups after Cornelissen *et al.* (2003).

Table 2.1 – Classification of the functional species groups for the vegetation of Terra Nova National Park, Newfoundland, Canada. Non-native species are indicated in bold, following the VASCAN database. Functional groups after Cornelissen *et al.* (2003).

Functional group	Species
Lichen	*Cladina* sp., *Cladonia* sp., other lichen species
Bryophyte	*Dicranum* sp., ground moss, *Hylocomium splendens, Lepidozia reptans, Pleurozium schreberi, Polytrichum* sp., *Ptilidium* sp., *Ptilium crista-castrensis, Rhytidiadelphus* sp., *Sphagnum* sp.
Pteridophyte	*Lycopodium* sp., *Gymnocarpium disjunctum*, *Dryopteris* sp., *Equisetum* sp., *Pteridium aquilinum*
Graminoides	*Carex* sp., *Poaceae* sp.
Early succession forbs	*Anaphalis margaritacea,* ***Cerastium fontanum*** **subsp.** ***vulgare***, *Chamerion angustifolium*, *Fragaria* sp., *Galium triflorum, Hieracium vulgatum,* ***Pilosella aurantiaca***, ***Rumex acetosella,*** *Solidago rugosa,* ***Taraxacum officinale***, *Viola macloskeyi*
Late succession forbs	*Aralia nudicaulis, Clintonia borealis, Coptis trifolia, Cornus canadensis, Lysimachia borealis, Maianthemum canadense*
Short shrub (<0.4m)[1]	*Gaultheria hispidula*, *Linnaea borealis, Vaccinium* sp., *Rubus pubescens*
Medium shrub (0.4 – 2m)[1]	*Diervilla lonicera, Ilex mucronata, Kalmia angustifolia, Rhododendron* sp., *Rubus idaeus*. *Taxus canadensis*
Tall shrub (>2m)[1]	*Acer spicatum, Acer rubrum*[2], *Alnus viridis* subsp. *crispa, Amelanchier* sp., *Sambucus racemosa*, *Sorbus* sp., *Viburnum nudum* var. *cassinoides*
Deciduous tree[1]	*Betula papyrifera, Populus tremuloides*
Coniferous tree[1]	*Abies balsamea*, *Picea glauca*, *Picea mariana, Pinus strobus*

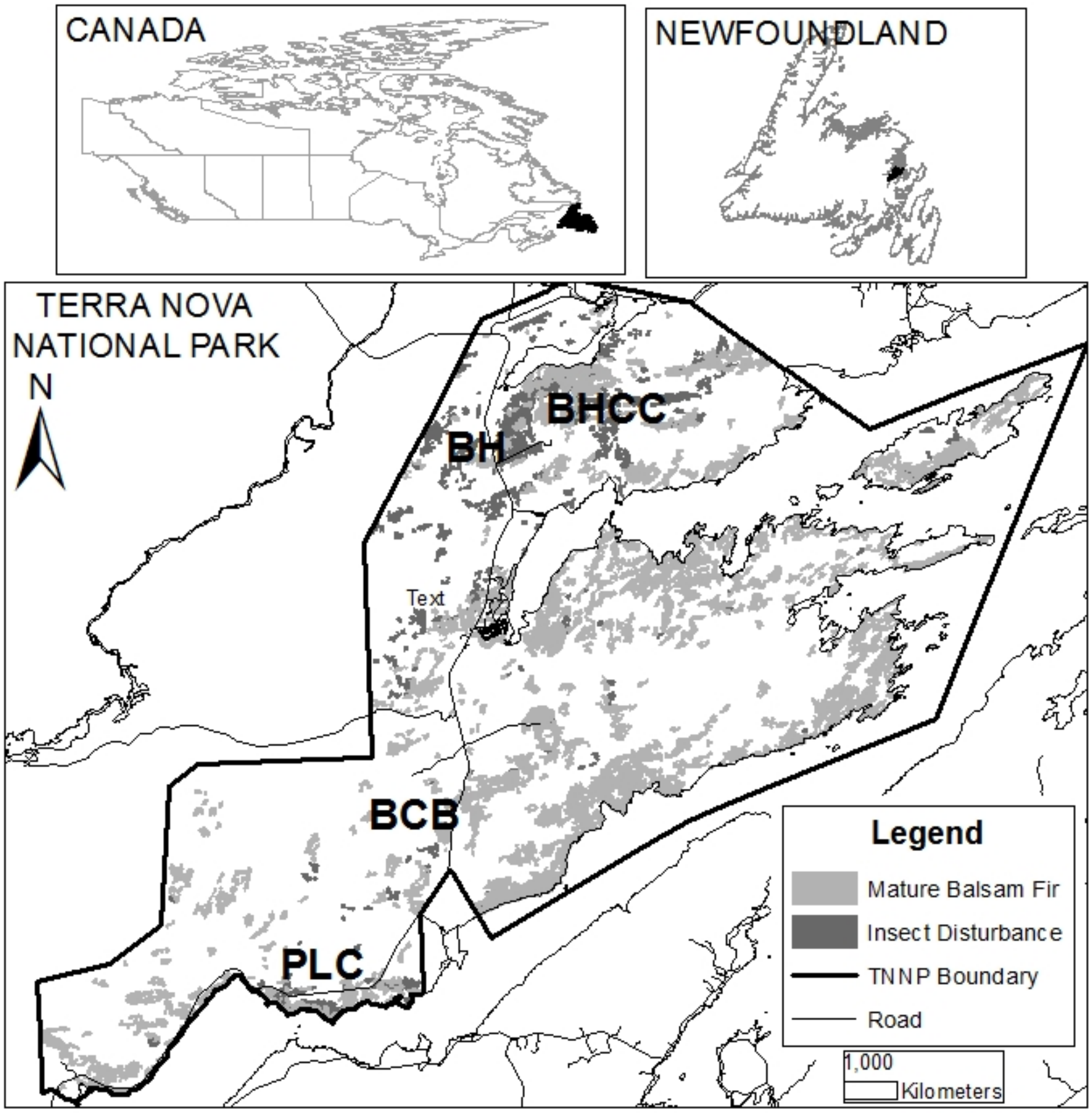
[1]Shrubs and tree classification following Ryan (1995)
[2]Assigned as a tall shrub, because of it multi-trunk growth form in TNNP

Table 2.2 – Environmental variables mean (± SE) for a disturbance gradient in Terra Nova National Park, Newfoundland, Canada. Letters indicated the significant difference (p<0.05[1]) between sites indicated by nested ANOVAs (F and p-value in Table E2). See Fig 1 for study site locations and descriptions.

	Closed BHCC	Small opening BCB	Medium opening PLC	Large opening BH
PAR 25cm (%)[1]	21.86 ± 3.36 (a)	57.11 ± 8.93 (b)	51.20 ± 5.85 (b)	72.01 ± 2.98 (c)
PAR 100cm (%)	24.24 ± 3.27 (a)	78.97 ± 6.03 (b)	82.31 ± 4.42 (b)	95.71 ± 1.24 (c)
Soil pH	4.19 ± 0.06 (a)	4.62 ± 0.09 (b)	4.87 ± 0.06 (b)	4.67 ± 0.05 (b)
Soil temperature (°C)[1]	14.7 ± 0.1 (a)	17.9 ± 0.2 (b,c)	18.0 ± 0.2 (c)	17.1 ± 0.1 (b)
Soil moisture (%V/V)[1]	22.8 ± 1.4 (a)	18.4 ± 2.7 (a,b)	14.9 ± 1.3 (b)	15.4 ± 0.8 (b)
Soil resistance (N)[1]	280.7 ± 27.9 (a)	739.1 ± 106.1 (b)	607.2 ± 93.1 (b)	754.5 ± 48.8 (b)
Decomposition rate (%)[1]	13.22 ± 2.38 (a)	15.51 ± 5.48 (a,b)	33.51 ± 4.04 (b)	34.68 ± 4.06 (b)
Moose habitat use	3.9 ± 0.8 (a)	8.5 ± 1.5 (a)	3.8 ± 0.8 (a)	3.3 ± 1.2 (a)

[1] P-value was adjusted following Bonferroni correction for additionnal *a posteriori* comparisons.

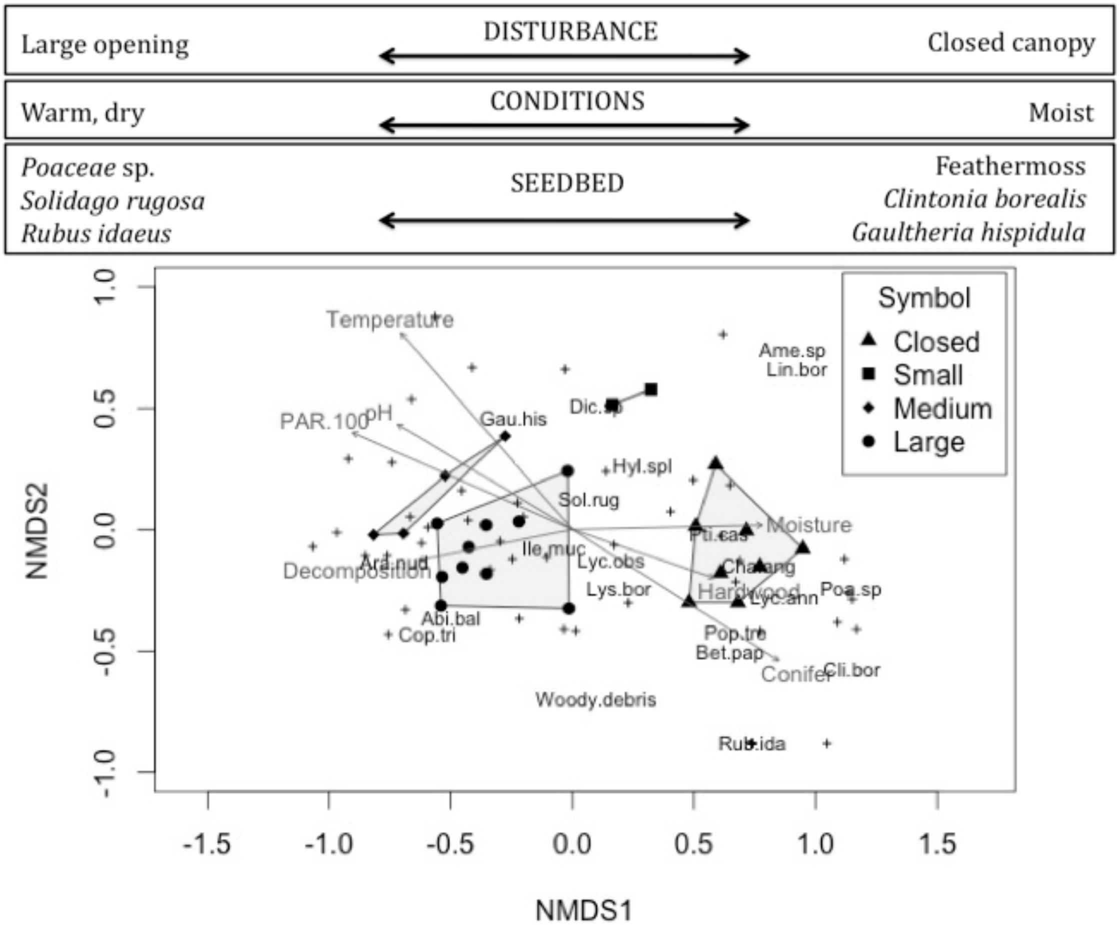
Figure 2.1



Disturbance type	Site	Disturbance size (ha)	# plots
No insect outbreak gap & moose	Blue Hill Closed Canopy (BHCC)	NA (40)[1]	8
Small insect outbreak & moose	Bread Cove Brook (BCB)	2.7 – 4.2	2
Medium insect outbreak & moose	Platter's Cove (PLC)	14.6	4
Large insect outbreak & moose	Blue Hill (BH)	52.3	10

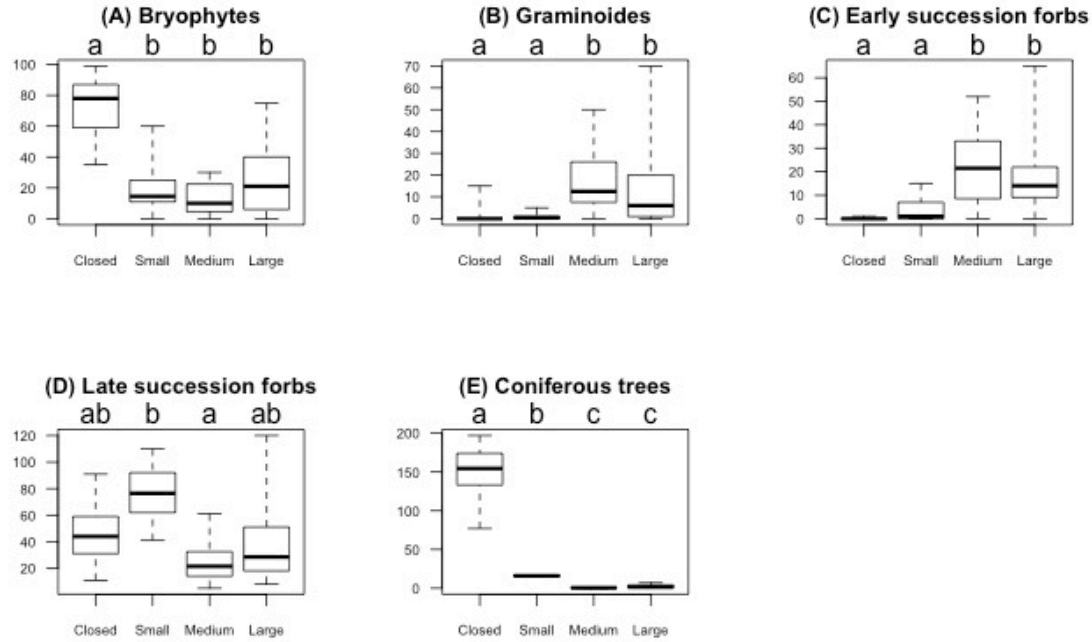
[1] Approximate area of the closed canopy stand

Figure 2.2



Large opening
DISTURBANCE
Closed canopy
Warm, dry
CONDITIONS
Moist
Poaceae sp.
Solidago rugosa
Rubus idaeus
SEEDBED
Feathermoss
Clintonia borealis
Gaultheria hispidula
Symbol
Closed
Small
Medium
Large
Temperature
PAR.100
pH
Gau.his
Dic.sp
Ame.sp
Lin.bor
Hyl.spl
Sol.rug
Moisture
Pti.cas
Ile.muc
Lyc.obs
Decomposition
Ara.nud
Cha.ang
Lys.bor
Hardwood
Lyc.ann
Poa.sp
Abi.bal
Cop.tri
Pop.tre
Bet.pap
Conifer
Cli.bor
Woody.debris
Rub.ida
NMDS2
NMDS1
1.0
0.5
0.0
-0.5
-1.0
-1.5
-1.0
-0.5
0.0
0.5
1.0
1.5

Figure 2.3


(A) Bryophytes
a b b b
Closed Small Medium Large
(B) Graminoides
a a b b
Closed Small Medium Large
(C) Early succession forbs
a a b b
Closed Small Medium Large
(D) Late succession forbs
ab b a ab
Closed Small Medium Large
(E) Coniferous trees
a b c c
Closed Small Medium Large

CHAPTER 3

3 SIMPLICITY IS THE KEY: RESTORATION PROTOCOLS FOR NON-REGENERATING FORESTS DEGRADED BY OVERABUNDANT HERBIVORES

3.1 Abstract

Global forests are being degraded at an alarming rate; hence ecological restoration becomes an integral component, ensuring future forest health. Beneficial effects of restoration will arise from scientifically based practices within an adaptive management framework. On the island of Newfoundland, moose (*Alces alces*) have become overabundant since their introduction in early 1900's causing regeneration failure. Intensive moose selective browsing on foundation species such as balsam fir (*Abies balsamea*) has limited advanced forest regeneration, creating "spruce-moose meadows". Experimental restoration was implemented in the boreal forest of Terra Nova National Park (Newfoundland, Canada), along a gradient of disturbance from closed canopy forest to large insect-disturbed stands. Seedling planting was carried out under various ground preparation treatments (field planting, aboveground suppression, scarification) and planting densities (5,000 and 20,000 seedlings/ha). Seedlings success (survival, growth and browsing intensity) was monitored and mixed-effects models were constructed to determine seedling responses. Results show minimal effects of ground treatments and planting density along the gradient of disturbance; environmental conditions and seedling individual traits explained most of seedling responses. Considering that no substantial

benefits were detected following ground treatments that are costly to implement in terms of human and financial resources, active restoration in boreal forest can be implemented using standard field planting protocols, without any ground preparation, independently of the forest degradation state.

3.2 Introduction

Global forests are being degraded at an increasing rate, with a documented net loss of 1.5 million km^2 over a period of 12 years (Hansen *et al.*, 2013); hence ecological restoration becomes an integral component to ensure future forest health, biodiversity conservation and community livelihood (Lamb *et al.*, 2005; Chazdon, 2008; Lamb, 2015). For example, in North-western Vietnam, the degradation of limestone forests following fuelwood and timber extraction in the Phuc Sen communities between 1960's and 1970's has led to protection and planting of indigenous trees, recovering lost biodiversity and spring water flow (Poffenberger, 2006). The importance of implementing restoration efforts with specific conservation goals to overcome failed regeneration is integral to uphold stated ecological integrity targets within protected areas (Parks Canada, 2008; Keenleyside *et al.*, 2012; Wiens and Hobbs, 2015). Given the challenges faced by protected areas, such as external pressure, surrounding landscape and species diversity representation, the use of restoration techniques is justify to conserve ecosystem integrity (Rodrigues *et al.*, 2004; DeFries *et al.*, 2005; Gaston *et al.*, 2008; Leroux and Kerr, 2013). To ensure restoration success, consideration must be given to ecological, social and financial aspects at the planning stage (Hobbs *et al.*, 2014). For instance, Palmer *et al.* (2014) found that of 644 river projects considered, a large proportion failed to reach their restoration goals mainly because of techniques focusing on channel design, which do not consider broader ecological processes, such as productivity or nutrient cycling. Therefore, experimentation within an adaptive management framework to select the most effective restoration protocol will best foster restoration success.

Forests around the world are home to a high diversity and abundance of herbivores. Where herbivore densities are high, they can create a new disturbance regime by selective browsing of preferred species, which may impede natural regeneration (McInnes *et al.*, 1992; Vourc'h *et al.*, 2001; Wardle *et al.*, 2001; Côté *et al.*, 2014). It is especially severe on islands where ungulates were introduced (e.g. Anticosti Island, Côté *et al.* (2014); Haida Gwaii, Vourc'h *et al.* (2001); Isle Royale, McInnes *et al.* (1992); Newfoundland, McLaren *et al.* (2004); New Zealand archipelago, Wardle *et al.* (2001)). Changes in environmental conditions in these degraded forests make passive recovery inadequate and active restoration a preferred solution (Yates *et al.*, 2000; Tremblay *et al.*, 2007; Gosse *et al.*, 2011; Hidding *et al.*, 2013; Côté *et al.*, 2014). On the island of Newfoundland (Canada) moose (*Alces alces*) were introduced in the early 1900's with their number increasing quickly (150,000 moose island-wide by 1960), degrading the boreal balsam fir (*Abies balsamea*) forest to the state of "spruce-moose meadows" in some areas (McLaren *et al.*, 2004; Gosse *et al.*, 2011). In an effort to lower browsing by overabundant moose and restore ecological integrity within their protected areas in Newfoundland, Parks Canada implemented a recreational moose hunt beginning in the fall of 2011. The licence quota for the protected areas is designed to decrease the moose density to that under natural levels of predation by wolf (*Canis lupus*), which was extirpated from the island in the early 1930's.

Seeding is often a solution used in restoration to assist natural regeneration (Whisenant, 1999); however in Newfoundland post-dispersal seed predation, seedling herbivory by various non-native species and shifts in environmental conditions impede balsam fir emergence (Noel, 2004; Gosse *et al.*, 2011), hence seedling stock is preferred to restore degraded areas. Previous restoration projects within balsam fir forests both in Québec and Newfoundland have examined how to optimize survival, growth and browsing occurrence of seedlings (Beguin *et al.*, 2009a; Beguin *et al.*, 2009b; Humber and Hermanutz, 2011; Faure-Lacroix *et al.*, 2013; Côté *et al.*, 2014). For example, results of Faure-Lacroix *et al.* (2013) show the key effect of seedling size, with medium size balsam fir (200cm^3 containers, ~25cm tall seedling) being the best compromise between surviving competition with other species and visibility to browsing.

Environmental conditions have also been documented as important factors affecting tree seedlings establishment success (Brooker *et al.*, 2006; Gómez-Aparicio *et al.*, 2008; Prévosto and Ripert, 2008; Prévosto *et al.*, 2010; Hibsher *et al.*, 2013; Palik *et al.*, 2015). To improve environmental conditions, ground preparation techniques such as scarification, mounding or subsoiling can positively influence ground conditions and density of competing vegetation (Löf *et al.*, 2012). All techniques affect ground structure by exposing mineral soil (scarification, mounding), mixing organic layer (scarification, mounding), creating elevated planting spots (mounding) and/or ripping compact surface layer (subsoiling; Löf *et al.*, 2012). Scarification can improve seedling survival by increasing soil moisture, temperature and nutrient availability, reducing compaction and controlling competing vegetation (Prévost, 1992; Löf *et al.*, 2012). In Mediterranean woodlands, Aleppo pine (*Pinus halepensis*) recruitment was enhanced by the soil decompaction that increased moisture and volume accessible to the root system in the ground, following scarification treatment (Prévosto and Ripert, 2008). However, aboveground vegetation removal did not improve pine recruitment (Prévosto and Ripert, 2008), but could be a good option for balsam fir, as it does not disrupt the moist seedbed, preferred over mineral soil (Frank, 1990) while reducing the competition of surrounding vegetation. As well, limiting competition for resources with the surrounding plant community, or other seedlings of the same species may be critical for successful seedlings planting (Bégin *et al.*, 2001; Wright *et al.*, 2014). Therefore, planting density is a crucial aspect that must balance financial constraint and restoration goals, by reducing cost and intraspecific competition, while ensuring sufficient seedlings to compensate for loss through browsing and interspecific competition. The target adult density needed to regenerate a closed canopy forest, based on similar boreal forests would be ~2,500 trees/ha (Tremblay *et al.*, 2007). Densities of 5,000 and 20,000 seedlings/ha were tested, which is greater than conventional forestry techniques. Considering that no seedlings avoid moose pressure remaining at < 1 m (Parks Canada, *unpubl.*), the densities were chosen to ensure the growth of a proportion of seedlings over moose browsing height.

As well, Hobbs *et al.* (2014) advocate for restoration planning at the landscape level, to more effectively use resources on the full spectrum of degraded ecosystems, and achieved multiple management goals. In this study we tested various restoration protocols in Terra Nova National Park (TNNP) with the target of re-establishing the foundation species, balsam fir. The forest landscape in TNNP is a mosaic of different disturbance intensities caused by insect disturbance, wind and moose browsing (Charron & Hermanutz, 2016). There is a gradient that includes: (1) closed canopy mature balsam fir forest, (2) small, (3) medium and (4) large canopy gaps created by spruce budworm (*Choristoneura fumiferana)* – hemlock looper (*Lambdina fiscellaria*) insect disturbance followed by windfall (Fig. 2.1; Chapter 2). Charron & Hermanutz (2016) found differences in plant community, light availability, soil chemistry and physical attributes along the disturbance gradient; therefore restoration was implemented across the disturbance gradient to evaluate the experimental planting and permit subsequent adaptive management. Two major responses were predicted based on previous work (Charron & Hermanutz, 2016), (1) passive, natural recovery would proceed in closed canopy and small gap stands, while, (2) active restoration would be needed in medium and large gaps areas.

The aim of the restoration in Terra Nova National Park is the re-establishment of closed canopy balsam fir forest stands complete with all the inherent ecosystem functions. To achieve this goal, balsam fir seedlings were experimentally planted across a disturbance gradient from closed canopy forest to large insect-disturbed stands. The objective of the study is to assess scientifically-sound procedures for the reestablishment of balsam fir in TNNP forests, by (1) evaluating the effect of various ground treatments on seedling success (survival, growth and browsing intensity): (i) aboveground vegetation removal and (ii) ground scarification; and (2) evaluating the effect of planting density on seedling success: (i) low density of 5,000 seedlings/ha and (ii) high density of 20,000 seedlings/ha. We hypothesized that: (1) an early response of the seedlings to the ground treatment, which will enhance early seedling establishment and growth, but will increase the visibility for browsing; and (2) a later effect of density after establishment, with denser planting expected to reduce the seedling survival, growth and increased browsing intensity by increasing intraspecific competition and herbivore attraction once the seedlings are large enough to potentially interfere with neighbors. Density effects are not anticipated for at least 5 years (Scott *et al.*, 1998); therefore minimal response after 2 years are expected. The outcomes of this study will contribute to best practices (ground treatment and density) to use for adaptive restoration across the disturbance gradient experienced in balsam fir forest of TNNP. This study will support broader conservation management initiatives such as lichen, mammal and bird conservation (e.g. *Erioderma pedicellatum*, Newfoundland pine marten [*Martes Americana atrata*] and Newfoundland red Crossbill [*Loxia curvirostra percna*]); all species that depend on closed-canopy forest and its resources. In addition, reinstatement of closed canopy forest will assist in minimizing the invasion of non-native plants such as Canada thistle (*Cirsium arvense*; Humber and Hermanutz, 2011)

3.3 Methods

3.3.1 Study Site

The experimental restoration was implemented in Terra Nova National Park (TNNP; 48°30'N, 54°00'W), a protected area of ~400km^2 located in Newfoundland, Canada. The climate is maritime with a mean temperature of -6.8°C and 16.1°C in January and July, respectively, and mean annual precipitation of 311.0 cm and 872.7 mm of snow and rain respectively (Environment Canada, 1971-2000). TNNP boreal forests are dominated by black spruce (*Picea mariana*) inland and coastal balsam fir forests. Balsam fir forest covers 15% of the park and is restricted to richer soil, predominantly humo-ferric podzols (Deichmann and Bradshaw, 1984). For a complete description of the environmental conditions at the restoration sites, see Charron and Hermanutz (2016).

3.3.2 Experimental design

Twenty-four plots of 24 m × 24 m were planted with balsam fir seedlings in July 2013. Between 251 and 1156 seedlings were planted per plot, a function of planting density (5,000 and 20,000 plant per ha) and terrain quality, for a total of 9,685 seedlings. Seedlings were 3-4 years old and were grown at Wooddale Provincial Tree Nursery (Newfoundland, Canada); to decrease moose attraction to the seedlings, fertilizer was only applied for the first two years of growth. Seeds were originally collected in Port Saunders, Newfoundland. Exceptionally, there was no precipitation in early July, and dead-by-drought seedlings were replaced (N=596) two weeks after planting. Survival and growth was assessed for these seedlings and the mortality estimates did not include the first set of seedlings that died due to transplant shock.

To assess seedling planting effort across the landscape, seedlings were planted at four different sites along a gradient of disturbance encompassing: (1) closed canopy mature balsam fir forest, (2) small, (3) medium and (4) large canopy gaps created by insect disturbance, which act as a baseline response. Within medium and large canopy gaps sites, plots were located at the centre and the edge of the opening, but analysis found no difference in environmental conditions and seedling success, and therefore, location (centre/edge) were pooled and not considered as a variable in the analyses (Table 6.1).

The ground and density treatments were established at the two extreme conditions of the disturbance gradient (closed canopy and large opening) because of limited resources. We used closed canopy forest as a control because environmental conditions were similar to undisturbed balsam fir forest, and passive natural regeneration was expected to allow recovery following moose population decrease. Prior to seedling planting (June 2013), three different ground treatments were applied: (1) Control, no ground treatment, (2) Aboveground treatment, cutting aboveground plant biomass over 10cm high, and (3) Soil scarification, combined with aboveground plant removal prior to scarification. At the location of each seedling, the soil was scarified with a Pulaski axe ~15cm belowground and ~30cm radius around the seedling. Two different densities were used: (1) low density of 5,000 and (2) high density of 20,000 seedlings per ha. It was not a fully factorial design, with no interaction between ground treatment and densities. All combinations of Site/Treatment/Density were replicated at least twice (Table 3.1). At the small and medium gaps sites, all seedlings were planted using the control ground treatment (i.e. no intervention) and the low density, acting as a baseline response throughout the landscape.

3.3.2.1 Plant community

In TNNP, plant community is highly correlated with environmental conditions, and is therefore a good proxy of environmental conditions (Charron & Hermanutz, 2016). For each restoration plot, percentage cover of all species < 2 m was estimated to the nearest 5% in 5 × 1m^2 quadrats located equally along a diagonal transect running between two opposite corners (4 sites, 24 plots × 5 quadrat; n=120). Grass species were grouped to family level (*Poaceae*), and rare or unidentifiable species at time of survey (e.g. species that were not flowering) were identified to the genus. The presence of palatable species (e.g. *Viburnum nudum*, *Betula papyrifera, Taxus canadensis* and *Cornus stolonifera*) within 50 cm of the seedling was recorded, following Tanner and Leroux (2015) and Pimlott (1953).

3.3.2.2 Individual seedling traits

Individual seedlings were surveyed after the first growing season (October 2013), after winter (May 2014) and after the second growing season (October 2014). Seedling success was defined by survival, growth and browsing intensity at each survey date. Survival was recorded as a binomial variable, a seedling being either alive or dead. If the seedling was dead, the probable cause of death was recorded (drought, herbivore (moose, hare [*Lepus americanus*]), or unknown). Growth traits recorded were: total height, new growth length of the terminal leader, basal diameter, and number of buds on the terminal leader. Total height was measured from the ground to the tip of the leader. New growth was measured from the last year bud scar to the tip of the leading branch, excluding buds. Basal diameter was measured with a caliper at the root collar. In addition, the initial number of branches and, for more complex tree structure, the initial number of possible leader branches was recorded. Browsing was recorded as a binomial variable, either present or absent, with no differentiation between old and new browse event and the browser (moose or hare) was also recorded.

3.3.3 Statistical Analysis

3.3.3.1 Plant community

For modeling purposes, each species percentage cover was summarized using ordination techniques on the understory vegetation survey data, and ordination scores used as proxy of environmental conditions. Principal component analysis (PCA) was performed using the "rda" function of the Vegan package. To ensure adequate data redundancy (Peck, 2010), mosses were pooled by genus for analysis, which did not affect the results, as the dominant mosses were monospecific. However, considering non-linearity condition and a zero-rich dataset, the same dataset was analyzed with the "metaMDS" (Non-metric multidimensional scaling analysis; NMDS) and a procrustean analysis was performed to ensure consistent result. The procrustean superimposition approach overlays two ordination solutions, rotates and scales them to optimize their fit (Jackson, 1995). In addition, a permutation procedure was done to evaluate the significance of the fit (Jackson, 1995; Peres-Neto and Jackson, 2001). The procrustean superimposition analysis was performed with the function “procrustes” and significance was tested with the “protest” function in R.

3.3.3.2 Seedling success modeling

To test the effects of the various restoration treatments on seedling success, we constructed mixed-models with plot as a random effect (n=2 or 4; Table 3.1), accounting for spatial autocorrelation. We used logistic regression with seedling survival and browsing intensity on the living seedlings as our response variables and linear models with new growth length, basal diameter and number of buds as our response variables to predict seedling success according to uncorrelated covariates: PCA scores, presence of palatable species in the area surrounding the seedling, initial seedling height and number of leading branches, planting density and ground treatment (Table 6.2). For each model, correlation coefficients between explanatory variables were $0.4< r >-0.4$, signifying there were no significant correlations between any treatment and the plant community (PCA scores and palatable species presence). To extract the effect of each treatment, models were sequentially constructed by ordering the covariates, with the restoration treatment as the last model covariate ((1) plant community, (2) individual seedling traits and, finally, (3) treatment). All plots were used, even with the absence of ground treatment and varying planting density in the small and medium insect opening (Table 3.1) because using all plots allowed the best resolution possible of seedling success under the controlled conditions of field planting at low density, along the entire disturbance gradient. Models were constructed using the functions “glmer” (logistic regression) and “lmer” (linear mixed-models) of the “lme4” packages. Confidence intervals (CI 95%) were computed for the treatments coefficient estimates, and significance level was set such that the CI did not overlap 0.

To evaluate the importance of plant community and individual traits on seedling success, we performed model selection on a constant set of candidate models (Table 6.3) and determined the models with most of the evidence based on Akaike's information criterion (AIC). Marginal and conditional goodness-of-fit (R^2) was computed following the procedure of Nakagawa *et al.* (2013). Models with pretending variables were eliminated from the AIC selection routine. Summary of the best predictive models allowed us to determine the important covariate(s) affecting seedling success.

3.4 Results

3.4.1 Plant community

The principal component analysis (PCA) on the understory plant community was explained by the first two axes (53.3% and 21.1% variance explained, respectively). The procrustean superimposition of the PCA and NMDS ordination techniques gave a high fit (m_{12} = 0.2517, p-value= 0.001) and therefore PCA scores can be used with confidence. The first axis represents a gradient from early succession communities, adapted to open, warm and dry conditions, to a shade tolerant and moist adapted communities, while the second axis show a gradient from communities with deciduous species, to coniferous and feathermoss dominated communities. PCA results and all axis scores for the two axes are included in Appendix II (Figure 6.1 and Table 6.4).

3.4.2 Seedling success

Seedling survival was very high after the first two growing seasons (90.5%; Table 3.2), with < 2% (75) of the seedlings not found during the survey. Cause of death was mainly attributed to drought (6.1%), with small loss to moose browsing (3.2%) and other causes (0.2%; Table 3.2). Growth measured as number of buds, new growth and basal diameter increment, was dependant on the year, with better growth in 2013 than 2014 (Table 3.2). Browsing appears to be minimal; of the surviving seedlings (6,645), 5% were browsed in October 2014, all by moose, except one occurrence of hare browsing and one unknown cause. Closed canopy stands had better survival and statistically fewer browsing occurrences, but statistically less growth compared to the insect disturbed areas (Table 3.2).

3.4.3 Effect of treatment on seedling success

The impact of the restoration treatments was minimal, with only the scarification treatment and, to a lesser measure, the density treatment showing statistically significant effects, compared to the control conditions of field planting at low density. Contrary to prediction, the sequentially constructed mixed model shows that soil scarification diminished the seedling's survival after the first growing season (CI95%: -1.94, -0.49; Figure 3.1). However, the effect of scarification was dependent on the environmental conditions, and a marginally better survival than the control treatment was seen in the closed canopy site that has preserved the environmental conditions of a mature balsam fir forest (scarification: 98% vs. control: 95%, by October 2014; Figure 3.2). In the open deforested area, a negative effect was experienced by seedlings (scarification: 82% vs. control: 86%, by October 2014; Figure 3.2). After the second growing season, scarification treatment did not affect survival, but difference from the first growing year were still present (Figure 3.2). Growth measures (length of the new terminal growth, number of buds on the leader and basal diameter) increased marginally with the scarification treatment after the second growing season (control: 1.1cm, 2.0 buds, 0.6mm; scarification: 1.7 cm, 2.2 buds, 0.8, respectively; Figure 3.1). In terms of the density treatment, the only significant effect seen was basal diameter increment, where seedlings planted in high-density plots had significantly lower basal diameters (CI95%: -0.58 – 0.014) after the second growing season. No other effects of density were observed. No effect of the aboveground treatment was seen on the seedling success. As well, browsing was not affected by any experimental restoration treatment.

3.4.4 Selection of predictive models for seedling success

Since the impacts of the active restoration treatments tested were minimal, individual seedlings traits and the plant community (PCA score and presence of palatable species) were examined to predict seedling success using AIC selection. Top models for each seedling success attributes (growth, survival, browsing) and season are summarized in Table 3.3. The relative importance of individual seedling traits and plant community varied as a function of the response variable and time since planting (Fig. 3.3, Table 3.3). Individual seedlings traits mainly explained the growth pattern after the first growing season (new growth R^2: 7.1%, number of buds R^2: 16.2), with taller seedlings at planting having a greater new growth and more buds. As well, seedlings with one leading branch had a shorter new growth, but more buds, compare with two or more leading branches seedlings (1 leader: 4.81cm growth and 2.98 buds; ≥2 leaders: 4.89cm growth and 2.60 buds). However, smaller seedlings with more leading branches had a better survival following the first growing season, than taller seedlings with only one leader.

Plant community (PCA score and palatable species presence) was mainly driving the second growing season growth (new growth R^2: 11.8%, number of buds R^2: 24.3 and basal diameter R^2: 19.7%). Seedlings planted under closed canopies and in moist environments, and close to palatable species had a better survival than those planted in open and dry areas, but the latter seedlings grew better, with greater new growth, more buds and thicker basal diameter

(Table 3.2). For the seedlings that were still alive after the second growing season, the chance of being browsed was explained by the environmental conditions and the individual traits (initial height) of the seedling (R^2: 29.8% and 11.1%, respectively), with taller seedlings growing in open and dry environments having a higher incidence of browsing. Therefore, better growth, lower survival and higher browsing intensity were observed with increasing forest disturbance.

3.5 Discussion

Ecological restoration is becoming a key part of forest health and conservation; however to be effective, it must be based on scientifically-sound protocols. Seedlings were planted under different ground treatments and densities to enhance their success and establish the optimal planting density. Our study showed that although statistically significant, no biologically significant impacts of ground and density interventions influenced seedling success; after two growing seasons, there was no increase in survival or growth or a reduction in browsing pressure. Contrary to our hypothesis, ground treatments did not have a consistent positive effect on seedling success, especially in focal restoration areas that had undergone significant degradation. As expected, no density-dependent effects were documented on seedling success, but longer-term monitoring is needed to confirm our preliminary findings.

Considering the cost in both financial and human resources needed to implemented ground restoration treatments, (scarification: ~$325/ha, planting: ~$450/ha; hence upwards of ~$775/ha; costs in Newfoundland; S. Avery, *pers. comm.*) it seems most cost efficient to limit invasive treatments such as scarification, and simply plant seedlings into the surrounding communities using the standard forestry tree planting protocols. As well, for restoration efforts within protected areas, limiting the human impact created by ground treatment is advantageous and may limit non-native plant invasions. Despite the interaction between the environment and ground treatment; with (1) improved growth, but lower survival in degraded areas, and (2) improved growth and survival in closed canopy forest, amelioration provided by the ground treatments were limited; hence the recommendation of using the control treatment of field planting.

Therefore, based on the results of the first two years, restoration of balsam fir forest can be implemented using field planting in the Park, independently of the past disturbance regime.

Despite observed ground physical improvement and successful revegetation, especially in Mediterranean dry sites and for broadleaves species Löf *et al.* (2012), the ground treatment did not have the expected positive effect on the success of our seedlings. Moreover, soil scarification resulted in lower survival in open and degraded areas; the highest priority stands for the ecological restoration in TNNP (Charron & Hermanutz, 2016). Results are consistent with Beguin *et al.* (2009b), where scarification led to disturbed understory vegetation, soil desiccation and modified microclimate in a boreal forest. In the closed canopy forest, scarification did not have the negative effect seen in open and disturbed area, because of the moister conditions provided by the shaded forest and the thick feathermoss seedbed (Place, 1956; Côté and Bélanger, 1991; McLaren and Janke, 1996; Parent *et al.*, 2003). Aboveground removal treatment had no significant effect, compared to the control, showing that aboveground competition for light is not a limiting factor for the shade-tolerant balsam fir seedlings (Messier *et al.*, 1999; Duchesneau *et al.*, 2001). Moreover, it was noted that the aboveground removal treatment had a shorter-lasting effect than the scarification treatment on the suppression of the competing vegetation (Prévosto and Ripert, 2008), which was mostly dominated by herbaceous species in the open areas. Ground treatments did not affect the browsing intensity, despite the visibility of the seedlings. Moose preference for taller seedlings and/or effective moose reduction from the recreational hunting program could explain the low browsing occurrence (8.1%, compare to 97% browsing of < 60 cm seedlings (Gosse *et al.*, 2011)) and limited effect of vegetation protection (Brooker *et al.*, 2006; Gómez-Aparicio *et al.*, 2008).

As expected, on the short time scale of two growing seasons, density did not affect the seedling success. Continued monitoring of the experiment is needed to assess possible density dependent effects on future seedling success. However, it can be predicted that higher density will reduce survival and growth through intraspecific competition (Bégin *et al.*, 2001) and increased browsing proportion, as the seedlings are more apparent (Feeny, 1976). A better understanding of density relation to seedling survival will inform the minimal density of seedlings to plant and achieve an optimal adult stand density of 2,500 tree/ha (Tremblay *et al.*, 2007).

The main factors affecting seedlings success were related to seedling traits and the surrounding plant community. As demonstrated by Faure-Lacroix *et al.* (2013), taller seedling stock had higher survival and growth, but also increased browsing pressure. Restoration work should then favor taller seedlings to increase success; but planting older, larger seedlings would be a more expensive intervention, and is a trade-off that is project dependent and would need to be evaluated for each situation (Newton *et al.*, 1993; South and Mitchell, 1999). As well, the conditions in which seedlings are planted in the landscape affect their success. However, we found that growth of our fir seedlings after the first growing season was excellent, and differences may be masked by the good conditions experienced by the seedlings in the prior year spent in the nursery; hence continued monitoring is needed to evaluate this effect. Along the disturbance gradient, from closed canopy forest to large open areas, conditions spanned from moist and shaded, to warm, dry and open, affecting survival, growth and browsing occurrence of the seedlings. The highest priority stands for restoration are the medium and large open areas (Charron & Hermanutz, 2016), which experienced lower survival, higher growth and more browsing occurrence, than the other areas. Variable seedling responses, with more or less growth and survival, are observed across the landscape; hence varying the minimal planting density can be used in a cost-effective manner to reach the optimal forest stand stocking. For example, using the average survival curve (logarithmic function) for both areas (Fig. 3.2), the density to reach 2,500 trees/ha after 20 years would need to be 2,570 trees/ha in the closed canopy and 2,870 trees/ha in the disturbed large area.

The statistical models constructed to predict seedling success in function of restoration treatments, plant communities and individual traits have a high proportion of unexplained variation, underscoring the need for further research (highest marginal R^2: 0.36; Table 3.3). Sources of variations could be due to: (1) the genetic variation, only assessed indirectly through individual seedlings traits (Thomas *et al.*, 2014) and (2) the microhabitat heterogeneity, not represented by the large size of the plots (Ameztegui and Coll, 2015). Ameztegui and Coll (2015), found that seedling browsing intensity and mortality was partially explained by microhabitat factor, represented by the distance to shrubs. Future work could include experiment evaluating shrub nurse-based restoration, as it provides higher initial biodiversity and has been proven to enhance microhabitat quality and protection from herbivory (Brooker *et al.*, 2006; Gómez-Aparicio *et al.*, 2008; Anthelme *et al.*, 2014; Löf *et al.*, 2014). In terms of planting density for restoration, the experiment was not designed to establish early response; however further surveys and comparison with a broader range of densities will establish if density-dependent effect are seen on competition and browsing intensity, affecting seedlings success.

In conclusion, as moose negatively affect large tracts of forested areas, implementing effective active restoration strategies are crucial in reaching restoration targets. The experimental restoration tested in this study is part of an adaptive management framework showing that no significant improvement was provided by ground treatment. Planting seedlings following tested standard field planting protocols without further ground intervention is the recommended practice for balsam fir forests in Newfoundland. The short time scale of the study does not permit to recommend any planting density, but further survey in the future would elucidate this question.

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Table 3.1 – Experimental restoration planting protocols established in Terra Nova National Park (Newfoundland, Canada) in 2013. Controls were established in closed canopy, small, medium and large insect gaps, while treatments were only tested in Blue Hill Closed Canopy (BHCC) and Blue Hill (BH).

Table 3.2 – Summary of balsam fir seedling success during two growing season along a gradient of disturbance (closed canopy, small, medium and large insect gaps) in Terra Nova National Park. Values correspond to mean ± SD.

Table 3.3 – Model selection results on a constant set of candidate models (Table 6.3). Vegetation (Veg) refers to the first and second PCA axis score and the presence of palatable species; individual traits (Ind) refer to height and number of leading branches at planting; ground (Gr) refers to ground treatment; and density (Den) refers to planting density.

Figure 3.1 – Coefficient confidence intervals (95%) for the ground treatment compare to control planting (AGC: aboveground removal, SCA: scarification); on (A) basal diameter, (B) new growth, and (C) number of buds after the second growing season. Coefficients come from sequentially constructed models: Y~ Vegetation + Individual + Ground. Significant effect for CI95% that does not overlap 0 (dotted line).

Figure 3.2 – Survival curves of balsam fir seedlings after two growing season in Terra Nova National Park (Newfoundland, Canada). Each site is identified by line (dashed: BH = large insect gap, dotted; BHCC = closed canopy mature forest) and each ground treatment by a symbol (●: control; ■: aboveground cut; ▲: scarification). The average survival curve equation (logarithmic) for BH is $y = -4.32\ln(x) + 100$ (R^2 : 0.87) and for BHCC is $y = -0.911\ln(x) + 100$ (R^2: 0.70).

Figure 3.3 – Coefficient confidence intervals (95%) for all variables under studies; P1: PCA axis 1; P2: PCA axis 2; Psp: presence of palatable species; H: height at planting; L1/2: Presence of 1/2 leader(s) compare to >2 leaders; Agc: Aboveground cut treatment; Sca: Scarification; D: High density. Coefficients come from sequentially constructed models: Y~ Vegetation + Individual + Ground +Density. Significant effect for CI95% that does not overlap 0 (dotted line).

Table 3.1 – Experimental restoration planting protocols established in Terra Nova National Park (Newfoundland, Canada) in 2013. Controls were established in closed canopy, small, medium and large insect gaps, while treatments were only tested in Blue Hill Closed Canopy (BHCC) and Blue Hill (BH).

Site[1]	**Ground Treatment**	**Density** (seedlings/ha)	**Number of plot replicates**	**Number of planted seedlings**
BHCC	Control	5,000	2	512
		20,000	2	2312
	Aboveground cut	5,000	2	512
	Scarification	5,000	2	512
BCB	Control	5,000	2	508
PLC	Control	5,000	4[2]	1024
BH	Control	5,000	4[2]	1016
		20,000	2	2266
	Aboveground cut	5,000	2	511
	Scarification	5,000	2	512

[1] BHCC = Blue Hill Closed Canopy = closed canopy mature forest;
BCB = Bread Cove Brook = small insect gap;
PLC = Platter's Cove = medium insect gap;
BH = Blue Hill = large insect gap
[2] Edge and center plots are pooled and give 4 replicates

Table 3.2 – Summary of balsam fir seedling success during two growing season along a gradient of disturbance (closed canopy, small, medium and large insect gaps) in Terra Nova National Park. Values correspond to mean ± SD.

	Overall	Closed	Small opening	Medium opening	Large opening
Number surveyed[1]	7316	2692	461	1024	3139
Proportion dead (%):	9.5	3.6	11.9	10.7	13.8
Drought	6.1	2.4	7.8	4.8	9.4
Moose	3.2	1.2	3.4	5.6	4.2
Other (hare, unknown)	0.2	> 0 [2]	0.7	0.3	0.2
Proportion browsed (%)[3]:	8.1	2.0	14.3	15.7	9.8
New growth increment (cm):					
2013	4.8 ± 2.5	4.7 ± 2.4	4.7 ± 2.4	4.9 ± 2.7	4.9 ± 2.5
2014	1.2 ± 1.5	0.6 ± 1.0	0.8 ± 1.0	2.1 ± 1.8	1.5 ± 1.6
Basal diameter increment (mm):					
2014	0.63 ± 0.73	0.24 ± 0.61	0.61 ± 0.70	1.13 ± 0.65	0.85 ± 0.68
Number of leader buds:					
2013	2.9 ± 1.0	2.9 ± 1.0	3.0 ± 1.0	3.1 ± 0.9	2.9 ± 1.0
2014	2.0 ± 1.0	1.4 ± 0.7	1.7 ± 0.8	2.6 ± 0.8	2.5 ± 0.9

[1] Not all surveyed seedlings were found during the course of the study
[2] Only 1 hare browsing occurrence
[3] All occurrences of browsing were caused by moose, except 2 occurrences in the closed canopy site which were caused by hare (1) and unknown (1) cause

Table 3.3 – Model selection results on a constant set of candidate models (Table 6.3). Vegetation (Veg) refers to the first and second PCA axis score and the presence of palatable species; individual traits (Ind) refer to height and number of leading branches at planting; ground (Gr) refers to ground treatment; and density (Den) refers to planting density.

Variable	Date	Model	K	AICc	Delta AICc	AICc weight	Log Likelihood	Marginal R^2	Conditional R^2
Survival	October 2013	Veg+Gr	7	1469.11	0.00	0.89	-727.55	0.23	0.28
		Veg	5	1473.36	4.25	0.11	-731.68	0.19	0.29
	May 2014	Veg+Ind	8	2960.08	0.00	1.00	-1472.03	0.23	0.27
	October 2014	Veg+Ind	8	4186.05	0.00	1.00	-2085.01	0.16	0.21
Browsing	October 2014	Veg+Ind	8	2293.74	0.00	1.00	-1138.86	0.36	0.45
New growth	May 2014	Ind+Gr	8	31448.88	0.00	0.48	-15716.43	0.07	0.09
		Veg+Ind	9	31449.47	0.59	0.36	-15715.72	0.07	0.09
		Ind	6	31451.00	2.12	0.17	-15719.49	0.07	0.09
	October 2014	Veg+Ind+Gr	11	22367.07	0.00	0.98	-11172.52	0.18	0.26
Basal diameter	October 2014	Veg+Den	7	804.59	0.00	0.52	-395.16	0.23	0.33
		Veg+Gr	8	805.71	1.12	0.29	-394.68	0.23	0.33
		Veg	6	806.58	1.99	0.19	-397.19	0.20	0.32
Buds	October 2013	Veg+Ind	9	18710.20	0.00	0.87	-9346.09	0.16	0.17
		Ind	6	18713.95	3.75	0.13	-9350.97	0.16	0.17
	October 2014	Veg+Ind+Gr	11	15703.95	0.00	1.00	-7840.95	0.29	0.34

Figure 3.1

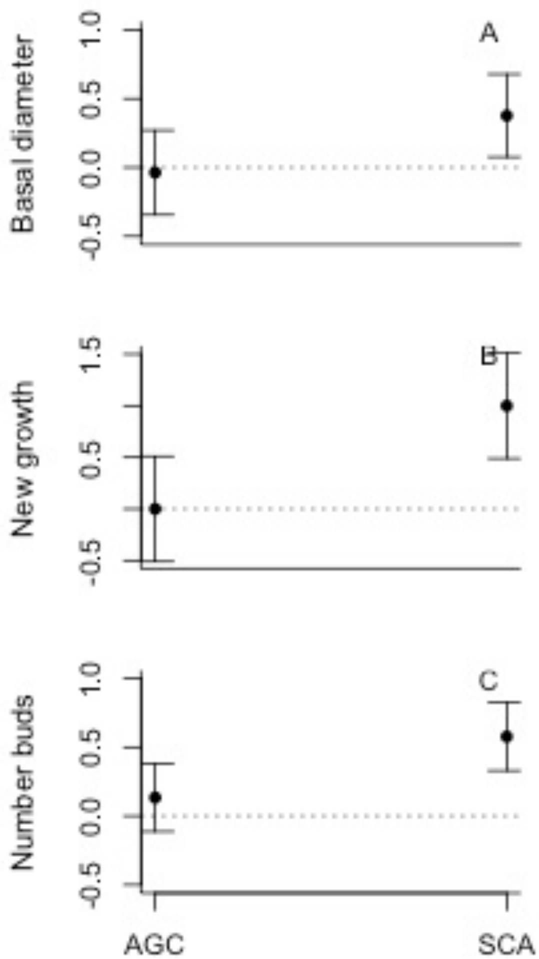
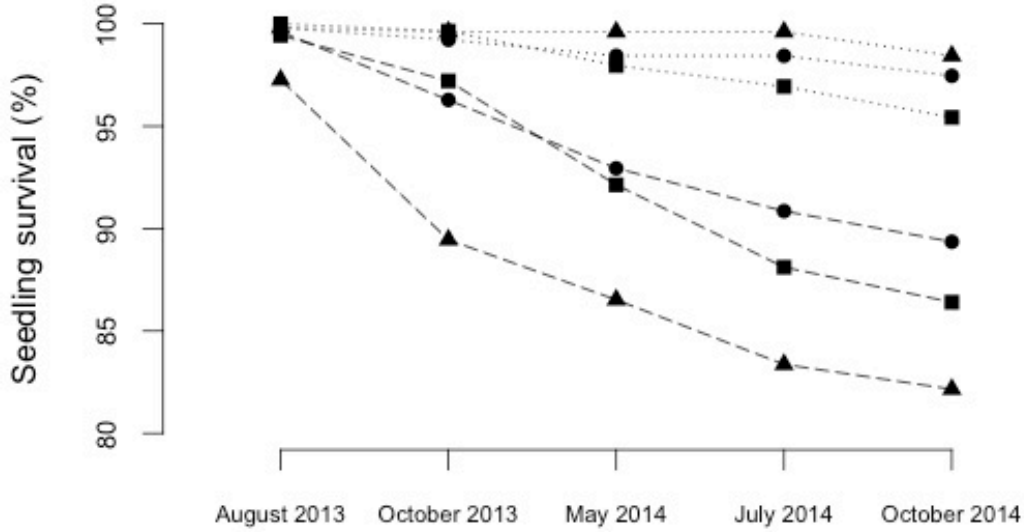
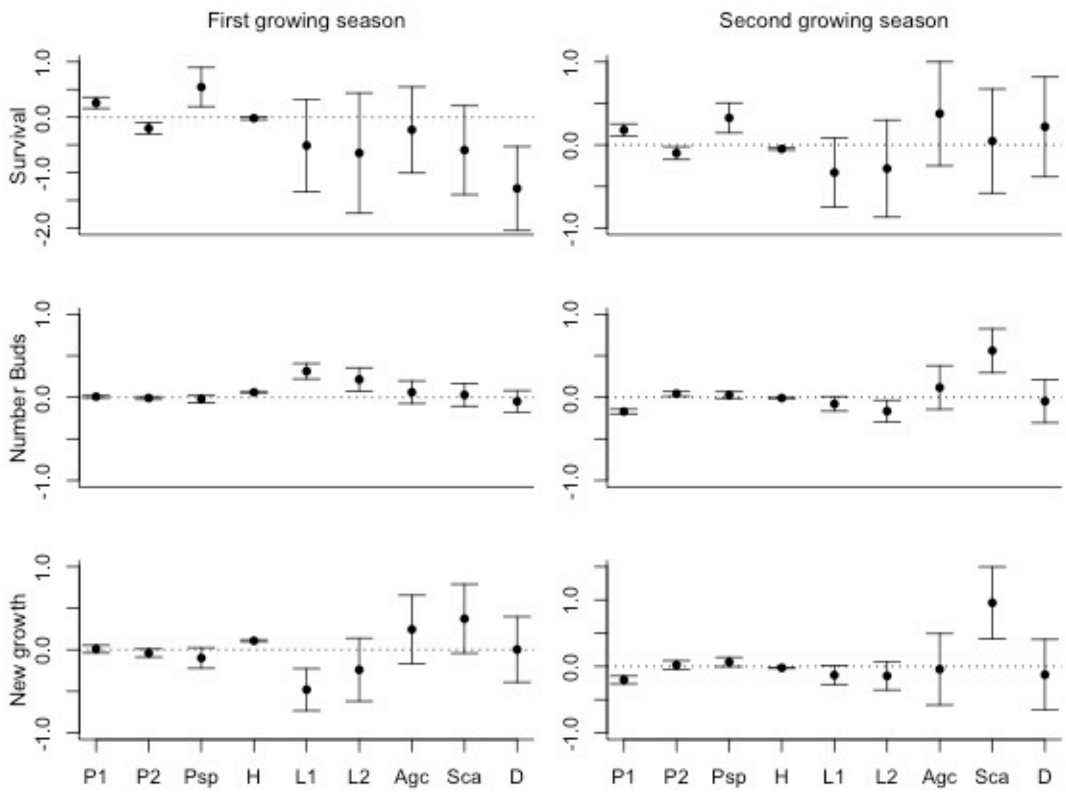

A
B
C
Basal diameter
New growth
Number buds
1.0
0.5
0.0
-0.5
1.5
0.5
-0.5
1.0
0.5
0.0
-0.5
AGC
SCA

Figure 3.2



Seedling survival (%)
100
95
90
85
80
August 2013
October 2013
May 2014
July 2014
October 2014

Figure 3.3


First growing season
Second growing season
Survival
Number Buds
New growth
1.0
0.0
-1.0
-2.0
P1
P2
Psp
H
L1
L2
Agc
Sca
D

CHAPTER 4

4 SUMMARY AND CONCLUSIONS

Forest area is declining at an increasing rate (Hansen *et al.*, 2013), which emphasizes the importance of ecological restoration as a key part of forest health and conservation. To be successful in the long-term, restoration effort must be efficient and effective, and based on scientifically sound protocols. Here, restoration of over-browsed balsam fir forests was investigated, focusing on the *where* and *how* restoration should be implemented to achieve future multi-aged balsam fir forests in Newfoundland. Like many other islands around the globe, the introduction of large herbivores, specifically moose in Newfoundland, has created a new disturbance (McInnes *et al.*, 1992; Vourc'h *et al.*, 2001; Wardle *et al.*, 2001; McLaren *et al.*, 2004; Côté *et al.*, 2014). Selective browsing of palatable species has modified the forest, creating spruce-moose meadows in some areas of the island (McLaren *et al.*, 2004; Gosse *et al.*, 2011). Considering that large tracts of forest have been negatively affected, long-term successful restoration will only be attained if it is implemented efficiently and effectively, and based on tested protocols. In the present study, the efficiency and effectiveness of balsam fir forest restoration was approached by: (1) determining *where* restoration should be prioritized on the landscape (Chapter 2), and (2) experimentally testing *how* to best carry out active restoration, based on the findings of (1) (Chapter 3).

Efficient restoration is ensured by limiting active restoration efforts to areas where environmental conditions have exceeded an ecological threshold preventing natural regeneration. In Terra Nova National Park (TNNP), priority should be given to areas > 5 ha that were naturally disturbed by insect (spruce budworm [*Choristoneura fumiferana*] and hemlock looper [*Lambdina fiscellaria*]) (Chapter 2). Areas > 5 ha were shown to have crossed an ecological threshold with significant environmental changes such that once the disturbance, over-browsing by moose, had been removed, it did not follow a natural regeneration trajectory (McLaren *et al.*, 2009). Plant communities had shifted towards early succession, light tolerant and competitive grasses and forbs, compared to shade-tolerant late succession forbs and seed-bearing adult balsam fir in areas < 5 ha. The feathermoss seedbed, optimal for balsam fir establishment, was limited, replaced by suboptimal leaf litter in the > 5 ha disturbed areas (Place, 1956; Côté and Bélanger, 1991). Moreover, abiotic conditions of the closed canopy forest (moist, shade, etc.) were replaced by warmer, drier and compacted soil without canopy cover in > 5 ha disturbed areas, such that disturbed areas > 5 ha have environmental conditions that create barriers for balsam fir establishment (Davies, 1987) and lack adequate seed rain (Noel, 2004), a critical aspect, given that balsam fir seed viability is < 9 months (Greene *et al.*, 1999). Therefore, the novel conditions experienced does not allow natural recovery, contrary to the < 5 ha insect-disturbed areas, which could regenerate naturally without intervention.

Our findings enable land managers to efficiently and effectively address landscape level restoration by focusing active restoration on heavily degraded areas both within TNNP and across the island of Newfoundland. More broadly, it underscores how disturbance regime can identify ecological thresholds, generating priorities for restoration. As well, implementing restoration strategies based on disturbance regime will create a heterogeneous landscape, as balsam fir forest reestablishment will follow different trajectories with various regeneration speeds, between active (e.g. seedling planting) and passive restoration (natural recovery) (Benayas *et al.*, 2008; Holl and Aide, 2011).

Effective restoration is ensured by testing scientifically based protocols and allowing adaptive management following experimentation results (Cummings *et al.*, 2005; Palmer *et al.*, 2014). In TNNP, active restoration was implemented by planting seedlings. The herbivory by various non-native species and the deep shift in environmental conditions is expected to impede balsam fir emergence, hence seedling stock is preferred (Noel, 2004; Gosse *et al.*, 2011). I tested if environmental conditions would be improved by ground treatments (aboveground suppression and scarification), as well as different planting densities (5,000 and 20,000 seedlings/ha) to assess the minimal density required to establish a closed canopy forest. I found that standard field planting protocols (i.e. just planting seedlings in the ground) were optimal for all areas (Chapter 3). Ground treatment (aboveground suppression and scarification) had disturbance-dependent effects; with (1) improved growth, but compromised survival in degraded areas, and (2) improved growth and survival in closed canopy forest. Although there was a slight increase in survival in the closed canopy forest and growth in all areas, it came at a price – decreased survival in degraded areas and higher financial cost; hence the recommendation of using standard field planting protocol.

The short time span of the research did not allow the evaluation of density dependent effects on seedling growth, survival and browsing prevalence; continued monitoring will be necessary to determine which density is optimal to generate a functioning closed canopy forest. Individual seedling traits such as total height, and plant community were the two aspects that explained most of the variation in seedling success, underscoring the importance of selecting appropriate seedling stock and planting of according to environmental conditions.

The findings are included within an adaptive management framework, adjusting active restoration practices based on experimental restoration methodology. Scientifically based restoration protocols had never been developed previously for moose-impacted boreal forest, an important component for the preservation of ecological integrity in the protected areas that Parks Canada manages in Eastern Canada. As well, the findings show that standard field planting, the simplest practice tested, is the optimal method to use. It has a dual positive effect by (1) reducing the time and cost associated with active restoration, and (2) limiting the human impact on the landscape created by ground treatment implementation (aboveground cut and scarification). On a global scale, scarification treatment can enhance ground conditions, benefiting planted tree stock (Löf *et al.*, 2012). However, research in the boreal forest does not always confirm this trend (Prévost, 1992; Beguin *et al.*, 2009). My outcomes were consistent with these boreal forest studies.

The mandate of Parks Canada is to preserve ecological integrity within their protected areas. For TNNP balsam fir forest, it means the reestablishment of multi-aged stands throughout the landscape. Multi-aged forests are the habitat of many native boreal species and of various species at risk, such as the Newfoundland marten, the red crossbill and the boreal felt lichen. Since the island of Newfoundland is experiencing pressure from the introduction of many non-native species, ensuring native habitat is a key part in preserving the native biodiversity of the island.

4.1 RECOMMENDATIONS

Based on the findings of this research project, I recommend the following to land managers, both within and outside of protected areas that have been overbrowsed by herbivores:

- Efficient restoration can be achieved by prioritizing active restoration practices to areas disturbed by insect on > 5 ha.
- Natural regeneration can operate in the closed canopy forest and areas < 5 ha.
- Dual restoration effort (passive-active) will generate a heterogeneous landscape of balsam fir stands at different stage and speed of recovery, optimal for a range of native species.
- Effective restoration of balsam fir forest can be achieved by planting seedlings following standard field planting protocols.
- The short time scale of the study did not permit to recommend any planting density, but future monitoring of the density experiment should elucidate this question.
- The experimental restoration tested in this study is encompassed in the adaptive management framework, informing best restoration practices based on scientifically sound protocols.
- Individual seedlings traits and environmental conditions have an important effect on the success of planted seedlings for restoration. Future restoration effort would benefit from experimentation examining seedling genetic stock, microhabitat conditions and nurse-based restoration practices.

4.2 REFERENCES

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5 APPENDIX I: Chapter 2 Method and Results

Table 5.1 – Distribution of natural tree species regeneration across the study sites of Terra Nova National Park, Newfoundland, Canada (mean percentage ± SE). Values are based on 5 x $1m^2$ quadrats per plots, except for tree density, which was measured within the entire plot. Seedlings are considered < 50 cm, saplings 50-200 cm and tree > 200 cm tall. Proportion browsed is calculated for the seedlings and saplings classes.

Table 5.2 – *Poaceae* species cover across the study sites of Terra Nova National Park, Newfoundland, Canada.

Table 5.3 – Species identified to the genus level across the study sites of Terra Nova National Park, Newfoundland, Canada.

Table 5.4 – Distribution of feathermoss species across the study sites within Terra Nova National Park, Newfoundland, Canada (mean percentage ± SE).

Table 5.5 – Correlation coefficient (r-value) with NMDS ordination axes, goodness of fit statistic (R^2) and p-values for each environmental variable. R-values indicate strength and direction of linear correlations between variables and NMDS axes. Codes in parenthesis are provided for the variables plotted in Figure 2.2.

Table 5.6 – Pearson's product-moment correlation coefficient (r-value) of vegetation variables with NMDS ordination axes. R-values indicate strength and direction of linear correlations between variables and NMDS axes. Bold values indicate significance at $p<0.05$[1]. Species codes

are provided in parenthesis after species name for those with significant correlation coefficient plotted in Figure 2.2.

Table 5.7 – Summary of F-values and p-values for the nested analysis of variance on the various species functional groups in relation to the disturbance gradient in Terra Nova National Park, Newfoundland, Canada. Bold values indicate significant p-value (0.05).

Table 5.8 – Summary of F-values and p-values for the nested analysis of variance on the environmental variables in relation to the disturbance gradient in Terra Nova National Park, Newfoundland, Canada. Bold values indicate significant p-value (0.05).

Figure 5.1 – Pictures of three sites along the gradient of disturbance: (A) closed canopy forest, Blue Hill closed canopy (BHCC); (B) small insect opening, Bread Cove Brook (BCB); and (C) large insect opening, Blue Hill (BH) in Terra Nova National Park, Newfoundland, Canada.

Figure 5.2 – Functional group cover distribution for a disturbance gradient in Terra Nova National Park, Newfoundland, Canada. Panels A-E show percentage cover of the functional groups and panel F shows the number of trees per plot. The box and whiskers show the extent of the data, with indication of the upper and lower quartile, and median (bold line). Functional groups after Cornelissen *et al.* (2003).

Table 5.1 – Distribution of natural tree species regeneration across the study sites of Terra Nova National Park, Newfoundland, Canada (mean percentage ± SE). Values are based on 5 x $1 m^2$ quadrats per plots, except for tree density, which was measured within the entire plot. Seedlings are considered < 50 cm, saplings 50-200 cm and tree > 200 cm tall. Proportion browsed is calculated for the seedlings and saplings classes.

Species	Measurement	Closed BHCC[3]	Small opening BCB[3]	Medium opening PLC[3]	Large opening BH[3]
Abies balsamea[1]	Seedling density (m^{-2})[2]	2.7 ± 0.7	0.1 ± 0.1	0	0
	Sapling density (m^{-2})	0	0	0	0
	Proportion browsed (%)	1.8 ± 1.8	0	NA	NA
	Tree density (ha^{-1})	2289.5 ± 191.6	60.8 ± 60.8	0	0
Betula papyrifera	Seedling density (m^{-2})	0	0	0.4 ± 0.1	0.3 ± 0.1
	Sapling density (m^{-2})	0	0	0	0
	Proportion browsed (%)	NA	NA	75.0 ± 25.0	60.0 ± 24.5
	Tree density (ha^{-1})	26.0 ± 10.4	17.4 ± 0	8.7 ± 5.0	6.9 ± 3.8
Acer rubrum	Seedling density (m^{-2})	0.2 ± 0.1	0	0.1 ± 0.1	0.1 ± 0.1
	Sapling density (m^{-2})	0	0	0	0.02 ± 0.02
	Proportion browsed (%)	33.3 ± 33.3	NA	0	66.6 ± 33.3
Picea mariana	Tree density (ha^{-1})	71.6 ± 39.7	208.3 ± 52.1	4.3 ± 4.3	27.8 ± 5.9

[1] According to Damman (1964) [Damman, A.W.H., 1964. Some forest types of central Newfoundland and their relation to environmental factors. Society of American Foresters, Washington D.C.], closed canopy forest is achieved with balsam fir advanced regeneration of 5,000- 50,000 stems/ha

[2] 15% of balsam fir seedlings were newly germinated seedlings, and all seedlings were < 30 cm high

[3] BHCC = Blue Hill Closed Canopy; BCB = Bread Cove Brook; PLC = Platter's Cove and; BH = Blue Hill

Table 5.2 – *Poaceae* species[1] cover across the study sites of Terra Nova National Park, Newfoundland, Canada.

	Closed BHCC[3]	Small opening BCB[3]	Medium opening PLC[3]	Large opening BH[3]
Mean cover	0	0.8	17.1	13.1
Standard deviation	0	1.5	14.1	17.5
Maximum cover[2]	0	5	50	70

[1]The dominant species is *Calamagrostis canadensis*
[2] Maximum cover observed in a quadrat
[3] BHCC = Blue Hill Closed Canopy; BCB = Bread Cove Brook; PLC = Platter's Cove and; BH = Blue Hill

Table 5.3 – Species identified to the genus level across the study sites of Terra Nova National Park, Newfoundland, Canada.

Genus	Reasons for identification to the Genus
Amelanchier sp.	Rare[1], not flowering and hard to identified, because of hybridization
Carex sp.	Rare[1]
Cladina sp.	Rare[1]
Cladonia sp.	Rare[1]
Dryopteris sp.	Hard to identified, because of hybridization
Equisetum sp.	Rare[1], only one occurrence (monospecific)
Fragaria sp.	Rare[1], not flowering and probably monospecific
Other lichen	Rare[1]
Ptilium sp.	Rare[1], only one occurrence (monospecific)
Sphagnum sp.	Most occurrence in the closed canopy site, one observation in the large gap area, cumulative cover of 120% for all surveys

[1] <5% cover in each plot

Table 5.4 – Distribution of feathermoss species across the study sites within Terra Nova National Park, Newfoundland, Canada (mean percentage ± SE).

Genus	Species	Closed BHCC[1]	Small opening BCB[1]	Medium opening PLC[1]	Large opening BH[1]
Hylocomium	*splendens*	44.3 ± 4.1	8.3 ± 4.3	7.6 ± 2.0	4.5 ± 0.8
Pleurozium	*schreberi*	13.0 ± 2.9	4.5 ± 1.6	0.1 ± 0.1	13.2 ± 2.5
Ptilium	*crista-castrensis*	6.8 ± 1.4	0.6 ± 0.5	0.5 ± 0.5	1.2 ± 0.4
Rhytidiadelphus	*loreus*	0.7 ± 0.3	5.1 ± 5.0	0.3 ± 0.3	0.02 ± 0.02
	squarrosus	1.0 ± 0.6	NA	1.5 ± 1.0	1.1 ± 0.7
	triquetrus	0.03 ± 0.03	NA	0.8 ± 0.8	2.3 ± 0.8
Dicranum	*polysetum*	1.6 ± 0.4	1.8 ± 0.7	NA	0.3 ± 0.1
	scoparium	1.3 ± 0.4	0.5 ± 0.5	0.3 ± 0.3	NA
	majus	0.9 ± 0.3	NA	0.3 ± 0.3	0.7 ± 0.3
Polytrichum	*piliferum*	0.1 ± 0.1	NA	NA	1.1 ± 0.8
	juniperinum	NA	0.5 ± 0.5	NA	0.5 ± 0.3
	commune	0.03 ± 0.03	NA	NA	0.1 ± 0.1

[1] BHCC = Blue Hill Closed Canopy; BCB = Bread Cove Brook; PLC = Platter's Cove and; BH = Blue Hill

Table 5.5 – Correlation coefficient (r-value) with NMDS ordination axes, goodness of fit statistic (R^2) and p-values for each environmental variable. R-values indicate strength and direction of linear correlations between variables and NMDS axes. Codes in parenthesis are provided for the variables plotted in Figure 2.2.

Environmental variables	Axis 1	Axis 2	R^2	P-value
% PAR at 25cm	- 0.853	0.523	0.547	0.001
% PAR at 100cm (PAR.100)	- 0.915	0.404	0.736	0.001
Conifer trees (Conifer)	0.844	- 0.537	0.760	0.001
Hardwood trees (Hardwood)	0.946	- 0.324	0.284	0.024
Moose density	0.304	0.953	0.023	0.790
Soil pH (pH)	- 0.856	0.516	0.529	0.001
Soil resistance	- 0.850	0.526	0.421	0.001
Soil decomposition rate (Decomposition)	- 0.981	- 0.194	0.314	0.020
Soil temperature (Temperature)	- 0.657	0.754	0.866	0.001
Soil moisture (Moisture)	1.000	0.023	0.459	0.003

Table 5.6 – Pearson's product-moment correlation coefficient (r-value) of vegetation variables with NMDS ordination axes. R-values indicate strength and direction of linear correlations between variables and NMDS axes. Bold values indicate significance at $p<0.05$[1]. Species codes are provided in parenthesis after species name for those with significant correlation coefficient plotted in Figure 2.2.

Species	Axis 1	Axis 2	Species	Axis 1	Axis 2
Abies balsamea (Abi.bal)	**0.768**	- 0.295	Live trunk	0.364	- 0.061
Acer rubrum	- 0.119	- 0.218	*Lycopodium annotinum* (Lyc.ann)	- 0.179	**0.421**
Alnus viridis subsp. *crispa*	- 0.098	0.032	*Lycopodium clavatum*	0.249	0.217
Amelanchier sp. (Ame.sp)	**0.525**	- 0.141	*Lycopodium obscurum* (Lyc.obs)	**0.419**	- 0.096
Anaphalis margaritacea	- 0.183	0.358	*Lysimachia borealis* (Lys.bor)	**0.513**	- 0.003
Aralia nudicaulis (Ara.nud)	**0.436**	0.123	*Maianthemum canadense*	- 0.315	0.146
Bare ground	0.187	- 0.253	Moose pellet	0.028	0.066
Betula papyrifera (Bet.pap)	**- 0.424**	- 0.266	*Pilosella aurantiaca*	- 0.349	0.168
Broadleaf litter (Leaf.litter)	0.137	**0.862**	*Pleurozium schreberi*	0.263	- 0.366
Carex sp.	0.007	- 0.262	*Poaceae* sp. (Poa.sp)	**- 0.772**	- 0.094
Cerastium fontanum subsp. *vulgare*	- 0.129	- 0.058	*Polytrichum* sp.	- 0.275	- 0.219
Chamerion angustifolium (Cha.ang)	**- 0.576**	0.038	*Populus tremuloides* (Pop.tre)	0.126	**0.485**
Cladina sp.	- 0.127	- 0.012	*Pteridium aquilinum*	0.086	- 0.121
Cladonia sp.	0.141	0.160	*Ptilidium* sp.	0.229	0.226
Clintonia borealis (Cli.bor)	**0.703**	- 0.236	*Ptilium crista-castrensis* (Pti.cas)	**0.629**	**- 0.550**
Coniferous litter	0.301	- 0.105	*Rhododendron groenlandicum*	0.187	- 0.253
Coptis trifolia (Cop.tri)	**0.410**	- 0.040	*Rhododendron canadense*	- 0.008	0.203
Cornus canadensis (Cor.can)	0.296	**0.675**	*Rhytidiadelphus* sp.	- 0.085	- 0.065
Dead stump	0.168	- 0.140	Rock	- 0.330	- 0.173
Diervilla lonicera	- 0.358	0.005	*Rubus idaeus* (Rub.ida)	**- 0.618**	- 0.067
Dicranum sp. (Dic.sp)	**0.796**	0.014	*Rubus pubescens*	- 0.352	- 0.164
Dryopteris sp.	- 0.092	- 0.087	*Rumex acetosella*	- 0.366	0.053
Equisetum sp.	- 0.270	- 0.014	*Sambucus racemosa*	- 0.170	0.317
Fragaria sp.	- 0.376	0.377	*Solidago rugosa* (Sol.rug)	**- 0.681**	- 0.038
Galium triflorum	- 0.321	0.130	*Sorbus americana*	0.374	0.139
Gaultheria hispidula (Gau.his)	**0.616**	- 0.147	*Sorbus decora*	0.314	- 0.121
Ground moss	0.036	- 0.293	*Sphagnum* sp.	0.389	- 0.274
Gymnocarpium disjunctum	- 0.023	- 0.282	*Taraxacum officinale*	- 0.138	0.016
Herbaceous litter (Herb.litter)	**- 0.927**	- 0.159	*Taxus canadensis*	0.187	- 0.253
Hieracium vulgatum	- 0.157	0.029	*Vaccinium angustifolium*	0.144	- 0.037
Hylocomium splendens (Hyl.spl)	**0.870**	- 0.171	*Vaccinium vitis-idaea*	0.265	- 0.253

Ilex mucronata (Ile.muc)	0.299	**0.470**	*Viburnum nudum* var.*cassinoides*	0.187	- 0.253
Kalmia angustifolia	0.408	- 0.242	*Viola macloskeyi*	- 0.365	0.178
Lepidozia reptans	0.381	- 0.214	Water	0.187	- 0.253
Lichen sp. (other)	- 0.179	- 0.147	Woody debris (Woody.debris)	**- 0.531**	0.385
Linnaea borealis (Lin.bor)	**0.631**	0.341			

[1]Critical r-value for significance at 5% (N=24) = 0.404 (Appendix III, Upton & Cook (2008))
[Upton, G., Cook, I., 2008. A Dictionnary of Statistics. Oxford University Press.]

Table 5.7 – Summary of F-values and p-values for the nested analysis of variance on the various species functional groups in relation to the disturbance gradient in Terra Nova National Park, Newfoundland, Canada. Bold values indicate significant p-value (0.05).

		Disturbance		**No – small gap**	**Small – medium gap**	**Medium – large gap**	**No- Medium gap**	**No – large gap**	**Small – large gap**
Bryophyte	$F_{3,4}$	34.72	$F_{1,4}$	30.53	0.86	3.94		70.94	
	p-value	**0.0025**	p-value[1]	**0.0052**	0.41	0.12		**0.001**	
Pteridophyte	$F_{3,4}$	0.13							
	p-value	0.94							
Graminoides	$F_{3,4}$	92.47	$F_{1,4}$	3.08	64.70	10.16			43.02
	p-value	**0.00038**	p-value[1]	0.15	**0.0013**	0.033			**0.0028**
Early succession	$F_{3,4}$	88.44	$F_{1,4}$	11.58	30.73	0.76			30.61
forbs	p-value	**0.00041**	p-value[1]	0.027	**0.0052**	0.43			**0.0052**
Late succession	$F_{3,4}$	9.15	$F_{1,4}$	10.55	24.86	2.82	8.17	2.54	18.42
forbs	p-value	**0.029**	p-value[2]	0.031	**0.0076**	0.17	0.046	0.19	0.013
Short shrubs	$F_{3,4}$	3.70							
	p-value	0.12							
Medium shrubs	$F_{3,4}$	1.32							
	p-value	0.39							
Tall shrubs	$F_{3,4}$	2.05							
	p-value	0.25							
Coniferous tree	$F_{3,20}$	173.02	$F_{1,(8/4/12/10)}$	100.62	67.57	6.91		21.71	
	p-value	**$1.8 e^{-14}$**	p-value[1]	**$8.3 e^{-6}$**	**0.0012**	0.022		**0.00090**	
Deciduous tree	$F_{3,20}$	0.62							
	p-value	0.61							

[1]Bonferri significance at 0.01
[2]Bonferri significance at 0.008

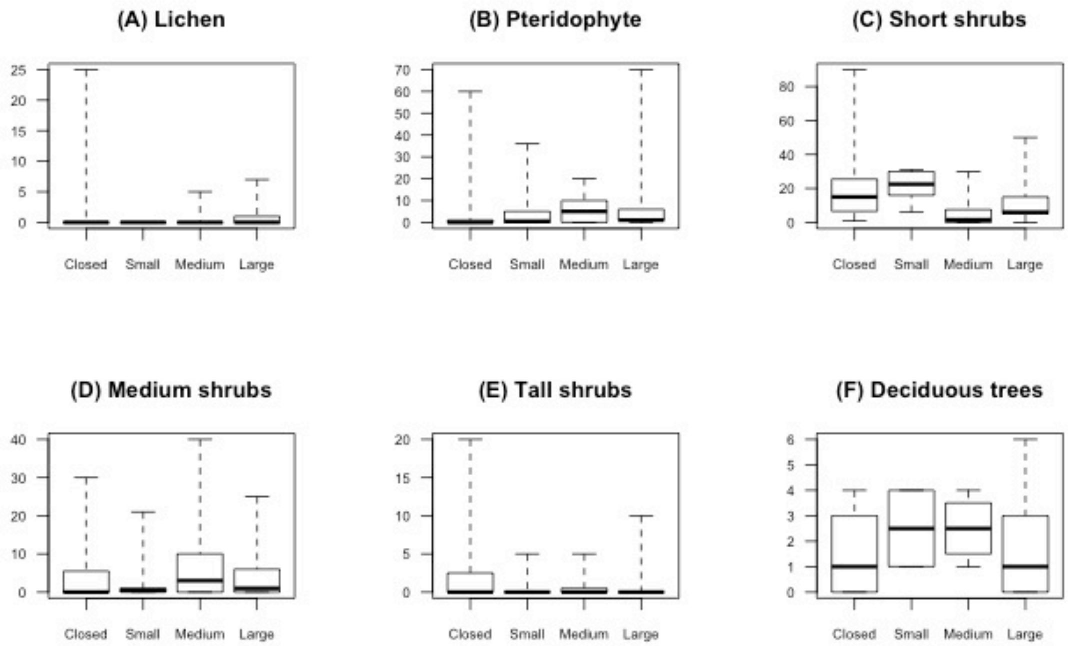
Table 5.8 – Summary of F-values and p-values for the nested analysis of variance on the environmental variables in relation to the disturbance gradient in Terra Nova National Park, Newfoundland, Canada. Bold values indicate significant p-value (0.05).

		Disturbance		**No – small gap**	**Small – medium gap**	**Medium – large gap**	**No-Medium gap**	**No – large gap**	**Small – large gap**
PAR 25cm (%)	$F_{3,20}$	NA[1]	$F_{1,20}$	NA[1]					
	p-value	**0**	p-value[2]	**0**	0.14	**0**	**0**		**0**
PAR 100cm (%)	$F_{3,20}$	NA[1]	$F_{1,20}$	NA[1]					
	p-value	**0**	p-value	**0**	0.53	**0**			
Soil pH	$F_{3,20}$	18.11	$F_{1,20}$	9.82	3.00	4.01			
	p-value	**$6.4\ e^{-6}$**	p-value	**0.0052**	0.099	0.059			
Soil temperature	$F_{3,20}$	89.83	$F_{1,20}$	100.4	0.28	15.55		162.58	5.85
(^{o}C)	p-value	**$8.9\ e^{-12}$**	p-value[2]	**$3.1\ e^{-9}$**	0.60	**0.00080**		**$4.6\ e^{-11}$**	0.025
Soil moisture	$F_{3,20}$	4.27	$F_{1,20}$	1.30	0.77	0.03		10.69	
(%V/V)	p-value	**0.018**	p-value[3]	0.27	0.39	0.86		**0.0038**	
Soil resistance (N)	$F_{3,20}$	19.75	$F_{1,20}$	18.58	1.17	3.14	16.26		
	p-value	**$3.4\ e^{-6}$**	p-value[3]	**0.00034**	0.29	0.092	**0.00065**		
Decomposition rate	$F_{3,20}$	5.25	$F_{1,20}$	0.26	3.60	0.69	11.09		2.17
(%)	p-value	**0.0078**	p-value[2]	0.62	0.072	0.42	**0.0033**		0.16
Moose habitat use	$F_{3,20}$	1.69							
	p-value	0.20							

[1] No unique F-value, since a restricted permutation test was used
[2] Bonferri significance at 0.01
[3] Bonferri significance at 0.013

Figure 5.1

Figure 5.2


(A) Lichen
(B) Pteridophyte
(C) Short shrubs
(D) Medium shrubs
(E) Tall shrubs
(F) Deciduous trees
Closed
Small
Medium
Large

6 APPENDIX II: Chapter 3 Method and Results

Table 6.1 – Mixed-model results of the seedling success in function of the planting location (centre, edge). Coefficients come from sequentially constructed models: Y~ Vegetation + Individual + Location; coefficient illustrate the success of seedlings planted on the edge of a gap, compared to centre-planted seedlings. Significant effect when the 95% CI does not overlap 0.

Table 6.2 – Explanatory variables description.

Table 6.3 – Candidate models for AIC selection. Explanatory variable codes are provided in Table 6.2.

Table 6.4 – Scores of the two first axes of the principal component analysis (PCA) on the understory plant community. Both axes explained a cumulative 74.4% of the variance. The plot identifier can be read: Site – Location – Ground treatment –Density – Replicate. See below for specific details on sites names.

Figure 6.1 – Ordination scatterplot (principal component analysis; PCA). Each site is represented by a different symbol and enclosed in a convex hull by solid lines. Species are represented by the “+” symbol or their code name (code are provided in Chapter 2). PCA ordination resulted in a 2-dimensional solution with cumulative explained variance of 0.744.

Table 6.1 – Mixed-model results of the seedling success in function of the planting location (centre, edge). Coefficients come from sequentially constructed models: Y~ Vegetation + Individual + Location; coefficient illustrate the success of seedlings planted on the edge of a gap, compared to centre-planted seedlings. Significant effect when the 95% CI does not overlap 0.

Variable	**Date**	**Coefficient estimate**	**Coefficient SE**	**CI95%**	**p-value**
Survival	October 2013	0.498	0.448	-0.38 – 1.38	0.267
	May 2014	0.220	0.301	-0.37 – 0.81	0.465
	October 2014	0.145	0.300	-0.44 – 0.73	0.629
Browsing	October 2014	0.494	0.437	-1.35 – 0.36	0.258
New growth	May 2014	0.073	0.218	-0.35 – 0.50	0.370
	October 2014	0.283	0.337	-0.94 – 0.38	0.205
Basal diameter	October 2014	0.147	0.177	-0.49 – 0.20	0.206
Buds	October 2013	0.005	0.070	-0.14 – 0.13	0.474
	October 2014	0.120	0.175	-0.46 – 0.22	0.249

Table 6.2 – Explanatory variables description.

Variable code	Description	Type	Range
PCA1 (P1)	PCA score for first axis of plant community ordination	Linear	-4.7 – 4.6
PCA2 (P2)	PCA score for second axis of plant community ordination	Linear	- 4.4 – 7.5
Specie (SP)	Presence or absence of neighbouring palatable specie	Categorical	0/1
Height (HE)	Height at planting	Linear	7.6 – 48.7 cm
Leader (BR)	Number of leading branches at planting	Categorical	1, 2, ≥ 3
Ground treatment (GR)	Ground treatment applied before planting	Categorical	Control/Aboveground cut/Scarification
Density treatment (DE)	Density of planting	Categorical	Low/High

Table 6.3 – Candidate models for AIC selection. Explanatory variable codes are provided in Table 6.2.

Candidate model	Model formulation
Vegetation	Y ~ P1 + P2 + SP + (1|Plot)
Individual	Y~ HE + BR + (1|Plot)
Ground	Y~ GR + (1|Plot)
Density	Y~ DE + (1|Plot)
Vegetation + Individual	Y ~ P1 + P2 + SP + HE + BR + (1|Plot)
Vegetation + Ground	Y ~ P1 + P2 + SP + GR + (1|Plot)
Vegetation + Density	Y ~ P1 + P2 + SP + DE + (1|Plot)
Individual + Ground	Y~ HE + BR + GR + (1|Plot)
Individual + Density	Y ~ HE + BR + DE + (1|Plot)
Vegetation + Individual + Ground	Y ~ P1 + P2 + SP + HE + BR + GR + (1|Plot)
Vegetation + Individual + Density	Y ~ P1 + P2 + SP + HE + BR + DE + (1|Plot)
Vegetation + Individual + Ground + Density	Y ~ P1 + P2 + SP + HE + BR + GR + DE + (1|Plot)
NULL	Y~ 1 + (1|Plot)

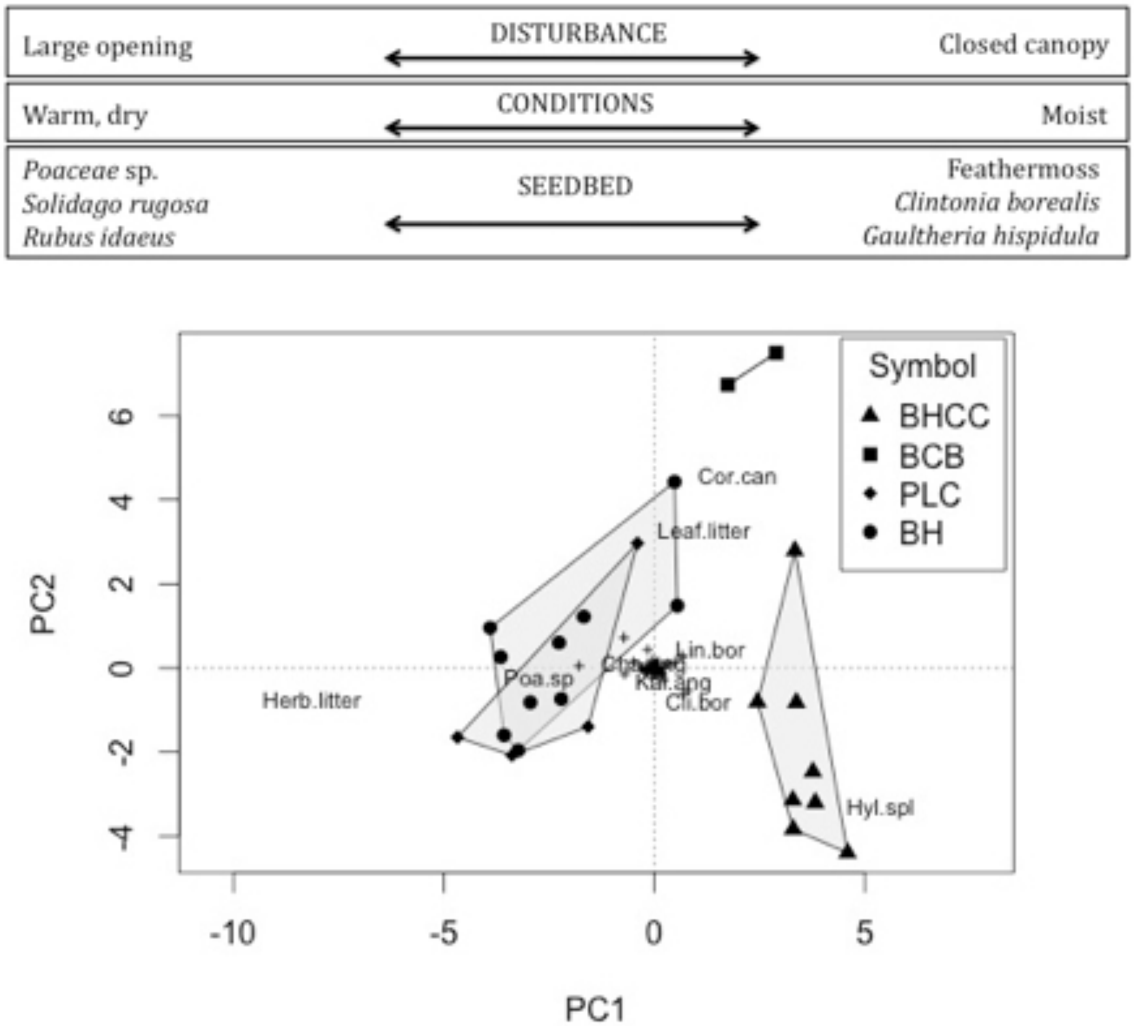
Y stand for every seedling response variable studied: Survival, browse, new growth, basal diameter, number of buds

Table 6.4 – Scores of the two first axes of the principal component analysis (PCA) on the understory plant community. Both axes explained a cumulative 74.4% of the variance. The plot identifier can be read: Site – Location – Ground treatment –Density – Replicate. See below for specific details on sites names.

Plot[1]	PCA axis 1 score	PCA axis 2 score
BH-C-CTL-5-A	-3.9038900	0.9536073
BH-C-CTL-5-B	0.5414547	1.4823313
BH-E-CTL-5-A	-2.2685403	0.6000602
BH-E-CTL-5-B	-3.2364007	-1.9632203
BH-C-AGC-5-A	-1.6789171	1.2190286
BH-C-AGC-5-B	-3.6510035	0.2584788
BH-C-SCA-5-A	0.4766878	4.4284447
BH-C-SCA-5-B	-2.9489840	-0.8183323
BH-C-CTL-20-A	-3.5723060	-1.5996618
BH-C-CTL-20-B	-2.2160419	-0.7381758
BHCC-C-CTL-5-A	3.3325681	2.7907883
BHCC-C-CTL-5-B	3.3683719	-0.8228965
BHCC-C-AGC-5-A	3.8165189	-3.2048667
BHCC-C-AGC-5-B	3.2902652	-3.8349144
BHCC-C-SCA-5-A	3.2822155	-3.1426265
BHCC-C-SCA-5-B	4.5847680	-4.3969493
BHCC-C-CTL-20-A	3.7602151	-2.4700232
BHCC-C-CTL-20-B	2.4441414	-0.8108543
PLC-C-CTL-5-A	-1.5778178	-1.3983441
PLC-C-CTL-5-B	-3.3833161	-2.0795724
PLC-E-CTL-5-A	-4.6802448	-1.6501634
PLC-E-CTL-5-B	-0.4049834	2.9684730
BCB-C-CTL-5-A	2.8877001	7.4948299
BCB-C-CTL-5-B	1.7375388	6.7345588

[1](Site) BH: Blue Hill, BHCC: Blue Hill Closed Canopy, PLC: Platter's Cove, BCB: Bread Cove Brook
(Location) C: Centre, E: Edge
(Ground Treatment) CTL: Control, AGC: Aboveground cut, SCA: Soil scarification
(Density) 5: low at 5,000/ha, 20: high at 20,000/ha

Figure 6.1


Large opening
DISTURBANCE
Closed canopy
Warm, dry
CONDITIONS
Moist
Poaceae sp.
Solidago rugosa
Rubus idaeus
SEEDBED
Feathermoss
Clintonia borealis
Gaultheria hispidula
Symbol
BHCC
BCB
PLC
BH
Cor.can
Leaf.litter
Lin.bor
Poa.sp
Herb.litter
Kal.ang
Cli.bor
Hyl.spl
PC2
6
4
2
0
-2
-4
-10
-5
0
5
PC1