

**Structure and composition of forest edges created by a spruce
budworm outbreak and maintained by moose browsing in
Cape Breton Highlands National Park**

By
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Abstract

Structure and composition of forest edges created by a spruce budworm outbreak and maintained by moose browsing in Cape Breton Highlands National Park

By Caroline Franklin

Natural forest edges created by a severe spruce budworm outbreak in Cape Breton Highlands National Park, Nova Scotia, Canada, have been maintained three decades post-disturbance by moose browsing. My overall research objective was to determine the direct and indirect effects of edge creation on vegetation structure and composition. Trees, deadwood, and understorey plants were sampled along 120 m transects perpendicular to six forest edges. The spruce budworm-induced forest edges were characterized by narrow transition zones where canopy cover, stem density, and structural diversity were intermediate between the disturbed area and forest. Severe moose browsing appears to be preventing sapling growth and altering species composition, particularly on the insect disturbed side of the edge. If moose continue to maintain the forest edge, contrasts in vegetation structure and composition between the severely browsed disturbed area and adjacent intact forest could increase and ultimately alter forest edge function.

October 2nd, 2013

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List of symbols

Abbreviation	Meaning
dbh	Diameter at breast height
DEI	Distance of edge influence
D.R.	Disturbed area reference
F.R.	Forest reference
GAMM	Generalized additive mixed models
RTEI	Randomized test of edge influence
SE	Standard error
UTM	Universal Transverse Mercator

Chapter 1: Introduction

The boreal forest of Cape Breton Highlands National Park, which is located on northern Cape Breton Island, Nova Scotia, Canada, offers a unique opportunity to study vegetation at forest edges. Natural forest edges were created by a spruce budworm outbreak nearly three decades earlier and have since been maintained by an introduced moose population. A better understanding of the structure, composition, and moose browse severity at the spruce budworm-induced forest edges reveals insight into the interplay between two herbivores and their effects on landscape dynamics.

1. Importance and classification of forest edges

Forest edges, defined as the interfaces between forested and adjacent ecosystems, are often prominent landscape features that can be characterized by distinct patterns and processes. The transition areas contribute to overall spatial heterogeneity and can therefore strongly influence habitat quality by providing environmental conditions different from those in the forest interior (Bannerman 1998; Disk 2007). Furthermore, forest edges play significant ecological roles by regulating flows of organisms, materials, and energy across adjoining communities (Cadenasso et al. 2003). A greater understanding of the complexity of edge function and of the related biological interactions is required for increased knowledge on landscape ecology.

Forest edges can be classified by origin and state. Inherent forest edges exist due to differences in soil type, microclimate, topography, or geomorphology between adjacent communities and are usually long-term features of the landscape (Thomas et al. 1979).

Meanwhile, induced forest edges result from natural disturbances or anthropogenic activities. Human induced edges are either maintained or left to regenerate depending on the anthropogenic function of the non-forested area. Since naturally induced edges result from disturbances such as wildfires, avalanches, windstorms, and insect outbreaks, these edges tend to regenerate once the disturbance agent has subsided. In this thesis, I focus on unique edges that were not only created by a natural disturbance (an insect outbreak) but are also being maintained by a natural process (moose browse activity).

2. Edge influence

Edge influence, also known as “edge effect,” results from differences in ecological conditions at the edge compared with the adjacent forest or non-forested areas. The abiotic and biotic gradients across forest edges induce primary responses to edge creation such as tree mortality (Harper et al. 2005). Indirect effects of edge creation resulting from the combination of primary responses and initial edge-related gradients are known as secondary responses. Subsequent edge effects resulting from these secondary influences are termed tertiary responses and include browsing of saplings and other plant-animal interactions (Harper et al. 2005). The extent and pattern of edge influence varies among response types (Harper et al. 2005) hence examinations of primary, secondary, as well as tertiary responses to edge creation provide a better understanding of edge dynamics.

In addition to the response variable of interest, edge origin, edge age, and the state of the edge also determine the pattern and extent of edge influence by contributing to the contrast in vegetation structure and composition between the adjoining communities on

either side of the forest edge. If the contrast in structure is strong, the edges are abrupt and generally have greater edge influence on vegetation compared to more gradual edges (Bannerman 1998). Human induced edges are usually more abrupt than natural edges (Matlack & Litvaitis 1999) and younger edges tend to be more abrupt than older edges (Harper et al. 2005). At regenerating edges, where the adjacent community undergoes forest succession, the contrast in structure between the adjoining ecosystems decreases over time hence edge influence is generally lower compared to that of maintained forest edges (Harper et al. 2005).

Geographical location also affects forest edge influence on vegetation. For instance, boreal and sub-boreal forest edges usually exhibit less edge influence compared to edges located in tropical forests (Harper et al. 2005). The weaker forest edge response in boreal ecosystems could be attributed to the ability of species to better adapt to ecological disturbances (Johnson 1992). At a smaller spatial scale, edge influence is also determined by the orientation of the edge. For example, light intensity and edge influence on vegetation tend to be greater at forest edges facing the equator compared to those facing other directions (Matlack & Litvaitis 1999). The combination of the various factors affecting edge influence on vegetation reveals the innate complexity of forest edges.

3. Prior research on forest edges

The majority of forest edge research has focused on edges created by human activity as opposed to edges induced by natural phenomena (Harper et al. 2005).

However, anthropogenic edges differ from natural ones because they are often more

abrupt and the adjacent clearings are usually larger (Matlack & Litvaitis 1999). While forest fragmentation becomes an increasingly important conservation issue, research related to the effects of edge creation and edge maintenance on ecosystem function is critical. Natural edge studies are particularly valuable because they provide a better understanding of natural processes, which can be used in the development of effective forest management practices. Sustainable forest management strategies often strive to emulate natural disturbances to minimize potentially negative anthropogenic impacts (Kuuluvainen & Grenfell 2012). Forest managers could use increased knowledge on natural forest edges to create or improve techniques involving the creation of forest edges resulting from otherwise ecologically detrimental human activities, such as clear cutting. Various forest disturbances affect landscape patterns and processes differently (Foster et al. 1998), hence a greater understanding of forest responses to individual disturbances is required for the development of landscape ecology studies.

Very few scientific studies have investigated forest edges adjacent to insect disturbances. One study examined the structure of forest edges created by mountain pine beetle (*Dendroctonus ponderosae*) outbreaks in central British Columbia and estimated the distance of edge influence on forest structure to be approximately 51 m (McIntire & Fortin 2006). A more recent study investigated the spatial patterns resulting from spruce budworm (*Choristoneura fumiferana*) defoliation in Ontario (James et al. 2010) but did not examine the actual influence of edge creation on abiotic or biotic response variables. Individual insect outbreaks result in different disturbance intensities; hence generalizations pertaining to the impact of insect outbreaks on forest dynamics cannot be based on findings from a single location or from a single outbreak (Bouchard et al. 2007).

4. Study area

Spruce budworm outbreaks are one of the major natural and stand initiating disturbances affecting forest dynamics in eastern boreal forests. The insect defoliator feeds mainly on *Abies balsamea* (balsam fir), but *Picea* (spruce) species are also suitable hosts. Populations of the spruce budworm tend to reach outbreak levels when there are large stands of mature host species and mild summer weather (Blais 1968). Outbreaks typically occur every three decades (Blais 1983) and persist for approximately ten years (Boulanger & Arseneault 2004).

The spruce budworm is native to the boreal forest of Cape Breton Highlands National Park, which encompasses 950 km² of northern Cape Breton Island, Nova Scotia. The latest outbreak (1974 - 1985) was considered to be the most severe compared to prior outbreaks in the area (Ostaff & MacLean 1989) and Cape Breton Highlands National Park management refrained from using aerial insecticides or other methods of pest control to suppress the outbreak. Defoliation caused by the insect resulted in tree growth reduction, tree mortality, and loss of wood production (MacLean 1984). More specifically, mortality of *Abies balsamea* and *Picea glauca* (white spruce) started two to three years after the beginning of the outbreak (Ostaff & MacLean 1989). By the collapse of the outbreak in 1985, affected stands experienced approximately 87% *Abies balsamea* mortality (MacLean & Ostaff 1989) and 27% *Picea* spp. mortality (Ostaff & MacLean 1989).

Due to the cyclic nature of the spruce budworm and balsam fir forest, it was expected that areas disturbed by the insect would regenerate after the outbreak collapse.

However, natural disturbances such as budworm defoliation create favourable moose (*Alces alces*) habitat by promoting sapling growth that is within reach of moose (Lautenschlager et al. 1997). Consequently, a large introduced moose (*Alces alces andersoni*) population is currently inhibiting forest regeneration in the Cape Breton Highlands (Smith et al. 2010).

Native moose (*Alces alces americana*) were extirpated from Cape Breton Island in the early 1900s as a result of over-hunting (Pulsifer & Nette 1995). In 1947 and 1948, 18 individual moose of the western sub-species (*Alces alces andersoni*) were introduced to northern Cape Breton from Elk Island National Park in Alberta (Pulsifer & Nette 1995). Since then, the population has increased dramatically due to hunting prohibition, an abundant food supply resulting from the spruce budworm outbreak, and a lack of natural predators. Although calves are occasionally preyed upon by black bear (*Ursus americanus*), moose are relieved from heavy predation pressure since wolves (*Canis* spp.) were extirpated from Nova Scotia in 1928 (Whitaker 2006). Furthermore, moose in the Cape Breton Highlands are not greatly affected by the transmission of the deadly parasite *Parelaphostrongylus tenuis* that is carried by white-tailed deer (*Odocoileus virginianus*) as deer are uncommon in the park. In 2013, the moose population for northern Cape Breton Island was estimated to be 5,000 (James Bridgland, personal communication). Moose feed mainly on *Abies balsamea* and *Betula papyrifera* (white birch) (Basquill & Thompson 1996); however, their diet may also include *Acer saccharum* (sugar maple), *Acer spicatum* (mountain maple), *Populus* (poplar) spp., and shrubs (Prescott 1968).

5. Research objectives

In this thesis, I considered the direct and indirect effects of spruce budworm induced-forest edges on vegetation structure and composition. In Chapter 2, I investigated primary structural responses (canopy cover, tree density, dead wood abundance) as well as a primary process response (decomposition rate) to edge creation. I then focused on secondary (sapling density, sapling height, understorey cover) and tertiary responses (moose browse activity) to edge creation in Chapter 3 to ultimately characterize the spruce budworm-induced forest edges in Cape Breton Highlands National Park. My objectives, which I address in the following two chapters, were:

1. To assess primary responses to edge creation by estimating the extent of edge influence on overstorey structure, deadwood abundance, and decomposition rate; and
2. To investigate edge maintenance by determining the spatial pattern and extent of edge influence for the severity of moose browse, understorey structure, and composition to ultimately gain insight into the effects of moose browsing on regeneration.

The natural forest edges resulting from the severe spruce budworm outbreak offered a unique opportunity to study forest edges because moose browsing was maintaining the edges (Figure 1-1), which were expected to abate after the collapse of the outbreak nearly three decades prior to sampling. All data were collected from the same transects in the study area to relate the effects of edge creation with the influence of moose herbivory on understorey characteristics in Chapter 4. Structural attributes (Chapter 2) and understorey variables (Chapter 3) were sampled in 5 x 20 m plots and

contiguous quadrats, respectively. The difference in sampling quadrat size was related to spatial scale due to the variability in vegetation size.



Figure 1-1. A spruce budworm-induced forest edge maintained by moose browsing in Cape Breton Highlands National Park, Nova Scotia. The insect disturbed area is in the foreground and the relatively undisturbed intact forest is in the background.

6. Literature cited

- Bannerman, S. 1998. *Biodiversity and interior habitats: The need to minimize edge effects* [Biodiversity - Management Concepts in Landscape Ecology Extension Note 21]. British Columbia Ministry of Forests, Victoria, BC, Canada.
- Basquill, S. & Thompson, R.G. 1996. *Moose (*Alces alces*) browse availability and utilization in Cape Breton Highlands National Park*. Parks Canada [report no. 010], Halifax, NS, Canada.
- Blais, J.R. 1968. Regional variation in susceptibility of eastern North American forests to budworm attack based on history of outbreaks. *The Forestry Chronicle* 44: 17-23.

- Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Canadian Journal of Forest Research* 13: 539-547.
- Bouchard, M., Kneeshaw, D. & Messier, C. 2007. Forest dynamics following spruce budworm outbreaks in the northern and southern mixedwoods of central Quebec. *Canadian Journal of Forest Research* 37: 763-772.
- Boulanger, Y. & Arseneault, D. 2004. Spruce budworm outbreaks in eastern Quebec over the last 450 years. *Canadian Journal of Forest Research* 34: 1035-1043.
- Cadenasso, M.L., Pickett, S.T., Weathers, K.C. & Jones, C.G. 2003. A framework for a theory of ecological boundaries. *BioScience* 53: 750-758.
- Disk, T.D. 2007. Incorporating edge effects into landscape design and management. In: Lindenmayer, D.B. & Hobbs, R.J. (eds.) *Managing and designing landscapes for conservation*, pp. 151-164. Blackwell Publishing Ltd, Malden, MA, US.
- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J.Q., Brosnoff, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. & Esseen, P.A. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19: 768-782.
- James, P.M., Fleming, R.A. & Fortin, M.-J. 2010. Identifying significant scale-specific spatial boundaries using wavelets and null models: spruce budworm defoliation in Ontario, Canada as a case study. *Landscape Ecology* 25: 873-887.
- Johnson, E.A. 1992. *Fire and vegetation dynamics: studies in the North American boreal forest*. Cambridge University Press, Cambridge, UK.
- Kuuluvainen, T. & Grenfell, R. 2012. Natural disturbance emulation in boreal forest ecosystem management – theories, strategies, and a comparison with conventional even-aged management. *Canadian Journal of Forest Research* 42: 1185-1203.
- Lautenschlager, R.A., Crawford, H.S., Stokes, M.R. & Stone, T.L. 1997. Forest disturbance type differentially affects seasonal moose forage. *Alces* 33: 49-73.
- MacLean, D.A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. *The Forestry Chronicle* 60: 273-279.
- MacLean, D.A. & Ostaff, D.P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. *Canadian Journal of Forest Research* 19: 1087-1095.

- Matlack, G.E. & Litvaitis, J.A. 1999. Forest edges. In Hunter, M.L. Jr. (ed.) *Maintaining biodiversity in forest ecosystems*, pp. 210-233. Cambridge University Press, Cambridge, UK.
- McIntire, E.J. & Fortin, M. -J. 2006. Structure and function of wildfire and mountain pine beetle forest boundaries. *Ecography* 29: 309-318.
- Ostaff, D.P. & MacLean, D.A. 1989. Spruce budworm populations, defoliation, and changes in stand condition during an uncontrolled spruce budworm outbreak on Cape Breton Island, Nova Scotia. *Canadian Journal of Forest Research* 19: 1077-1086.
- Prescott, W.H. 1968. *A study of winter concentration areas and food habits of moose in Nova Scotia*. M.Sc. thesis, Acadia University, Wolfville, NS, Canada.
- Pulsifer, M.D. & Nette, T.L. 1995. History, status and present distribution of moose in Nova Scotia. *Alces* 31: 209-219.
- Smith, C., Beazley, K., Duinker, P. & Harper, K.A. 2010. The impact of moose (*Alces alces andersoni*) on forest regeneration following a severe spruce budworm outbreak in the Cape Breton Highlands, Nova Scotia, Canada. *Alces* 46: 135-150.
- Thomas, J.W., Maser, C. & Rodiek, J.E. 1979. Edges. In Thomas, J.W. (ed.) *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*, pp. 48-59. U.S. Department of Agriculture Forest Service, Portland, OR, USA.
- Whitaker, A.N. 2006. *A preliminary exploration of the ecological and societal possibility of wolf recovery to Nova Scotia, Canada*. MES thesis, Dalhousie University, Halifax, NS, Canada.

Chapter 2: Structural responses to forest edge creation by a spruce budworm outbreak

Abstract

Natural disturbances such as insect outbreaks create boundaries that influence ecological patterns, processes, and functions. To better understand the effects of edge creation on forest structure, I examined live and decomposed structural attributes of 30 year-old forest edges created by a severe spruce budworm outbreak in Cape Breton Highlands National Park, Nova Scotia. My research objectives were 1) to determine the extent of initial effects of spruce budworm-induced edges on forest structure; 2) to gain insight into the structural development of the edges since creation; and 3) to investigate the impact of edge creation and subsequent structural development on structural diversity. Canopy cover, tree density, deadwood abundance, and decomposition rates were examined in 5 x 20 m plots located along 120 m transects across six edges. The forest edges were characterized by narrow zones of transition approximately 10 m wide over which structural diversity, live stem density, and canopy cover increased from the disturbed area into the forest. Vegetative structural changes resulting from edge creation were only apparent on the disturbed side of the spruce budworm-forest edges; however, the edges could have receded into the forest since creation. The unique and dynamic structure of spruce budworm-induced forest edges may play an important role in habitat function and therefore long-term monitoring of edge structure is encouraged.

1. Introduction

Natural disturbances, such as insect outbreaks, cause considerable changes in forest structure and consequently contribute to spatial heterogeneity (Bonan & Shugart 1989). The spruce budworm (*Choristoneura fumiferana*) is of particular importance to eastern boreal forest dynamics because outbreaks of this insect defoliator and balsam fir forests typically interact in a cyclic self-regulating system that enables forest succession (Baskerville 1975; MacLean 1984; MacLean 1988; Morin 1994). The insect feeds mainly on *Abies balsamea* (balsam fir) but *Picea* (spruce) spp. are also suitable hosts. Populations of the spruce budworm tend to reach outbreak levels every three decades (Blais 1983) when there are large stands of mature host species, especially in years of mild and dry summer weather (Blais 1968). Tree mortality begins within five years of severe defoliation (Belyea 1952) and the resulting deadwood contributes to increased structural diversity (Belle-Isle & Kneeshaw 2007). Outbreaks usually persist for approximately ten years (Boulanger & Arseneault 2004) and have increased in severity, extent, and frequency over the past 200 years in eastern Canada (Blais 1983). As spruce budworm outbreaks continue to cause large-scale forest fragmentation, an understanding of outbreak-induced forest edge function will increase knowledge of landscape patterns and processes.

Forest edges resulting from extensive tree mortality caused by insect outbreaks are the boundaries between insect disturbed areas and relatively undamaged intact forests. Although prior studies have examined the direct effects of spruce budworm outbreaks in disturbed areas (e.g. D'Aoust et al. 2004; Bouchard et al. 2006; Bouchard et al. 2007),

relatively few studies have explored the impact of insect outbreaks on the adjacent remaining forest stands. James et al. (2010) investigated the spatial patterns resulting from spruce budworm defoliation in Ontario but did not examine the actual influence of edge creation on abiotic or biotic response variables.

In Cape Breton Highlands National Park, Nova Scotia, natural forest edges created by the latest spruce budworm (*Choristoneura fumiferana*) outbreak approximately 30-40 years ago provide a unique opportunity to study naturally maintained forest edges. A large re-introduced moose (*Alces alces andersoni*) population has been inhibiting forest regeneration in the insect disturbed areas (Smith et al. 2010); hence forest edges continue to persist. Park management did not control the latest spruce budworm outbreak on Cape Breton Island, which began in 1974 and was the most severe compared to prior outbreaks in the area (Ostaff & MacLean 1989). By the collapse of the outbreak in 1985, affected stands on Cape Breton Island experienced mortality of approximately 87% *Abies balsamea* (MacLean & Ostaff 1989) and 27% *Picea* spp. (Ostaff & MacLean 1989). The influence of edge creation on forest structure and composition has yet to be investigated.

My research objectives were 1) to determine the extent of initial effects of spruce budworm-induced edges on forest structure by investigating canopy cover, live tree density, and deadwood abundance; 2) to gain insight into the structural development of the edges by examining deadwood decay stages and measuring decomposition rate; and 3) to investigate the impact of edge creation and subsequent structural development on structural diversity. A characterization of the spruce budworm-induced forest edge structure will ultimately help assess the potential habitat function of these specific edges.

2. Methods

Study area

The study was conducted in Cape Breton Highlands National Park (46°50'N, 60°30'W), which was established in 1936 and encompasses 950 km² of northern Cape Breton Island, Nova Scotia. The surrounding Atlantic Ocean to the east and the Gulf of St. Lawrence to the west of the island contribute to the park's maritime climate. Climatic normals (1971 – 2000) from nearby Pleasant Bay (46°49'N, 60°46'W) reported a mean January temperature of $-5.3 \pm 1.8^{\circ}\text{C}$, a mean July temperature of $18.1 \pm 1.8^{\circ}\text{C}$, and a mean annual precipitation of 1450.1 mm (Environment Canada 2013). The region is characterized by a plateau, which ranges in elevation from 350 m to 500 m above sea level and contains underlying Precambrian granitic and volcanic bedrock (Webb & Marshall 1999). The plateau experiences heavy snowfall, high winds, and frequent fog (Webb & Marshall 1999). Approximately 88% of Cape Breton Highlands National Park is forested by a unique combination of Acadian taiga and boreal vegetation (Parks Canada 2010). In the boreal land region, which dominates approximately 50% of the park, the dominant tree species is *Abies balsamea* interspersed with *Picea glauca* (white spruce) and *Betula papyrifera* (white birch). *Picea mariana* (black spruce) and *Larix laricina* (eastern larch) are also present in moist areas. Soils are mostly sandy loam of moderately coarse texture (Neily et al. 2003).

Site selection and data collection

Historical aerial photographs of Cape Breton Island taken in 1969 were compared to aerial photographs taken in 2009 to identify areas of forest canopy reduction caused by the outbreak. Ground surveys were subsequently used to select six forest edges that were created by the spruce budworm outbreak of 1974 – 1985 (Figure 2-1). The following criteria were used in the edge selection process, in order of decreasing importance: 1) the forest edge was adjacent to an area disturbed by the last spruce budworm outbreak, 2) the forest edge was accessible, 3) the forest area and the disturbed area extended at least 80 m from the edge in opposite directions, 4) the forest area and the disturbed area interiors (70 – 100 m from the edge) were located at least 100 m away from another edge, road, trail, or water body, 4) the forest area was fir-spruce dominated for at least 100 m from the edge into the interior, and 5) the elevation was relatively uniform across the edge gradient. A total of six sites were used in the study (Table 2-1). The furthest distance between two sites was 25 km while the shortest distance between two sites was 0.93 km.

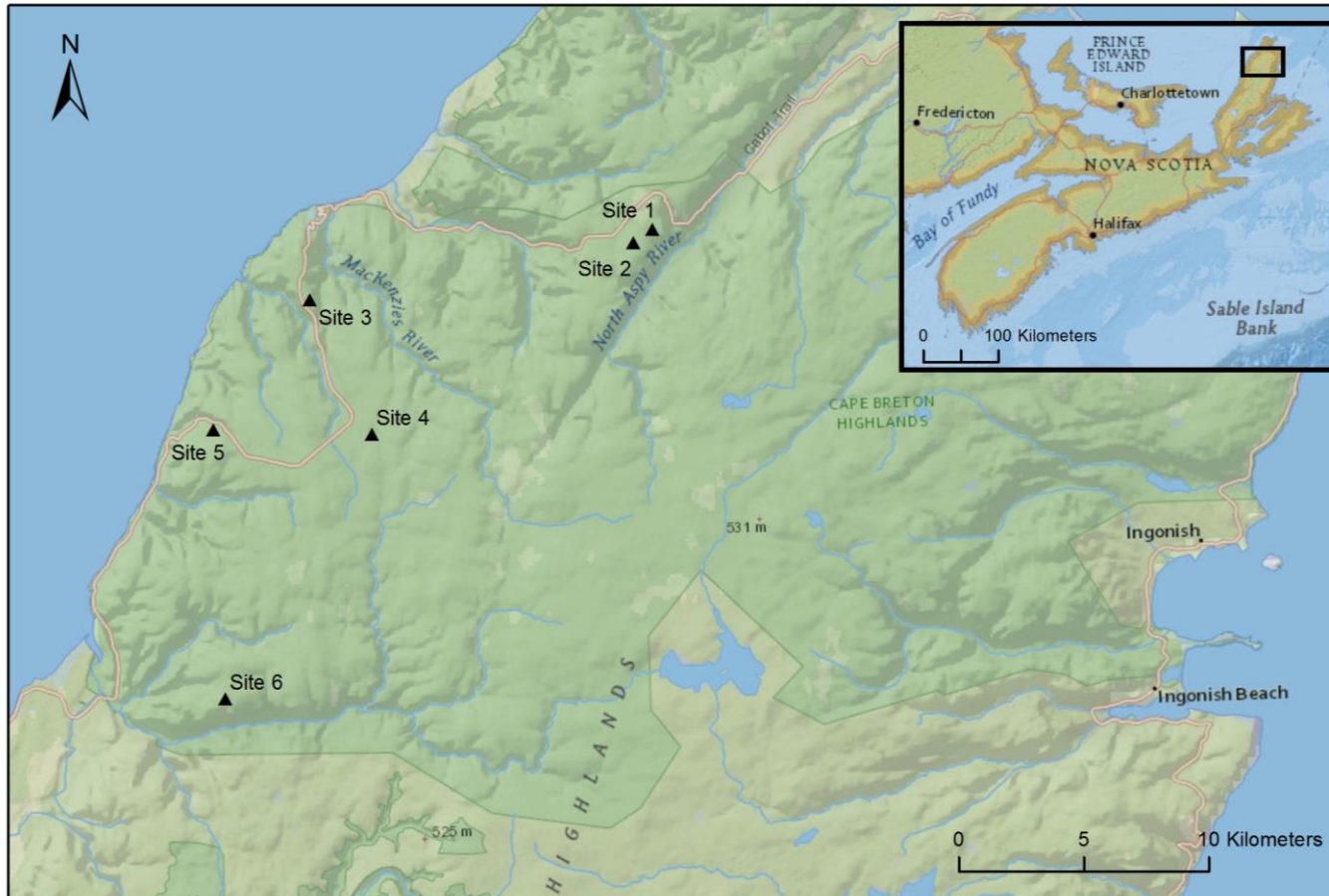


Figure 2-1. Map of study sites in Cape Breton Highlands National Park and the corresponding location in Nova Scotia (inset). Cartography credits by Caroline Franklin, National Geographic base map, National Geographic, Esri, DeLorme, NAVTEQ, iPC, NRCAN, METI, NASA Blue Marble, ESA GlobCover 2009 (Copyright notice: © ESA 2010 and UCLouvain), IUCN and UNEP-WCMC (2011), The World Database on Protected Areas (WDPA) Annual Release. Cambridge, UK: UNEP-WCMC.

Table 2-1. UTM coordinates, edge orientation, and elevation at the edge for individual study sites.

Site	UTM coordinates (East, North)*	Edge orientation (facing insect-disturbed area)	Elevation (metres above sea level)
1	678421, 5186826	213° SW	438
2	677648, 5186305	271° W	465
3	664632, 5184089	320° NW	352
4	667192, 5178624	39° NE	422
5	660735, 5178802	249° W	381
6	661314, 5168032	351° N	459

*Universal Transverse Mercator coordinates, Zone 20, NAD 83.

I established a 120 m long transect perpendicular to each of the six forest edges, which extended 60 m into both the forest and the disturbed area (Figure 2-2). The distance of 60 m was chosen to detect edge influence, which usually dissipates within 50 m from the edge in boreal forests (Harper et al. 2005). The forest edge in the middle of the transect at 0 m was defined as the point at which the intact forest transitioned into the insect disturbed area, or the limit of continuous canopy. Along each transect, nine 5 m x 20 m plots (length parallel to the forest edge) were established at the centres of the following distances from the edge: -60, -40, -20, -10, 0, 10, 20, 40, and 60 m (negative distances represent the insect disturbed side of the edge). Three plots (each 5 m x 20 m) were established in the insect disturbed area and in the forest area to represent reference conditions. The patchiness of the study area restricted disturbed area and forest reference plots from being established at every site so one site and two sites did not have disturbed area reference plots and forest reference plots, respectively. The majority of these plots were located 100 m away from the insect disturbed area-forest edge; however, some of the reference plots were located only 70 m away from the edge due to spatial constraints.

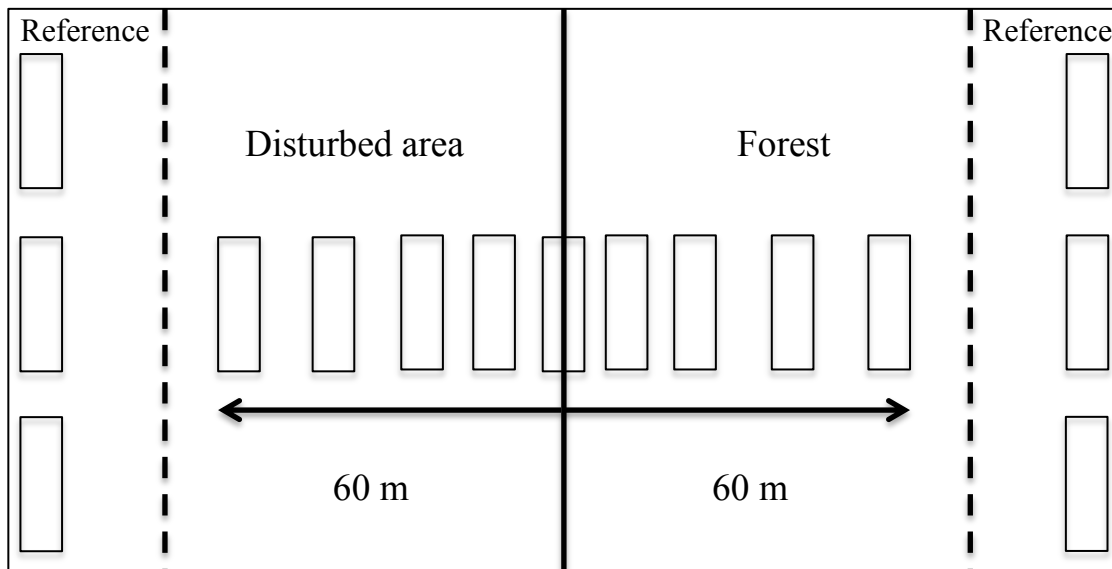


Figure 2-2. Sampling design illustrating an edge transect and corresponding reference plots at an insect disturbed area-forest study site used to measure primary response variables. Reference plots were 70 – 100 m away from the edge. Data were collected inside the rectangular plots (5 x 20 m each). Drawing is not to scale.

Data were collected from June to August 2012. Average canopy cover for each plot was calculated from four measurements taken facing each cardinal direction using a spherical densiometer. Species, relative canopy position, and diameter at breast height (dbh) of each tree (dbh \geq 5 cm) growing in the plots were recorded. The heights of the three tallest trees in each plot were measured using a laser rangefinder. The relative canopy position of the remaining trees was estimated as suppressed, intermediate, co-dominant, or dominant (Côté 2000). A classification system adapted from Thomas et al. (1979) (Table 2-2) was used to determine the decay stage of deadwood. Decay stage, relative canopy position, and diameter at breast height of each snag (\geq 5 cm dbh) located in the plots were recorded. The line intercept method was used to sample logs (\geq 5 cm in diameter) along the 20 m centre line of each plot and log diameter was measured at the point of line intersection.

Table 2-2. The classification system used to measure decay stage of deadwood (adapted from Thomas et al. 1979).

Decay class	Snags	Logs
Lightly decayed	Branches and twigs present; bark present	Boles with sound structural integrity; bark fully or somewhat intact; branch system may contain twigs and needles/leaves; little to no moss or other vegetation present on bole
Moderately decayed	Some branches detached; no twigs or needles/leaves; bark absent	Boles somewhat soft but maintain some structural integrity; bark detached; branch system absent; moss/vegetation covering bole
Severely decayed	No branches or bark; bole often hollow	Boles with very soft wood; often hidden as lumps on forest floor; covered in thick moss vegetation

The decomposition rate of wood was estimated using a time series approach with untreated popsicle sticks made of *Betula chinensis* (Chinese birch). Popsicle sticks were used as a standard substrate so that decomposition rates could be compared across the disturbed area-forest gradient. In the middle of each plot at five sites, six pre-weighed popsicle sticks were secured on the surface of the soil in June 2012. Two and four popsicle sticks from each plot were retrieved after 118 to 121 days (4 months) in October 2012 and after 337 to 342 days (11 months) in May 2013, respectively. Each stick was then oven dried at 60°C until a constant mass was achieved and subsequently weighed to determine percentage mass loss.

Due to time constraints, soil samples were collected only from three sites. Temperature, moisture, and pH were averaged from three sub-samples collected near the centre of each plot. In October 2012, a digital thermometer was used to obtain the temperature of soil approximately 15 cm below the surface. Soil moisture was determined using the gravimetric method (Jarrell et al. 1999) because it was inexpensive

and relatively simple compared to electronic methods (Strangeways 2003). The mass of each sub-sample (~ 5 g) was recorded prior to placing samples in an oven at 60°C. After a constant mass was achieved, initial mass was subtracted from final mass to estimate soil moisture. A digital pH meter was used to measure soil pH of each sub-sample (1:1 soil water mixture).

Data analysis

I analyzed edge influence on the following variables: canopy cover, live stem density of all trees together and of individual tree species (*Abies balsamea*, *Picea glauca*, *Betula papyrifera*, *Larix laricina*), tree species diversity, snag and log densities of three different decay classes (light decay, moderate decay, severe decay), snag breakage, decomposition rate, soil temperature, soil moisture, soil pH, and structural diversity. Tree species diversity was calculated using the Shannon-Weiner index. Structural diversity was determined separately for live trees, snags, and logs by creating mutually exclusive structural groups as ‘pseudo-species’ based on frequency (Appendix 2-A). The structural groups were then used to calculate the structural equitability index, which is a more suitable index compared to Shannon’s diversity index (structural diversity index = Shannon diversity index/ \ln (# pseudo-species)) (Valbuena et al. 2012). Total structural diversity index included all groups representing live stems, snags, and logs. Snag breakage was measured by calculating the percentage of snags with broken tops in each plot.

The randomized test of edge influence (RTEI) (Harper & Macdonald 2011) was used to quantify the distance of edge influence (DEI) for each of the variables under

investigation. Distance of edge influence is the distance over which a given response variable is significantly different compared to the reference ecosystem (Harper et al. 2005). Compared to other methodological approaches that estimate the distance of edge influence, the RTEI is considered one of the most effective as it considers randomization of the values in the reference ecosystem as well as of the values at the forest edge (Harper & Macdonald 2011). The no blocking method was used because not all of the study sites included reference plots. RTEI involved the following steps: 1) the observed difference between the mean of the reference values and the mean of the values at a given distance from the edge was calculated, 2) all values were combined and then randomly assigned as either edge or reference, 3) the calculation in step 1 was repeated for the randomized data, 4) steps 2 and 3 were repeated 5000 times to obtain a distribution of differences from the randomization of the data. The percentile of the observed difference within the distribution of randomized differences was subsequently used as the p-value. Using a two-tailed test, the mean edge value was considered to be significantly different than the reference values when the p-value was in the upper 97.5 or lower 2.5 percentiles. The analysis was performed for each distance along the edge transect (-60, -40, -20, -10, 0, 10, 20, 40, 60 m) using the disturbed area reference and forest reference separately. To address the issue of multiple testing, DEI was only considered significant if there were at least two consecutive significant p-values.

3. Results

Spruce budworm outbreak-forest edges were abrupt zones of transition between adjoining disturbed areas and relatively undisturbed forest. Edge influence did not extend into the forest for any of the response variables under investigation when compared to the forest reference, suggesting that the forest side of the edge was not significantly different from the undisturbed forest.

The transition zone was approximately 10 m in width and extended from what was arbitrarily defined as the forest edge (the limit of continuous canopy) into the disturbed area. Within this narrow zone of transition, live stem density and canopy cover were significantly different than both the disturbed area reference and forest reference (Figure 2-3a-b). Canopy cover was reduced by half and live stem density decreased from 1300 ± 358 trees/ha to 400 ± 103 trees/ha from the edge to 10 m into the disturbed area. Similar to canopy cover and live stem density, maximum tree height also increased from the disturbed area into the forest and revealed a sigmoidal shaped pattern across the edge gradient (Figure 2-3c). Maximum tree height was highest 10 m into the forest from the edge and was almost twice as high in the forest reference compared to the disturbed area reference.

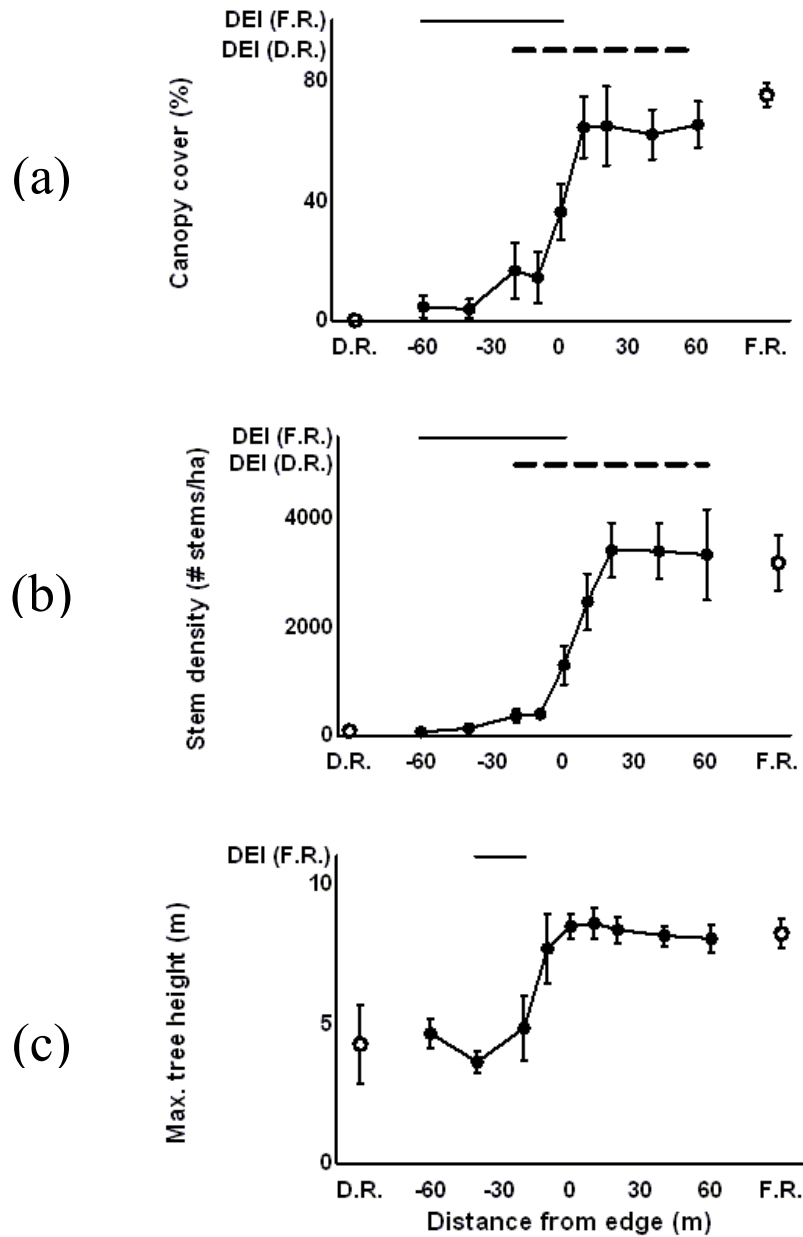


Figure 2-3. Mean (a) canopy cover, (b) live stem density, and (c) maximum tree height along the insect disturbed area-forest edge. Bars represent ± 1 standard error. Open circles represent values for the disturbed area reference (D.R.) and forest reference (F.R.). Solid and dashed horizontal lines at the top of plots indicate the distance of edge influence (DEI) for values compared to the forest reference and disturbed area reference, respectively.

Only four tree species were identified in the study area. *Abies balsamea* represented the greatest density at every distance from the edge, except in the disturbed area reference where *Picea glauca* and *Betula papyrifera* were the dominant species (Table 2-3). *Larix laricina* was absent except at 40 m and at 60 m from the edge into the forest and in the forest reference. Tree species diversity was zero at 20 m to 60 m from the edge into the disturbed area and values were significantly higher 0 m to 10 m from the edge into the forest compared to the disturbed area reference.

Table 2-3. Mean stem density of individual species and species diversity at different distances from the spruce budworm disturbed area-forest edge. Negative values represent the distances from the edge on the disturbed side. Distance of edge influence (DEI) is the set of consecutive distances that were significantly different than the disturbed area reference (D.R.) or the forest reference (F.R.).

Distance from edge (m)	Stem density (#/ha) (± 1 SE)				Species diversity (± 1 SE)
	<i>Abies balsamea</i>	<i>Picea glauca</i>	<i>Betula papyrifera</i>	<i>Larix laricina</i>	
D.R.	7 \pm 7	20 \pm 15	60 \pm 38	0 \pm 0	0.09 \pm 0.06
-60	50 \pm 50	17 \pm 17	0 \pm 0	0 \pm 0	0.00 \pm 0.00
-40	100 \pm 100	33 \pm 21	0 \pm 0	0 \pm 0	0.00 \pm 0.00
-20	283 \pm 145	83 \pm 54	0 \pm 0	0 \pm 0	0.00 \pm 0.00
-10	283 \pm 101	117 \pm 83	0 \pm 0	0 \pm 0	0.10 \pm 0.10
0	1083 \pm 376	217 \pm 75	0 \pm 0	0 \pm 0	0.46 \pm 0.11
10	1750 \pm 530	717 \pm 341	0 \pm 0	0 \pm 0	0.43 \pm 0.14
20	2250 \pm 706	1167 \pm 528	0 \pm 0	0 \pm 0	0.35 \pm 0.12
40	2167 \pm 685	1183 \pm 561	0 \pm 0	50 \pm 50	0.31 \pm 0.13
60	2067 \pm 1037	1200 \pm 636	17 \pm 17	50 \pm 50	0.43 \pm 0.14
F.R.	1458 \pm 545	1717 \pm 587	0 \pm 0	8 \pm 8	0.28 \pm 0.10
DEI (m)					
D.R.	-20 to 60	0 to 60	--	--	0 to 10
F.R.	-60 to -40	-60 to 0	--	--	-60 to -20

Snag density increased from the disturbed area into the forest, where density was highest 20 m from the edge on the forest side (Figure 2-4a). The majority of snags on the disturbed side of the edge were moderately or severely decayed whereas a greater proportion of snags located over 10 m from the edge into the forest were lightly decayed (Figure 2-4a) and of smaller diameter (Appendix 2-C). Edge influence on overall snag density extended further when compared to the disturbed area (DEI = - 20 m to 60 m) than when compared to the forest reference (DEI = -60 m to -40 m). Severely decayed snag density did not exhibit significant edge influence and extent of edge influence on lightly decayed snag density did not surpass the forest edge. Forest edge creation did not significantly affect the proportion of broken snags despite a general decrease from the disturbed area into the forest (Figure 2-4b).

In contrast to overall snag density, total log density generally declined from the disturbed area into the forest (Figure 2-4c) yet there was no significant edge influence. Moderately decayed log density was the only decay class to exhibit edge influence (DEI = -40 m to -20 m compared to the forest reference). Among the three decay classes, moderately decayed was the most dominant followed by severely decayed and then lightly decayed.

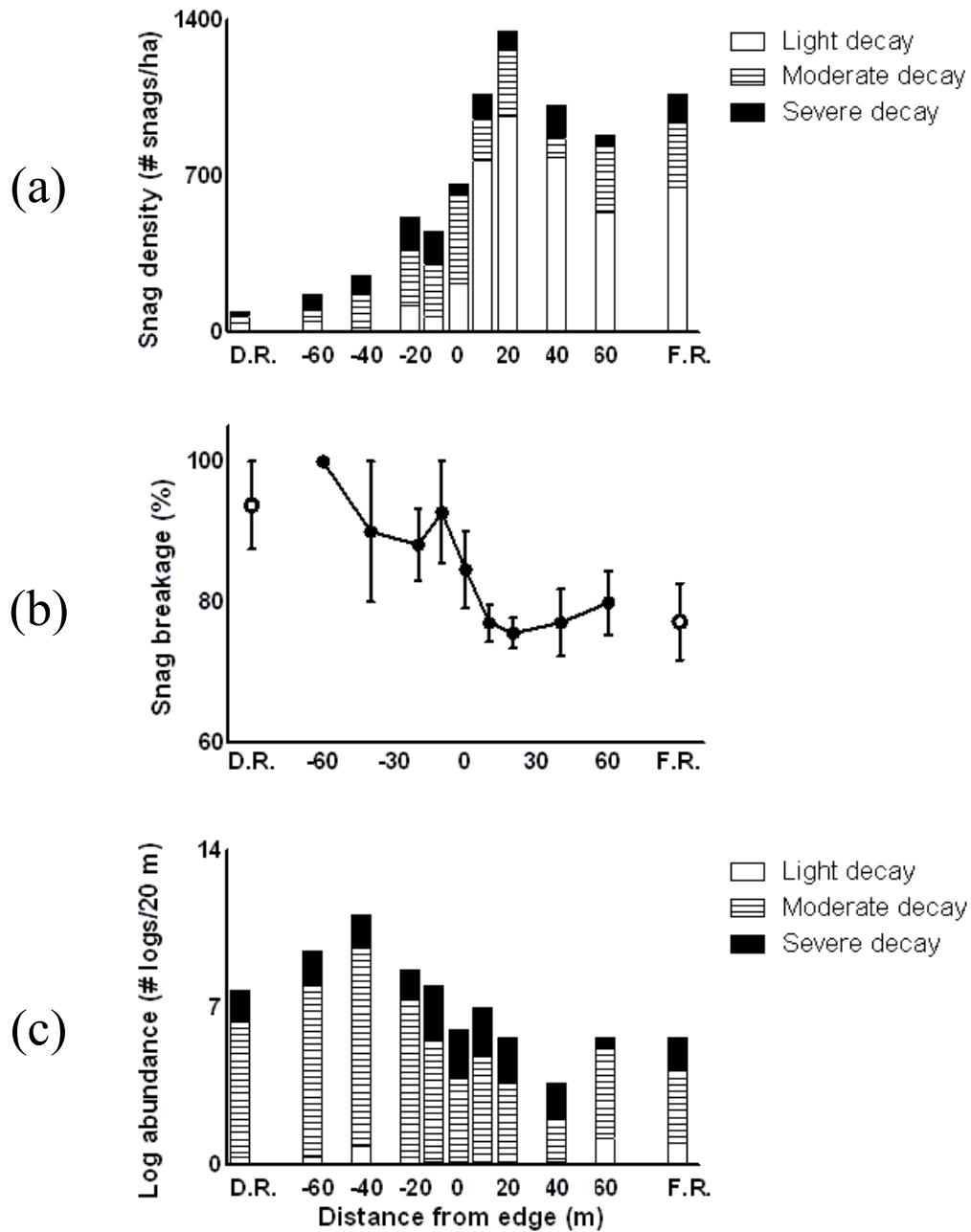


Figure 2-4. Mean (a) snag density by decay class, (b) snag breakage, and (c) log abundance by decay class along the insect disturbed area-forest edge. In (b), open circles represent values for disturbed area reference (D.R.) and forest reference (F.R.) and bars represent ± 1 standard error. Standard error values for (a) and (c) are included in Appendix 2-B.

Decomposition rate fluctuated across the spruce budworm-induced forest edges despite slower rates in the forest reference compared to the disturbed area reference (Table 2-4). Average decomposition rates after 4 months and 11 months were significantly greater 10 m from the edge into the forest compared to the disturbed area reference. Soil temperature, moisture, and pH did not exhibit significant edge influence (Table 2-4).

Table 2-4. Mean decomposition after 4 months and after 11 months, and soil temperature, moisture, and pH at different distances from the spruce budworm disturbed area-forest edge (D.R. = disturbed area reference, F.R. = forest reference). Negative values represent the distances from the edge on the disturbed side. Asterisks indicate distances from the edge that were significantly different than the disturbed area reference.

Distance from edge (m)	Decomposition \pm 1 SE (% mass change)		Soil variables		
	After 4 months	After 11 months	Temperature ($^{\circ}$ C) \pm 1 SE	Moisture (%) \pm 1 SE	pH \pm 1 SE
D.R.	21.9 \pm 2.3	36.3 \pm 2.1	17.7 \pm 0.7	49.4 \pm 5.9	4.3 \pm 0.1
-60	21.6 \pm 3.1	30.0 \pm 1.4	18.1 \pm 0.9	57.2 \pm 7.9	4.2 \pm 0.1
-40	14.9 \pm 0.6	29.3 \pm 2.5	17.9 \pm 0.9	68.1 \pm 16.6	4.1 \pm 0.1
-20	15.7 \pm 1.9	30.9 \pm 3.0	17.0 \pm 0.7	64.9 \pm 11.7	4.5 \pm 0.1
-10	17.2 \pm 2.3	29.1 \pm 2.7	17.3 \pm 0.9	43.5 \pm 12.5	4.7 \pm 0.0
0	18.2 \pm 2.9	26.8 \pm 2.0	16.6 \pm 0.9	60.4 \pm 12.0	4.4 \pm 0.0
10	14.2 \pm 0.7*	24.9 \pm 2.2*	16.5 \pm 0.8	45.4 \pm 11.2	4.5 \pm 0.1
20	20.4 \pm 3.0	25.2 \pm 2.5	16.4 \pm 0.8	48.4 \pm 12.5	4.6 \pm 0.1
40	20.1 \pm 3.5	29.9 \pm 3.7	16.5 \pm 1.0	51.7 \pm 4.1	4.7 \pm 0.1
60	15.0 \pm 1.5	23.0 \pm 1.2*	16.6 \pm 1.0	50.5 \pm 9.0	4.7 \pm 0.0
F.R.	14.8 \pm 1.3	24.0 \pm 1.5	14.8 \pm 0.7	29.3 \pm 2.1	4.5 \pm 0.0

The forest side of the edge was characterized by greater tree and snag structural diversities but lower log structural diversity compared to the disturbed side of the edge (Figure 2-5). When compared to the forest reference, tree and snag structural diversities were only significantly different on the disturbed side (Figure 2-5a-b). Edge influence on tree structural diversity (DEI = -20 m to 60 m) was slightly less than snag structural diversity (DEI = -40 m to 60 m) when compared to the disturbed area reference. Log structural diversity did not experience significant edge influence compared to either reference (Figure 2-5c) and overall structural diversity was significantly different up to 10 m from the edge into the disturbed area when compared to the forest reference (Figure 2-5d).

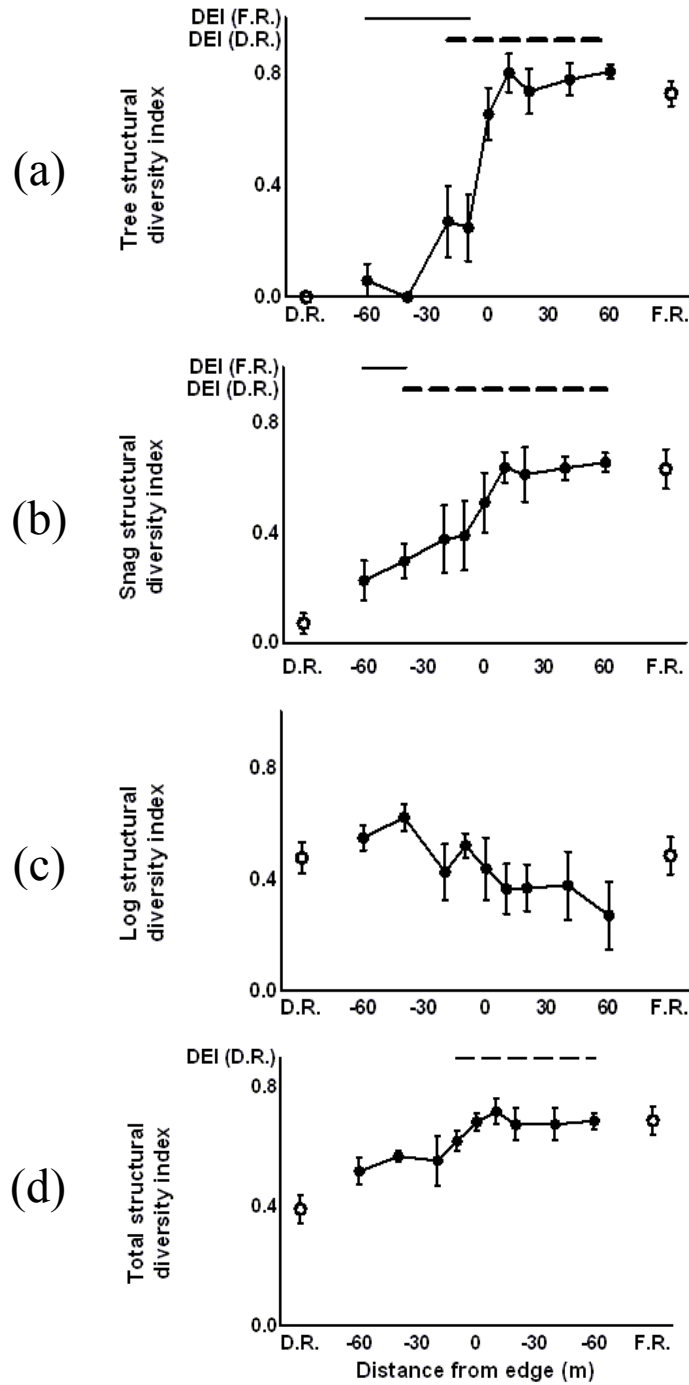


Figure 2-5. Mean structural diversity index for (a) live trees, (b) snags, (c) logs, and (d) all structural components combined along the insect disturbed area-forest edge. Bars represent ± 1 standard error. Open circles represent values for disturbed area reference (D.R.) and forest reference (F.R.). Solid and dashed horizontal lines at the top of plots indicate distance of edge influence (DEI) for values compared to the forest reference and disturbed area reference, respectively.

4. Discussion

Structural changes caused by the latest spruce budworm outbreak in Cape Breton Highlands National Park were still evident three decades post-edge creation. As expected, the disturbed side of the edge contained fewer trees and lower canopy cover than the forest side as a result of heavy tree mortality from the insect outbreak. Shorter trees, which were premature during heavy insect infestation, were the only surviving stems in the disturbed areas. The outbreak caused greater mortality in taller trees since the insect defoliator prefers more mature host trees. Tree growth rates in disturbed areas can be slower than those in intact forests (Chapman & Chapman 1997), which could also explain the relatively low tree height on the insect disturbed side of the edge. In addition to distinct structural differences between the disturbed area and the relatively undisturbed forest, overstorey structure at the interface between the areas was unique.

Narrow transition zones resulting from the spruce budworm outbreak

The narrowness of the 10 m wide transition zone that characterized the spruce budworm-induced edges suggests that the edges were abrupt as the contrast in vegetation structure between the disturbed area and adjacent forest was apparent over a relatively short distance. The underlying mechanisms responsible for the abruptness of the budworm-induced forest edges are unknown but here I present and discuss a few hypotheses. *Abies balsamea* and *Picea glauca*, the two main host species of the spruce budworm, were the dominant tree species on the forest side of the edge so host density was not the cause for cessation of the outbreak at the edge. Even though spruce budworm

populations can decline due to disease (Royama 1984) and predation (Régnière & Nealis 2007), these local ecological factors probably would have caused more gradual forest edges. The outbreak was most likely advancing steadily and then stopped due to inclement weather such as high rainfall and freezing temperatures at the time of larvae emergence and post-emergence, respectively (Sanders & Lucuik 1985). Therefore, the abruptness of the spruce budworm-induced forest edges throughout Cape Breton Highlands National Park was likely caused by sudden changes in regional climate.

It is also unclear why there was a lack of significant edge influence on forest structure using the forest reference, which suggests that the edge was structurally similar to undisturbed forest. High resilience to natural disturbances in boreal forests could be responsible for the negligible influence on vegetation although prior research indicated significant edge effects in boreal ecosystems. For instance, distance of edge influence on forest structure extended up to 10 m from the edge into the forest at anthropogenic edges (Harper & Macdonald 2002; Rheault et al. 2003; Harper et al. 2004). At inherent forest edges, the distance of edge influence on primary responses extended from the edge up to 20 m into forest (Harper & Macdonald 2001; Komonen 2009). At natural edges created by fire, forest structure response variables had distance of edge influence that extended up to 40 m from the edge into the forest (Harper et al. 2004). Boundaries created by different natural disturbances have distinct vegetative characteristics (McIntire & Fortin 2006), which could potentially explain the inconsistent findings for edge influence.

Structural development since edge creation

Forest edges are not static hence structural attributes, such as tree height, can change over time. Maximum tree height could have been highest 10 m from the edge into the forest due to increased resource availability such as light, which would enhance tree growth close to the edge. Murphy (2013) measured tree radial growth along some of the transects and found higher average growth rates post edge creation compared to pre-budworm outbreak growth rates at 10 m from the edge into the forest. Although trees growing at 0 m receive more light exposure than those growing at 10 m, they are also subjected to higher wind speeds (Chen et al. 1995; Davies-Colley et al. 2000), which may have restricted tree height directly at the edge.

Contributions to deadwood input and deadwood transformation continued to persist during the three decades after edge creation. Snag density increased yet log density decreased from the disturbed area into the forest interior. Insect caused-tree mortality initially resulted in standing deadwood. The majority of the stems that died from insect defoliation have since fallen and become logs hence the greater log density and lower snag density on the disturbed side of the edge compared to the forest side. After the collapse of the spruce budworm outbreak in Cape Breton, 17% of the dead trees had already blown down after four years (Ostaff & MacLean 1989). Furthermore, blowdown continues to play an important role in the transformation of snags to logs up to 15 years after outbreak collapse (Spence & MacLean 2012). Higher percentages of snag breakage in the disturbed area in my study and in Ostaff & MacLean (1989) suggest stronger winds compared to the forest. While studying maintained edges, Davies-Colley et al. (2000) concluded that wind speeds were consistently higher up to 80 m from the

edge into the disturbed area than in the forest side of the edge. Therefore, the majority of snags resulting from the insect outbreak have most likely already blown over within the last few decades to become logs.

An examination of deadwood in different stages of decay provides insight into the relationship between the process of decomposition and time since disturbance. Compared to the disturbed area reference, decomposition rate was significantly slower 10 m from the edge into the forest, where the abundance of lightly decayed snags was relatively high. According to results obtained from dendrochronology techniques used to correlate snag degradation classification systems with predictions of time since death (Campbell & Laroque 2007; Aakala et al. 2008; Angers et al. 2012), snags classified as light, moderate, and severe decay experienced death post-outbreak, during the outbreak, and pre-outbreak, respectively. Since lightly decayed snags are estimated to have died within the past 15 years (Aakala et al. 2008; Angers et al. 2012), higher proportions of lightly decayed, small diameter snags on the forest side of the edge compared to the disturbed side were most likely the result of self-thinning post-outbreak. Greater light availability on the forest side of the edge compared to the forest interior may have caused increased sapling growth following edge creation, which then led to self-thinning and higher lightly decayed snag density near the edge.

Previous research on forest edges created by wildfire indicated that the forest edge contained greater amounts of more recent deadwood compared to the disturbed area (Harper et al., unpublished) but a similar phenomenon was only observed for snags at the spruce budworm-induced edges. Three hypotheses for more recent deadwood at the edge compared to the disturbed area are: 1) mortality occurs later at edges compared to the

disturbed area due to partial disturbance at edges, 2) windthrow contributes more recent deadwood post-edge creation, and 3) decomposition is slower at the edge compared to the disturbed area (Harper et al., unpublished). More recently decayed snags at the spruce budworm-forest edges were more likely the result of self-thinning than partial disturbance due to the high abundance of small-diameter trees at the edge. The lack of significant edge influence on snag breakage and log abundance suggest that windthrow was indifferent at the edge. Therefore, my results support the third hypothesis because decomposition rate was statistically significantly slower 10 m from the edge into the forest when compared to the disturbed area reference.

The lack of extensive edge influence on decomposition may reflect the absence of significant edge influence on the abundance of logs in separate decay classes. The decomposition rates represent decomposition of deadwood on the ground rather than of standing deadwood because the sticks were placed on the surface of the soil similar to logs. Furthermore, although the popsicle sticks were used as a common substrate to provide comparisons of decomposition rates relative to distance from edge, they could not provide an accurate depiction of decomposition rates on all species in the study area since wood decay rates vary depending on plant species (Yatskov et al. 2003; Freschet et al. 2012).

Even though the spruce budworm outbreak contributed a substantial amount of deadwood to the area, the scarcity of live trees lowered total structural diversity in the severely disturbed area. Total structural diversity was highest 10 m from the edge into the forest, which suggests that the interface may function as a distinctive habitat containing a mixture of live trees, logs, and snags. Both snags and logs are important

habitat features for the endangered American marten (*Martes americana*) (Payer & Harrison 2000), therefore the insect disturbed area-forest edge may play an important role in habitat quality by providing a variety of structural components. Future studies could develop more complex structural indices that give extra weight to specific or desirable habitat characteristics (Spies & Franklin 1988).

Habitat quality and edge characteristics should be monitored over time. Forest edges recede after isolation (Gascon et al. 2000) hence the position of the spruce budworm-induced edges could have shifted since edge creation. More specifically, the distinct contrast in overstorey structure could have initially been situated approximately 10 m into the disturbed area from what was considered the edge at time of sampling. Future studies could incorporate long-term monitoring into sampling designs to better understand the temporal dynamics of vegetation structure at forest edges.

5. Conclusions

Transition zones of approximately 10 m between the disturbed areas and intact forests characterized the spruce budworm-induced edges in Cape Breton Highlands National Park. Initial effects of edge creation included reduced canopy cover and tree density compared to the undisturbed forest. Tree mortality caused by the insect outbreak resulted in snags, which have transformed into logs since the collapse of the outbreak. In contrast to higher log abundance on the disturbed side of the edge, the forest side of the edge contained more snags, the majority of which were recently decayed and resulted from self-thinning. Higher structural diversity at the spruce budworm outbreak-forest

edge compared to the disturbed area reference suggests that the edge may play a more important role in providing habitat for some species. Evidence of the initial effects of edge creation in addition to structural changes since the insect disturbance reveals that the spruce budworm-induced edges are not merely intermediate zones of transition between disturbed areas and adjacent forests, but are active features of the landscape characterized by unique structural attributes.

6. Literature cited

- Aakala, T., Kuuluvainen, T., Gauthier, S. & De Grandpré, L. 2008. Standing dead trees and their decay-class dynamics in the northeastern boreal old-growth forests of Quebec. *Forest Ecology and Management* 255: 410-420.
- Angers, V.A., Bergeron, Y. & Drapeau, P. 2012. Morphological attributes and snag classification of four North American boreal tree species: Relationships with time since death and wood density. *Forest Ecology and Management* 263: 138-147.
- Baskerville, G.L. 1975. Spruce budworm: Super silviculturist. *The Forestry Chronicle* 51: 138-140.
- Belle-Isle, J. & Kneeshaw, D. 2007. A stand and landscape comparison of the effects of a spruce budworm (*Choristoneura fumiferana* (Clem.)) outbreak to the combined effects of harvesting and thinning on forest structure. *Forest Ecology and Management* 246: 163-174.
- Belyea, R.M. 1952. Death and deterioration of balsam fir weakened by spruce budworm defoliation in Ontario. Part II. An assessment of the role of associated insect species in the death of severely weakened trees. *Canadian Journal of Forestry* 50: 729-738.
- Blais, J.R. 1968. Regional variation in susceptibility of eastern North American forests to budworm attack based on history of outbreaks. *The Forestry Chronicle* 44: 17-23.
- Blais, J.R. 1983. Trends in the frequency, extent, and severity of spruce budworm outbreaks in eastern Canada. *Canadian Journal of Forest Research* 13: 539-547.

- Bonan, G.B. & Shugart, H.H. 1989. Environmental factors and ecological processes in boreal forests. *Annual Review of Ecology and Systematics* 20: 1-28.
- Bouchard, M., Kneeshaw, D. & Bergeron, Y. 2006. Forest dynamics after successive spruce budworm outbreaks in mixedwood forests. *Ecology* 87: 2319-2329.
- Bouchard, M., Kneeshaw, D. & Messier, C. 2007. Forest dynamics following spruce budworm outbreaks in the northern and southern mixedwoods of central Quebec. *Canadian Journal of Forest Research* 37: 763-772.
- Boulanger, Y. & Arseneault, D. 2004. Spruce budworm outbreaks in eastern Quebec over the last 450 years. *Canadian Journal of Forest Research* 34: 1035-1043.
- Campbell, L.J. & Laroque, C.P. 2007. Decay progression and classification in two old-growth forests in Atlantic Canada. *Forest Ecology and Management* 238: 293-301.
- Chapman, C.A. & Chapman, L.J. 1997. Forest regeneration in logged and unlogged forests of Kibale National Park, Uganda. *Biotropica* 29: 396-412.
- Chen, J., Franklin, J.F. & Spies, T.A. 1995. Growing-season microclimatic gradients from clearcut edges into old-growth douglas-fir forests. *Ecological Applications* 5: 74-86.
- Côté, M. 2000. *Dictionnaire de la Foresterie. Dictionary of Forestry*. Ordre des ingénieurs forestiers du Québec, Les Presses de l'Université Laval, Québec, Canada.
- D'Aoust, V., Kneeshaw, D. & Bergeron, Y. 2004. Characterization of canopy openness before and after a spruce budworm outbreak in the southern boreal forest. *Canadian Journal of Forest Research* 34: 339-352.
- Davies-Colley, R.J., Payne, G.W. & van Elswijk, M. 2000. Microclimate gradients across a forest edge. *New Zealand Journal of Ecology* 24: 111-121.
- Environment Canada. 2013. Canadian climate normals or averages 1971-2000. National Climate Data and Information Archive. Retrieved from www.climate.weatheroffice.gc.ca on 30 March 2013.
- Freschet, G.T., Weedon, J.T., Aerts, R. van Hal, J.R. & Cornelissen, J.H.C. 2012. Interspecific differences in wood decay rates: insights from a new short-term method to study long-term wood decomposition. *Journal of Ecology* 100: 161-170.

- Gascon, C., Williamson, G.B. & da Fonseca, G. A. B. 2000. Receding forest edges and vanishing reserves. *Science* 288: 1356-1358.
- Harper, K.A. & Macdonald, S.E. 2001. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. *Ecology* 82: 649-659.
- Harper, K.A. & Macdonald, S.E. 2002. Structure and composition of edges next to regenerating clear-cuts in mixed-wood boreal forest. *Journal of Vegetation Science* 13: 535-546.
- Harper, K.A. & Macdonald, S.E. 2011. Quantifying distance of edge influence: a comparison of methods and a new randomization method. *Ecosphere* 2: art94.
- Harper, K.A., Lesieur, D., Bergeron, Y. & Drapeau, P. 2004. Forest structure and composition at young fire and cut edges in black spruce boreal forest. *Canadian Journal of Forest Research* 34: 289-302.
- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J.Q., Brososke, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. & Esseen, P.A. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19: 768-782.
- James, P.M., Fleming, R.A. & Fortin, M.-J. 2010. Identifying significant scale-specific spatial boundaries using wavelets and null models: spruce budworm defoliation in Ontario, Canada as a case study. *Landscape Ecology* 25: 873-887.
- Jarrell, W.M., Armstrong, D.E., Grigal, D.F., Kelly, E.F., Monger, H.C. & Wedin, D.A. 1999. In Robertson, G.P., Coleman, D.C., Bledsoe, C.S. & Sollins, P. (eds.) *Standard soil methods for long-term ecological research*, pp. 55-73. Oxford University Press, New York, NY, US.
- Komonen, A. 2009. Forest characteristics and their variation along the lakeshore-upland ecotone. *Scandinavian Journal of Forest Research* 24: 515-526.
- MacLean, D.A. 1984. Effects of spruce budworm outbreaks on the productivity and stability of balsam fir forests. *The Forestry Chronicle* 60: 273-279.
- MacLean, D.A. 1988. Effects of spruce budworm outbreaks on vegetation, structure, and succession of balsam fir forests on Cape Breton Island, Canada. In M.J.A. Werger, M.J.A., van der Aart, P.J.M., During, H.J. & Verhoeven, J.T.A. (eds.) *Plant form and vegetation structure*, pp. 253-261. SPB Academic Publishing, The Hague, The Netherlands.

- MacLean, D.A. & Ostaff, D.P. 1989. Patterns of balsam fir mortality caused by an uncontrolled spruce budworm outbreak. *Canadian Journal of Forest Research* 19: 1087-1095.
- Morin, H. 1994. Dynamics of balsam fir forests in relation to spruce budworm outbreaks in the boreal zone of Quebec. *Canadian Journal of Forest Research* 24: 730-741.
- Murphy, L. 2013. *Dendrochronological analysis of balsam fir (Abies balsamea) radial tree-ring growth across edges created by a spruce budworm outbreak*. H.BSc. thesis, Saint Mary's University, Halifax, NS, Canada.
- Neily, P.D., Quigley, E., Benjamin, L., Stewart, B. & Duke, T. 2003. *Ecological land classification for Nova Scotia (Volume 1 – Mapping Nova Scotia's Terrestrial Ecosystems)*. Nova Scotia Department of Natural Resources, Halifax, NS, Canada.
- Ostaf, D.P. & MacLean, D.A. 1989. Spruce budworm populations, defoliation, and changes in stand condition during an uncontrolled spruce budworm outbreak on Cape Breton Island, Nova Scotia. *Canadian Journal of Forest Research* 19: 1077-1086.
- Parks Canada. 2010. *Cape Breton Highlands National Park of Canada management plan*. Parks Canada, Ingonish Beach, NS, Canada.
- Payer, D.C. & Harrison, D.J. 2000. Structural differences between forests regenerating following spruce budworm defoliation and clear-cut harvesting: implications for marten. *Canadian Journal of Forest Research* 30: 1965-1972.
- Régnière, J. & Nealis, V.G. 2007. Ecological mechanisms of population change during outbreaks of the spruce budworm. *Ecological Entomology* 32: 461-477.
- Rheault, H., Drapeau, P., Bergeron, Y. & Esseen, P.-A. 2003. Edge effects on epiphytic lichens in managed black spruce forests of eastern North America. *Canadian Journal of Forest Research* 33: 23-32.
- Royama, T. 1984. Population dynamics of the spruce budworm *Choristoneura fumiferana*. *Ecological Monographs* 54: 429-462.
- Sanders, C.J., & Lucuik, G.S.M. 1985. Effect of weather on spruce budworm populations. In Sanders, C.J., Stark, R.W., Mullins, E.J. & Murphy, J. (eds.) *Recent advances in spruce budworms research: proceedings of the CANUSA spruce budworms research symposium, September 16-20, 1984, Bangor, Maine*, pp. 90-91. Minister of Supply and Services Canada, Ottawa, ON, Canada.

- Smith, C., Beazley, K., Duinker, P. & Harper, K.A. 2010. The impact of moose (*Alces alces andersoni*) on forest regeneration following a severe spruce budworm outbreak in the Cape Breton Highlands, Nova Scotia, Canada. *Alces* 46: 135-150.
- Spence, C.E. & MacLean, D.A. 2012. Regeneration and stand development following a spruce budworm outbreak, spruce budworm inspired harvest, and salvage harvest. *Canadian Journal of Forest Research* 42: 1759-1770.
- Spies, T.A. & Franklin, J.F. 1988. Old-growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. *Natural Areas Journal* 8: 190-201.
- Strangeways, I. 2003. *Measuring the Natural Environment*. 2nd ed. Cambridge University Press, Cambridge, UK.
- Thomas, J.W., Anderson, R.G., Maser, C. & Bull, E.L. 1979. Snags. In Thomas, J.W. (ed.) *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*, pp. 60-77. U.S. Department of Agriculture Forest Service, Portland, OR, USA.
- Valbuena, R., Packalén, P., Martín-Fernández, S. & Maltamo, M. 2012. Diversity and equitability ordering profiles applied to study forest structure. *Forest Ecology and Management* 276: 185-195.
- Webb, K.T. & Marshall, I.B. 1999. *Ecoregions and ecodistricts of Nova Scotia*. Agriculture and Agri-Food Canada, Truro, NS, and Environment Canada, Hull, QC, Canada.
- Yatskov, M., Harmon, M.E. & Krankina, O.N. 2003. A chronosequence of wood decomposition in boreal forests of Russia. *Canadian Journal of Forest Research* 33: 1211-1226.

Appendix 2-A: Classification of structural groups of trees, snags, and logs used to calculate structural diversity indices.

	Relative height	Diameter (cm)	Decay stage
Live trees			
Suppressed	Suppressed	> 5	
Small diameter intermediate height	Intermediate	5 – 10	
Large diameter intermediate height	Intermediate	> 10	
Small diameter tall	Co-dominant, Dominant	5 – 10	
Medium diameter tall	Co-dominant, Dominant	11 – 15	
Large diameter tall	Co-dominant, Dominant	> 15	
Snags			
Stump	< 3 m	All	1 – 3
Small diameter suppressed recent	Suppressed	5 – 10	1
Small diameter suppressed decayed	Suppressed	5 – 10	2, 3
Large diameter recent	Suppressed, Intermediate, Co-dominant, Dominant	> 10	1
Large diameter suppressed decayed	Suppressed	> 10	2, 3
Small diameter tall recent	Intermediate, Co-dominant, Dominant	5 – 10	1
Tall decayed	Intermediate, Co-dominant, Dominant	All	2, 3
Logs			
Small lightly decayed		5 – 10	1
Small moderately decayed		5 – 10	2
Small well decayed		5 – 10	3
Medium lightly decayed		11 – 15	1
Medium moderately decayed		11 – 15	2
Medium well decayed		11 – 15	3
Large lightly decayed		> 15	1
Large moderately decayed		> 15	2
Large well decayed		> 15	3

Appendix 2-B: Mean snag and log densities of each decay class at different distances from the spruce budworm disturbed area-forest edge and corresponding distance of edge influence (DEI) when compared to the disturbed area reference and forest reference.

Negative values represent the distances from the edge on the disturbed side.

Distance from edge (m)	Snag density (# snags/ha) \pm 1 SE			Log abundance (# logs/20 m) \pm 1 SE		
	Light decay	Moderate decay	Severe decay	Light decay	Moderate decay	Severe decay
Disturbed area reference	42 \pm 23	25 \pm 11	25 \pm 11	.3 \pm .2	6.1 \pm 1.0	1.4 \pm .4
-60	50 \pm 34	50 \pm 22	67 \pm 33	.3 \pm .3	7.7 \pm 3.4	1.5 \pm .5
-40	17 \pm 17	150 \pm 81	83 \pm 40	.8 \pm .5	8.8 \pm 1.3	1.5 \pm .4
-20	117 \pm 65	250 \pm 109	150 \pm 76	0 \pm 0	7.3 \pm 1.9	1.3 \pm .6
-10	67 \pm 42	233 \pm 61	150 \pm 81	.2 \pm .2	5.3 \pm 1.4	2.5 \pm .8
0	217 \pm 83	400 \pm 106	50 \pm 34	.2 \pm .2	3.7 \pm 1.3	2.2 \pm .7
10	767 \pm 211	183 \pm 48	117 \pm 48	.2 \pm .2	4.7 \pm 1.7	2.2 \pm 1.1
20	967 \pm 246	300 \pm 68	83 \pm 31	0 \pm 0	3.7 \pm 1.6	2.0 \pm .9
40	783 \pm 170	83 \pm 31	150 \pm 56	.2 \pm .2	1.8 \pm .7	1.7 \pm .7
60	533 \pm 184	300 \pm 93	50 \pm 34	1.2 \pm .8	4.0 \pm 1.7	.5 \pm .3
Forest reference	650 \pm 110	292 \pm 85	125 \pm 41	1.0 \pm .4	3.2 \pm .6	1.5 \pm .5
DEI (m)						
D.R.	0 to 60	-20 to 60	--	--	--	--
F.R.	-60 to 0	--	--	--	-40 to -20	--

Appendix 2-C: Mean snag densities of each decay class and dbh (diameter at breast height) class at different distances from the spruce budworm disturbed area-forest edge.

Negative values represent the distances from the edge on the disturbed side.

Snag decay class dbh class (cm)	Average snag density (# snags/ha) \pm 1 SE								
	Light			Moderate			Severe		
	5 – 10	11 – 15	> 15	5 – 10	11 – 15	> 15	5 – 10	11 – 15	> 15
Disturbed area reference	20 \pm 20	7 \pm 7	0 \pm 0	7 \pm 7	0 \pm 0	13 \pm 9	7 \pm 7	0 \pm 0	27 \pm 12
-60	50 \pm 34	0 \pm 0	0 \pm 0	17 \pm 17	0 \pm 0	33 \pm 21	17 \pm 17	33 \pm 21	50 \pm 22
-40	0 \pm 0	0 \pm 0	17 \pm 17	100 \pm 63	50 \pm 50	0 \pm 0	17 \pm 17	33 \pm 33	50 \pm 50
-20	50 \pm 50	33 \pm 33	33 \pm 21	133 \pm 115	83 \pm 48	50 \pm 22	50 \pm 22	167 \pm 17	83 \pm 65
-10	33 \pm 21	17 \pm 17	17 \pm 17	67 \pm 49	67 \pm 33	100 \pm 63	50 \pm 22	50 \pm 34	50 \pm 34
0	133 \pm 42	50 \pm 22	17 \pm 17	117 \pm 65	183 \pm 75	83 \pm 48	17 \pm 17	33 \pm 21	0 \pm 0
10	633 \pm 204	50 \pm 34	83 \pm 40	50 \pm 22	117 \pm 48	17 \pm 17	0 \pm 0	67 \pm 33	67 \pm 49
20	833 \pm 254	100 \pm 37	33 \pm 21	150 \pm 56	83 \pm 40	100 \pm 52	17 \pm 17	17 \pm 17	50 \pm 22
40	683 \pm 156	67 \pm 33	33 \pm 21	50 \pm 22	0 \pm 0	33 \pm 21	50 \pm 22	33 \pm 21	83 \pm 48
60	367 \pm 193	100 \pm 45	67 \pm 33	183 \pm 60	67 \pm 49	50 \pm 50	17 \pm 17	0 \pm 0	33 \pm 33
Forest reference	533 \pm 81	100 \pm 37	25 \pm 18	208 \pm 51	42 \pm 19	58 \pm 42	58 \pm 29	17 \pm 11	67 \pm 22

Chapter 3: Moose browse severity, regeneration, and understorey composition at spruce budworm-induced forest edges

Abstract

Natural forest edges were created from tree mortality caused by a severe spruce budworm outbreak in the early 1980s in Cape Breton Highlands National Park, Nova Scotia. An introduced moose population has since maintained these edges, thereby restricting forest succession. Patterns of moose browsing and vegetation at these edges provides insight into the processes that are hindering regeneration of large forested areas in the park. My objective was to determine patterns and extent of edge influence for 1) moose browse severity, 2) regeneration structure, and 3) species composition at the budworm-induced edges. Browse intensity, saplings, and understorey plant species were sampled in contiguous quadrats along 120 m transects across six edges and in reference forest and disturbed areas. Most saplings in the disturbed area were severely browsed and were shorter than those in the intact forest. Understorey diversity as well as shrub, herb, and fern cover were significantly lower whereas sapling height and the percentage of unbrowsed saplings were higher at 25 – 30 m from the forest edge into the forest compared to the disturbed area and forest references. The findings suggest that reduced browse pressure negatively affects unpalatable understorey growth. The insect disturbed area was characterized by more shade intolerant species, increased graminoid cover, and reduced bryophyte cover compared to the forest. Therefore, moose are maintaining the forest edges extending edge influence on forest regeneration into the forest by preventing sapling growth and altering species composition.

1. Introduction

Forest edges are often prominent landscape features that contribute to spatial heterogeneity and can be characterized by distinct ecological patterns and processes. Edges can be naturally inherent as a result of differences in soil type, microclimate, topography, or geomorphology (Thomas et al. 1979). Alternatively, forest edges can be induced by anthropogenic activities or natural disturbances including wildfires, avalanches, windstorms, and insect outbreaks. While inherent edges are typically permanent features of the landscape, naturally induced edges are usually short-term features that eventually dissipate due to regeneration in the disturbed area adjacent to the forest (Thomas et al. 1979). The majority of forest edge research has focused on edges created by human activity as opposed to edges induced by natural phenomena (Harper et al. 2005). However, anthropogenic edges differ from natural edges because they are often more abrupt and the adjacent clearings are usually larger (Matlack & Litvaitis 1999). An understanding of both edge types is required for increased knowledge of landscape processes and patterns.

Natural forest edges were created by the latest spruce budworm (*Choristoneura fumiferana*) outbreak approximately 30 years ago in the boreal forest of northern Cape Breton Island, Nova Scotia. Due to the cyclic nature of the spruce budworm and balsam fir forest (Baskerville 1975), it was expected that areas disturbed by the insect would regenerate after the outbreak collapse. However, natural disturbances, such as budworm defoliation, create favourable moose (*Alces alces*) habitat by promoting sapling growth that is within reach of moose (Lautenschlager et al. 1997). A large re-introduced moose

Alces alces andersoni) population has been inhibiting forest regeneration in the Cape Breton Highlands. Consequently, grasslands now dominate large tracts of previously forested land that was affected by the spruce budworm outbreak (Smith et al. 2010).

It has been recognized that moose are foraging heavily in areas affected by the latest spruce budworm outbreak in northern Cape Breton (Basquill & Thompson 1996; Smith et al. 2010); however, recent studies focused solely on areas that were severely affected by the insect outbreak. Therefore, there is a lack of knowledge related to the patterns of browse severity at the interface between forest stands that were not defoliated by the insect outbreak and disturbed areas. The edges between forested stands and disturbed areas have been observed to be sharp (Smith 2007), yet ecological processes and species composition at these particular edges have yet to be thoroughly examined.

Adequate moose habitat contains shelter from adverse weather conditions, optimal snow depth, and cover for predator avoidance (Timmermann & McNicol 1988). Despite these habitat requirements, moose densities tend to be highest in areas affected by fires (Telfer 1970; LeResche et al. 1974; Bangs & Bailey 1980), logging (Dodds 1960; Telfer 1967; Bergerud & Manuel 1968), and insect epidemics (Brassard et al. 1974; Forbes & Theberge 1993) due to superior forage production post-disturbance. A mixture of insect disturbed and undisturbed areas is ideal for moose as preferred winter moose habitat contains various palatable, young species interspersed with mature stands that consist of palatable coniferous species (Cowan et al. 1950). Therefore, forest edges are considered beneficial for moose because they supply cover adjacent to forage and provide a greater variety of palatable species (LeResche et al. 1974). Although researchers in other regions found no correlation between moose browse and distance to forest edge (Hamilton et al.

1980; Andrén & Angelstam 1993), only the non-forested sides of the edge were considered and the edges under investigation were anthropogenic.

An examination of herbivory in both the insect disturbed area and undisturbed forest is necessary to gain a better understanding of the interplay between natural edge creation and moose browsing as well as the potential effects on forest dynamics. In addition to moose browse, an investigation of understorey structure and composition will reveal insight into the processes that are preventing forest regeneration in the park.

My objective was to evaluate moose browse severity at spruce budworm-induced forest edges to ultimately determine the extent to which moose browsing is affecting understorey growth and composition. The following questions were addressed:

- 1) How does species-specific moose browse severity vary across the insect disturbed area-forest edge?
- 2) What size of saplings are most vulnerable to browse?
- 3) Do sapling height and density vary across the budworm-induced edge and/or among species?
- 4) How do overall understorey cover, species composition, and species diversity vary across the spruce budworm-induced forest edge?

2. Methods

Study area

The study area was located in Cape Breton Highlands National Park (46°50'N, 60°30'W), which was established in 1936 and encompasses 950 km² of northern Cape

Breton Island, Nova Scotia. The surrounding Atlantic Ocean to the east and the Gulf of St. Lawrence to the west of the island contribute to the Park's maritime climate. Climatic normals (1971 – 2000) from nearby Pleasant Bay (46°49'N, 60°46'W) reported a mean January temperature of $-5.3 \pm 1.8^{\circ}\text{C}$, a mean July temperature of $18.1 \pm 1.8^{\circ}\text{C}$, and a mean annual precipitation of 1450.1 mm (Environment Canada 2013). The region is characterized by a plateau, which ranges in elevation from 350 m to 500 m above sea level and contains underlying Precambrian granitic and volcanic bedrock (Webb & Marshall 1999). The plateau experiences heavy snowfall, high winds, and frequent fog (Webb & Marshall 1999). Approximately 88% of Cape Breton Highlands National Park is forested by a unique combination of Acadian taiga and boreal vegetation (Parks Canada 2010). In the boreal land region, which dominates approximately 50% of the park, the dominant tree species is *Abies balsamea* (balsam fir) interspersed with *Picea glauca* (white spruce) and *Betula papyrifera* (white birch). *Picea mariana* (black spruce) and *Larix laricina* (eastern larch) are also present in moist areas. Soils are mostly sandy loam of moderately coarse texture (Neily et al. 2003).

Site selection and data collection

Historical aerial photographs of Cape Breton Island taken in 1969 were compared to aerial photographs taken in 2009 to identify areas of forest canopy reduction caused by the outbreak. Ground surveys were subsequently used to select six forest edges that were created by the spruce budworm outbreak of 1974 – 1985 (Figure 2-1). The forest edge (0 m) was defined as the point at which the intact forest transitioned into the insect disturbed area, or the limit of continuous canopy. The following criteria were used in the edge

selection process in order of decreasing importance: 1) the forest edge was adjacent to an area disturbed by the last spruce budworm outbreak, 2) the forest edge was accessible, 3) the forest area and the disturbed area extended at least 80 m from the edge in opposite directions, 4) the forest area and the disturbed area interiors (70 – 100 m from the edge) were located at least 100 m away from another edge, road, trail, or water body, 4) the forest area was fir-spruce dominated for at least 100 m from the edge into the interior, and 5) the elevation was relatively uniform across the edge gradient. Since moose were located throughout the entire park, criteria related to moose activity were not required. A total of six sites were used in the study (Table 2-1). The furthest distance between two sites was 25 km while the shortest distance between two sites was 0.93 km.

I established a 120 m long transect perpendicular to each of the six forest edges, which extended 60 m into both the forest and the disturbed area (Figure 3-1). The distance of 60 m was chosen to detect edge influence, which usually dissipates within 50 m from the edge in boreal forests (Harper et al. 2005). The forest edge in the middle of the transect at 0 m was defined as the point at which the intact forest transitioned into the insect disturbed area, or the limit of continuous canopy. Contiguous 1 m² quadrats were used for sampling along the entire lengths of the transects. Plots composed of five contiguous quadrats (1 m²) were established separate from the transects in the insect disturbed area and in the forest area to represent reference conditions. The majority of these plots were located 100 m away from the insect disturbed area-forest edge; however, some of the reference plots were located only 70 m away from the edge due to spatial constraints. Moreover, the patchiness of the study area restricted six reference plots from

being established at every site, hence three plots were located in the disturbed area at five sites and three plots were established in the forest area at four sites.

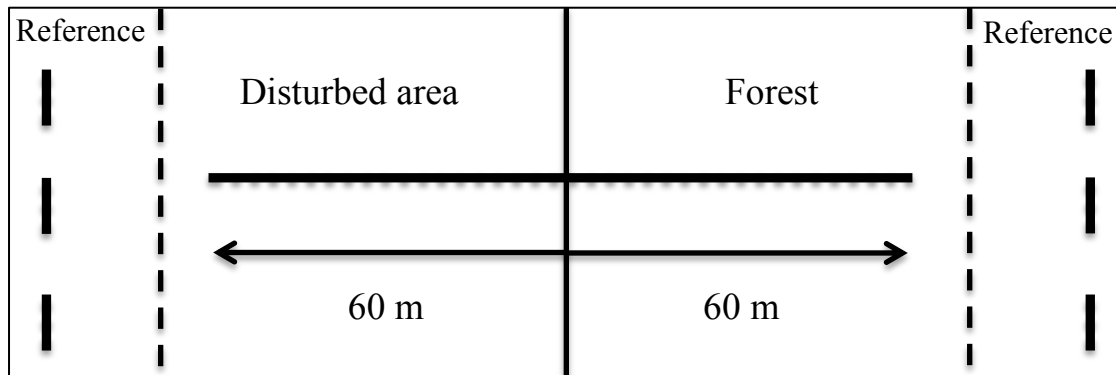


Figure 3-1. Sampling design illustrating an edge transect and corresponding reference plots at an insect disturbed area-forest study site used to measure secondary and tertiary response variables. Reference plots were 70 – 100 m away from the edge. Thick solid lines represent contiguous quadrats (1 m²) in which data were collected. Drawing is not to scale.

Data were collected from June to August 2012. The height and species of each seedling (height \leq 10 cm) and sapling (height $>$ 10 cm, diameter at breast height $<$ 5 cm) growing in the contiguous quadrats were recorded. Saplings were classified as short ($<$ 50 cm in height), intermediate (50 – 99 cm in height), or tall (\geq 100 cm in height). Each sapling was assessed for moose browsing using a classification system based on the presence of live foliage, the growth form, and the proportion of browsed stems (Table 3-1). The classification system was adapted from Smith et al. (2010) to include an additional category so that dead saplings could be identified as either browsed or unbrowsed. Some of the prior studies that evaluated moose browsing only considered whether a sapling was browsed or unbrowsed (e.g. Hamilton et al. 1980; Mastenbrook & Cumming 1989). Although classification systems may be subjective, the results provide additional details regarding the intensity of herbivory and have been applied in previous

studies (e.g. Dodds 1960; Peek 1963; Andrén & Angelstam 1993; Thompson & Curran 1993; Smith et al. 2010). For this study, all of the individual saplings located in the sampling quadrats were classified as one of six different classes: live unbrowsed, lightly browsed, moderately browsed, severely browsed, dead unbrowsed, and dead browsed. If there were fewer than five saplings found in a 5 m interval of contiguous quadrats, then the next closest saplings growing near the transect were evaluated for browse severity, up to 5 m from the transect. The number of *Abies balsamea*, *Betula papyrifera*, and *Picea glauca* saplings and seedlings were tallied in each 1 m² quadrat located along the edge transect and in the reference plots to obtain sapling and seedling densities.

Table 3-1. Criteria used on individual saplings for determining severity of moose browse. The classification system was adapted from Smith et al. (2010).

Browse Class	Live				Dead	
	Unbrowsed	Lightly browsed	Moderately browsed	Severely browsed	Unbrowsed	Browsed
Live foliage	Yes	Yes	Yes	Yes	No	No
Browse evidence	No	Yes	Yes	Yes	No	Yes
Altered growth form	No	No	Yes (some evidence)	Yes (drastic evidence)	No	Yes
Proportion of stems browsed	None	<1/3	>1/3, <2/3	>2/3	None	N/A
Cylindrical and dense (<i>Abies balsamea</i>)	No	No	No	Yes	No	Yes
Multiple dead stems (<i>Betula papyrifera</i>)	No	No	No	Yes	No	Yes

Overall cover of moose pellets, the shrub layer, the herbaceous layer, ferns, bryophytes, graminoids, fine woody debris, and litter were visually estimated to the nearest 1% up to 5%, and to the nearest 5% thereafter. Individual species cover was estimated for shrubs, herbs, and ferns with the exception of *Amelanchier* spp., *Aster* spp. (other than *A. acuminatus*), *Oxalis* spp., *Solidago* spp. (other than *Solidago macrophylla*), and *Dryopteris* spp., which were identified to genus but were treated as species for the purpose of analysis. Species with growth habits classified as either dwarf shrub or herb, according to CFIA and NRCan/CFS (2011), were considered to be part of the herbaceous layer vegetation while those classified as either small tree or shrub were considered as shrub layer vegetation. Visual estimation was used to determine cover because more rigorous methods, such as the use of point quadrats, would have been impractical and inaccurate due to dense and tall vegetation.

Data analysis

Percentages of *Abies balsamea* and of *Betula papyrifera* saplings in each browse class were calculated for each 5 m interval along the edge transects and for the reference sites. Proportions of species were calculated separately to detect differences associated with moose diet preferences. However, two species were excluded from analysis: *Picea glauca* saplings since none encountered at the study sites were browsed, and *Acer rubrum* saplings due to relatively low density, although some were lightly browsed. In addition to analyzing browse severity among sapling species, moose browse severity was also analyzed using height class categories. The percentages of saplings in each of the six

browse classes were calculated for each height class. The tallest sapling of each of the three most common tree species (*Abies balsamea*, *Betula papyrifera*, and *Picea glauca*) growing in every 5 m interval along the edge and in the reference plots was used to examine maximum sapling height. Species diversity was calculated using the Shannon-Weiner index and overall understorey diversity included shrubs, herbs, and ferns. Species found in at least 25 % of the 5 m transect intervals were examined on an individual level.

To determine patterns across the insect disturbed area-forest edge, data were analyzed using generalized additive mixed models (GAMM) in the *mgcv* package (Wood 2011) in the R software (R Core Team 2013). This type of model was used to give flexibility in the modeling process so that asymmetry could be more easily detected than generalized linear modeling (Yee & Mitchell 1991). Each site was recognized as a random variable in the models, therefore data collected at the same site were not considered independent from one another. Variables related to browse severity were analyzed with binomial distribution. Variables measured with count data (sapling and seedling densities) were analyzed with Poisson distribution while the remaining continuous variables (cover, species diversity) were analyzed using Gaussian distribution. Reference data were not included in the GAMM analysis due to the variation in the distances from the edge from which these data were collected. The sequential Bonferroni test was used to address the issue of multiple comparisons and highly correlated response variables were analyzed collectively.

The randomized test of edge influence (RTEI) (Harper & Macdonald 2011) was used to quantify the distance of edge influence (DEI) for each of the variables under investigation. Compared to other methodological approaches that estimate the distance of

edge influence, the RTEI is considered one of the most effective as it considers randomization of the values in the reference ecosystem as well as of the values at the forest edge (Harper & Macdonald 2011). The analysis compares the average difference of values at a specific distance from the edge and reference values to a distribution of randomized differences for the entire data set (Harper & Macdonald 2011). The no blocking method was used because not all of the study sites included reference plots. RTEI involved the following steps: 1) the observed difference between the mean of the reference values and the mean of the values at a given distance from the edge was calculated, 2) all values were combined and then randomly assigned as either edge or reference, 3) the calculation in step 1 was repeated for the randomized data, 4) steps 2 and 3 were repeated 5000 times to obtain a distribution of differences from the randomization of the data. The percentile of the observed difference within the distribution of randomized differences was subsequently used as the p-value. Using a two-tailed test, the mean edge value was considered to be significantly different than the reference values when the p-value was in the upper 97.5 or lower 2.5 percentiles. The analysis was performed for each distance along the edge transect (-60, -40, -20, -10, 0, 10, 20, 40, 60 m) using the disturbed area reference and forest reference separately. To address the issue of multiple testing, DEI was only considered significant if there were at least two consecutive significant p-values.

3. Results

Moose pellet cover and browse

Two different types of analyses provided separate results for moose pellet cover. The generalized additive mixed models (GAMM) indicated that the spatial pattern of moose pellet cover across the spruce budworm-forest gradient was not statistically significant (Figure 3-2). However, the randomized test of edge influence (RTEI) revealed that moose pellet cover was significantly higher from -10 m on the disturbed side to 5 m from the edge into the forest compared to both the forest and disturbed area references (Figure 3-2). Distances from the edge on the disturbed side and the forest side are represented using negative and positive values, respectively.

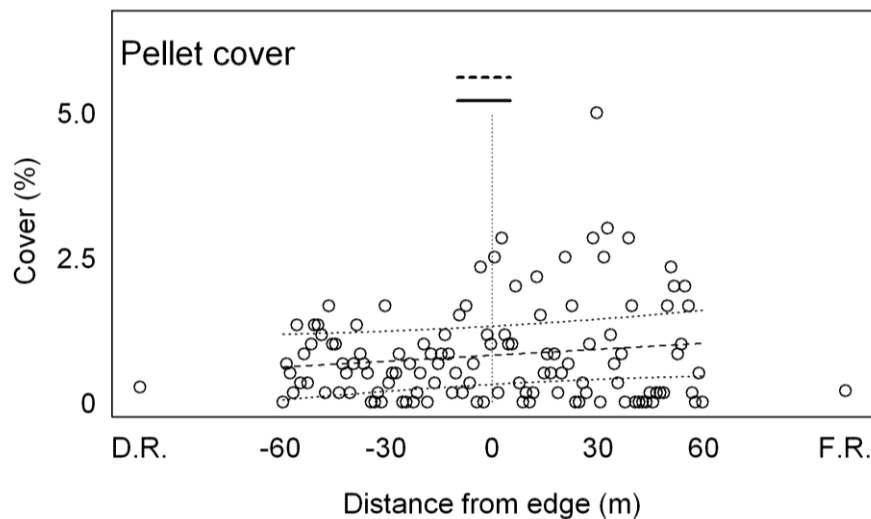


Figure 3-2. Percentage cover of moose pellets along the insect disturbed area-forest edge. Negative and positive values on the x-axis represent the disturbed and forest sides of edge, respectively (D.R. = disturbed area reference, F.R. = forest reference). Circles indicate average values from all sites at each 1 m distance along the transect and the trend line (dashed = $p \geq 0.05$) represents the fitted model with 95% CI (dotted lines). Horizontal lines near the top of graph represent significant DEI as compared to the forest (solid line) and disturbed area (dashed line).

Moose browsing was more prevalent on the disturbed side of the edge compared to the forest side (Figure 3-3). Of all *Abies balsamea* saplings examined, 15% and 45% were living and unbrowsed in the disturbed area reference and forest reference, respectively (Figure 3-3a). Similarly, the percentage of live, unbrowsed *Betula papyrifera* saplings also exhibited an increasing pattern from the disturbed area into the forest, yet percentages were significantly higher at the edge compared to the disturbed area reference (Figure 3-3b). The proportions of light and moderately browsed saplings were generally relatively low and did not reveal any edge influence (Figure 3-3c-f). The majority of browsed saplings were severely browsed and characterized by stunted and other abnormal growth forms. Both *Abies balsamea* and *Betula papyrifera* saplings exhibited significant decreasing patterns of severe browsing from the disturbed area into the forest (Figure 3-3g-h). Compared to *Abies balsamea*, a lower percentage of *Betula papyrifera* saplings were severely browsed overall although DEI was greater for *B. papyrifera* than *A. balsamea*.

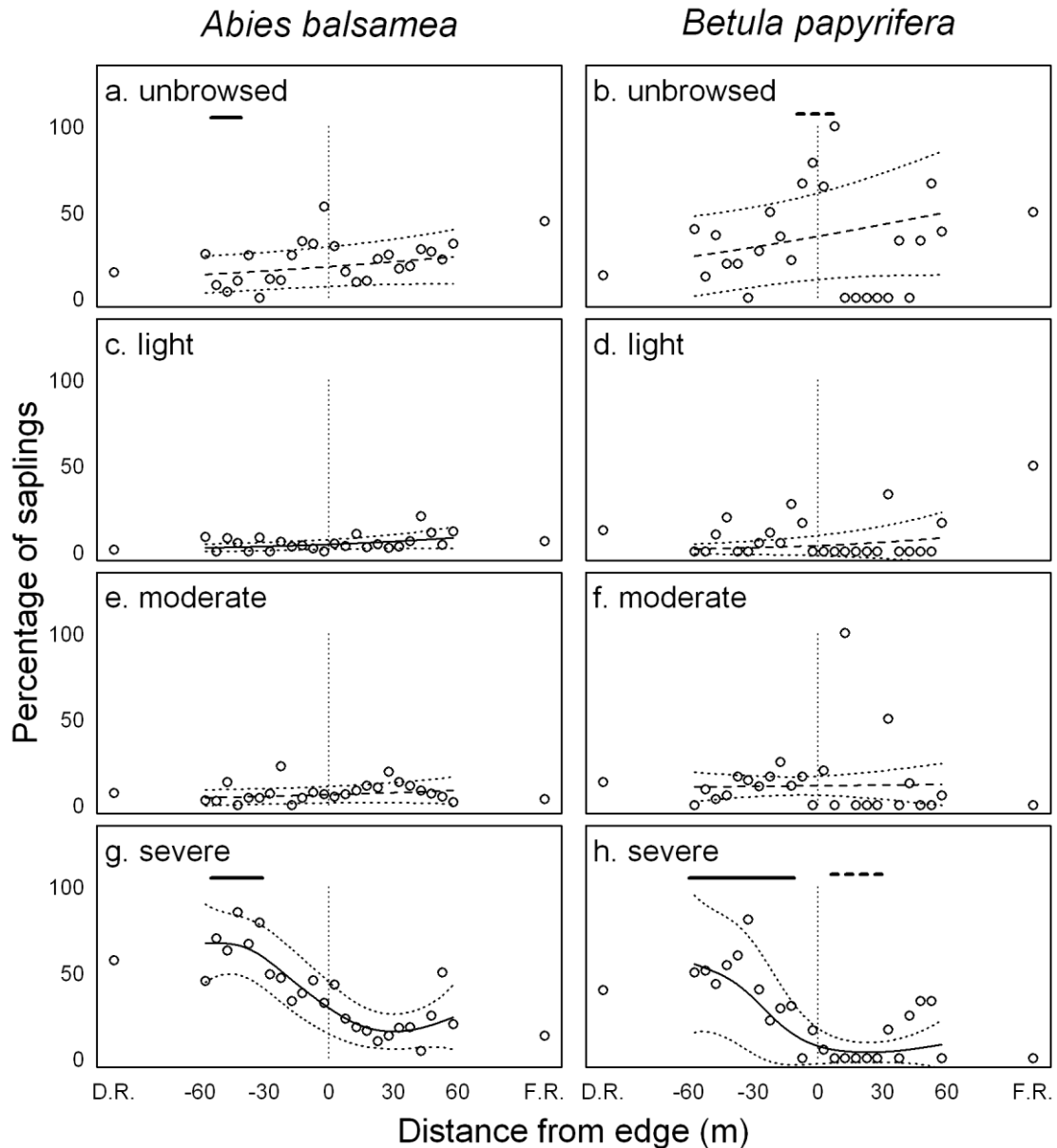


Figure 3-3. Percentage of *Abies balsamea* saplings (n = 824) and *Betula papyrifera* saplings (n = 315) in individual live browse severity classes (as a proportion of the total number of live and dead saplings) along the insect disturbed area-forest edge. Negative and positive values on the x-axis represent the disturbed and forest sides of edge, respectively (D.R. = disturbed area reference, F.R. = forest reference). Circles indicate mean values from all sites at each 5 m interval along the transect and the trend lines (dashed = $p \geq 0.05$, solid = $p < 0.05$ before Bonferroni correction) represent the fitted model with 95% CI (dotted lines). The pattern for lightly browsed *Abies balsamea* (c) was not significant at the 0.05 level after Bonferroni correction. Horizontal lines near the top of the graphs represent significant DEI as compared to the forest (solid line) and disturbed area (dashed line).

Overall, fewer saplings were dead than alive and causes of mortality varied between species and across the edge gradient (Figure 3-4). The percentages of unbrowsed dead saplings of *Abies balsamea* and of *Betula papyrifera* were significantly greater on the forest side of the edge compared to the disturbed area side; however, only the former species had significant DEI when compared to both references (Figure 3-4a-b). *Abies balsamea* saplings that had experienced mortality consequent of browse were more abundant on the disturbed area side of the edge compared to the forest side (Figure 3-4c). Conversely, an opposite, yet non-significant, pattern was revealed for the percentage of severely browsed dead *Betula papyrifera* saplings, which increased from the disturbed area into the forest (Figure 3-4d).

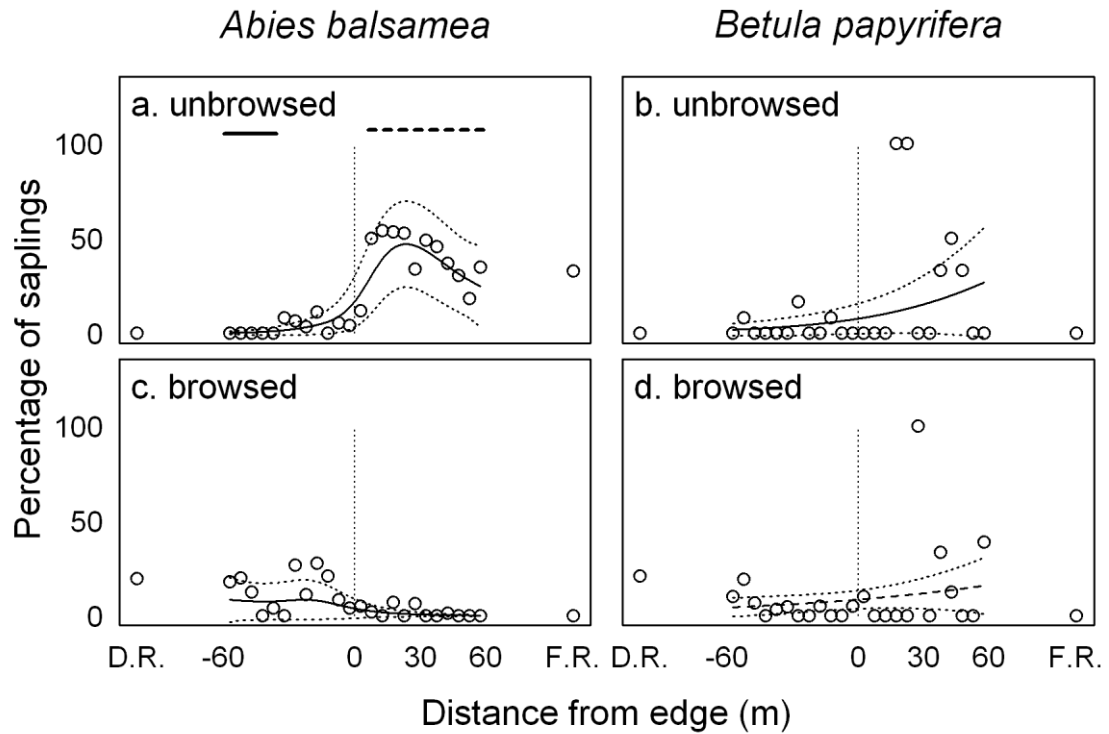


Figure 3-4. Percentage of *Abies balsamea* saplings (n = 824) and *Betula papyrifera* saplings (n = 315) in individual dead browse severity classes (as a proportion of the total number of live and dead saplings) along the insect disturbed area-forest edge. Negative and positive values on the x-axis represent the disturbed and forest sides of edge, respectively (D.R. = disturbed area reference, F.R. = forest reference). Circles indicate mean values from all sites at each 5 m interval along the transect and the trend lines (dashed = $p \geq 0.05$, solid = $p < 0.05$) represent the fitted model with 95% CI (dotted lines). Horizontal lines near the top of the graphs represent significant DEI as compared to the forest (solid line) and disturbed area (dashed line).

Browse severity classification patterns differed among distinct height classes as taller saplings were more severely affected by browsing (Figure 3-5). The majority of short saplings (< 50 cm in height) were unbrowsed, particularly at the edge (Figure 3-5a). The shortest browsed saplings were 11 cm in height and were found growing in the disturbed area. While the percentages of lightly browsed short saplings did not display a significant pattern across the disturbed area-forest gradient, short saplings that were moderately or severely browsed were more numerous in the disturbed area compared to the forest (Figure 3-5b-d). Similar trends were observed for saplings of intermediate height (50-99 cm), yet relatively fewer saplings were unbrowsed (Figure 3-5e) and more saplings were browsed (Figure 3-5f-h) compared to shorter saplings. No tall saplings (> 99 cm in height) were unbrowsed in the disturbed area and very few were unbrowsed even in the forest reference (Figure 3-5i). The percentages of tall saplings that were lightly browsed and moderately browsed increased from the disturbed area to the forest (Figure 3-5j-k). The percentage of severely browsed saplings was greatest for tall saplings (Figure 3-5l) and decreased with shorter height classes.

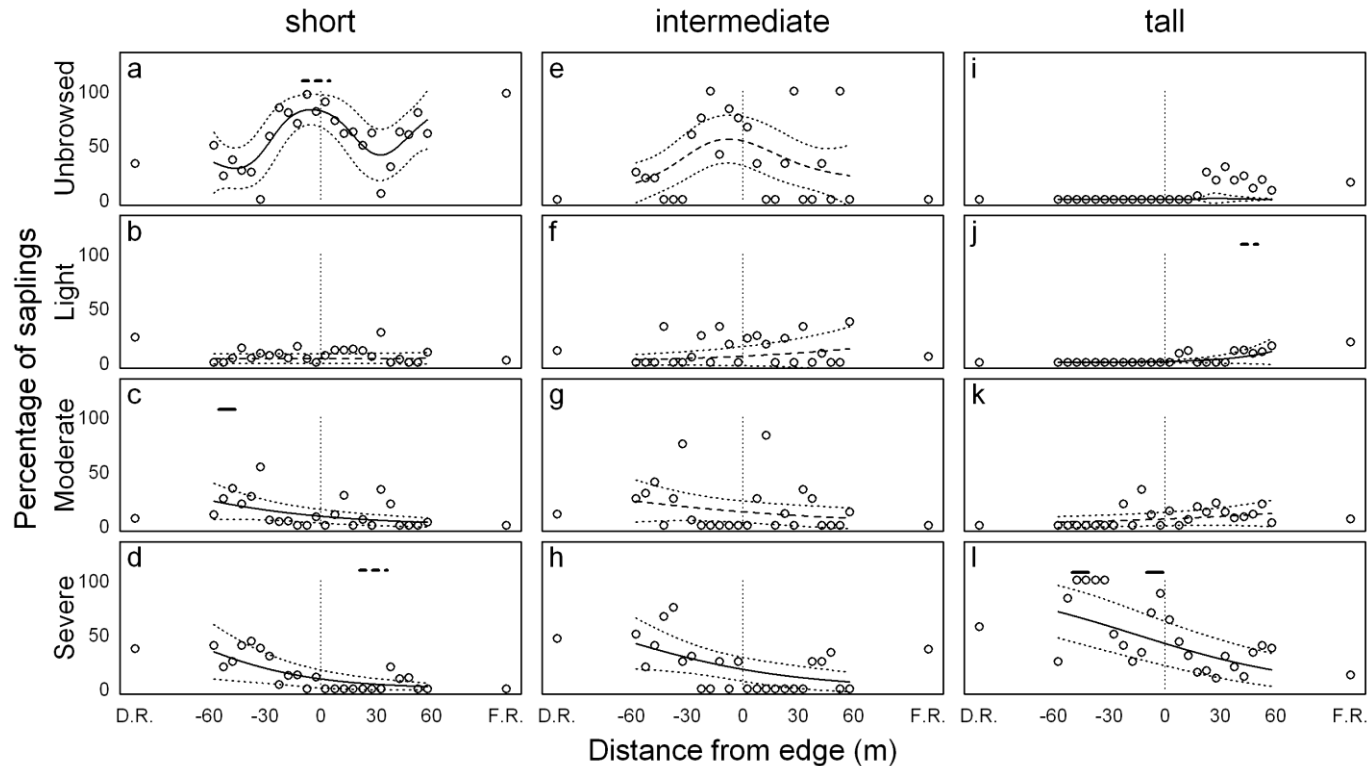


Figure 3-5. Percentage of *Abies balsamea* and *Betula papyrifera* saplings ($n = 1139$) divided by three height classes (short = < 50 cm, intermediate = $50 - 99$ cm, tall = > 99 cm) in individual live browse severity classes (as a proportion of the total number of live and dead saplings) along the insect disturbed area-forest edge. Negative and positive values on the x-axis represent the disturbed and forest sides of edge, respectively (D.R. = disturbed area reference, F.R. = forest reference). Circles indicate mean values from all sites at each 5 m interval along the transect and the trend lines (dashed = $p \geq 0.05$, solid = $p < 0.05$ before Bonferroni correction) represent the fitted model with 95% CI (dotted lines). The pattern for severely browsed intermediate saplings (h) was not significant at the 0.05 level after Bonferroni correction. Horizontal lines near the top of graphs represent significant DEI as compared to the forest (solid line) and disturbed area (dashed line).

Greater percentages of taller saplings were dead compared to saplings of shorter height (Figure 3-6). Among short saplings, percentages of unbrowsed dead saplings were higher in the disturbed area (Figure 3-6a). The maximum average percentage of severely browsed dead saplings was 25% and the proportion declined significantly from the insect disturbed area side of the edge into the forest (Figure 3-6b). The percentages of intermediate and tall saplings that died from causes unrelated to browsing were significantly greater 16 – 40 m and 6 – 60 m from the edge into the forest compared to the disturbed area reference, respectively (Figure 3-6c,e). Similar to short saplings, the average proportion of saplings of intermediate height representing severely browsed, dead saplings was zero in the forest reference (Figure 3-6d). The percentage of tall saplings that died from browsing was greater than the proportions associated with short and medium height classes (Figure 3-6f).

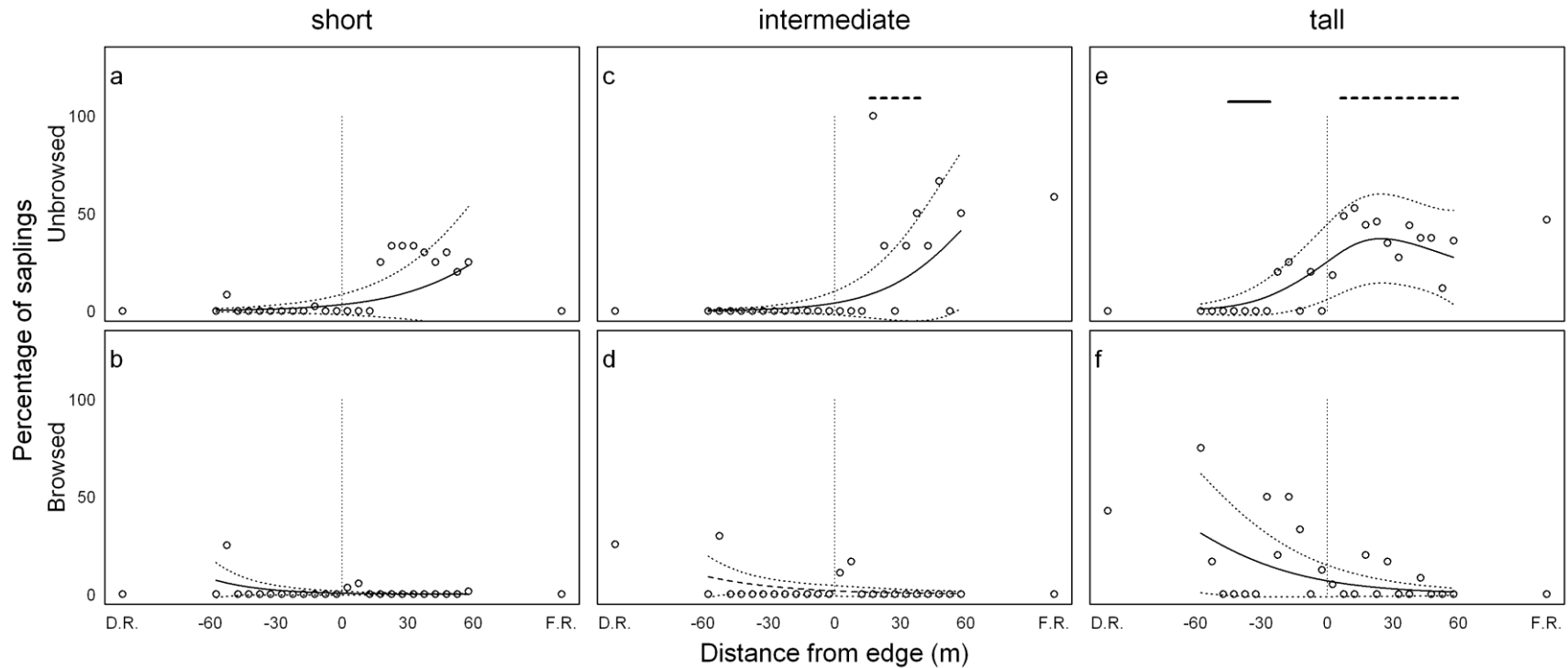


Figure 3-6, Percentage of *Abies balsamea* and *Betula papyrifera* saplings (n = 1139) divided by three height classes (short = < 50 cm, intermediate = 50 – 99 cm, tall = > 99 cm) in individual dead browse severity classes (as a proportion of the total number of live and dead saplings) along the insect disturbed area-forest edge. Negative and positive values on the x-axis represent the disturbed and forest sides of edge, respectively (D.R. = disturbed area reference, F.R. = forest reference). Circles indicate mean values from all sites at each 5 m interval along the transect and the trend lines (dashed = $p \geq 0.05$, solid = $p < 0.05$) represent the fitted model with 95% CI (dotted lines). Horizontal lines near the top of graphs represent significant DEI as compared to the forest (solid line) and disturbed area (dashed line).

Regeneration

Abies balsamea and *Picea glauca* were generally the tallest saplings on the disturbed side of the edge and on the forest side, respectively, whereas *Betula papyrifera* was the shortest species at the majority of distances from the edge (Figure 3-7a-c). In the disturbed area reference, *Picea glauca* maximum sapling height was over twice as high as both *Abies balsamea* and *Betula papyrifera* maximum sapling heights. Average maximum *Abies balsamea* sapling height was significantly higher 36 m to 60 m from the edge into the forest compared to the disturbed area reference (Figure 3-7a). Neither *Betula papyrifera* nor *Picea glauca* exhibited significant edge influence (Figure 3-7b-c).

Total sapling density did not differ significantly across the insect disturbed area-forest gradient due to contrasting patterns of density between species. *Abies balsamea* represented the greatest sapling density; however, there was no significant edge influence despite an overall increasing trend from the disturbed area to the forest interior (Figure 3-7d). In contrast, *Betula papyrifera* sapling density decreased significantly from the disturbed area to the forest (Figure 3-7e). Even though *Picea glauca* sapling density was significantly lower at the edge (11 – 20 m) compared to the forest reference, there was no significant spatial pattern for this response variable and overall density was lower compared to density of the browsed species. Total seedling density increased significantly from the disturbed area into the forest and the greatest average seedling density occurred 20 m from the edge into the forest (Figure 3-7f). *Abies balsamea* accounted for the majority of the seedlings and was the only species found as a seedling in the forest reference quadrats. Average seedling density of *Betula papyrifera* and *Picea glauca* did

not exceed one in any of the quadrats and neither species exhibited significant patterns across the edge gradient.

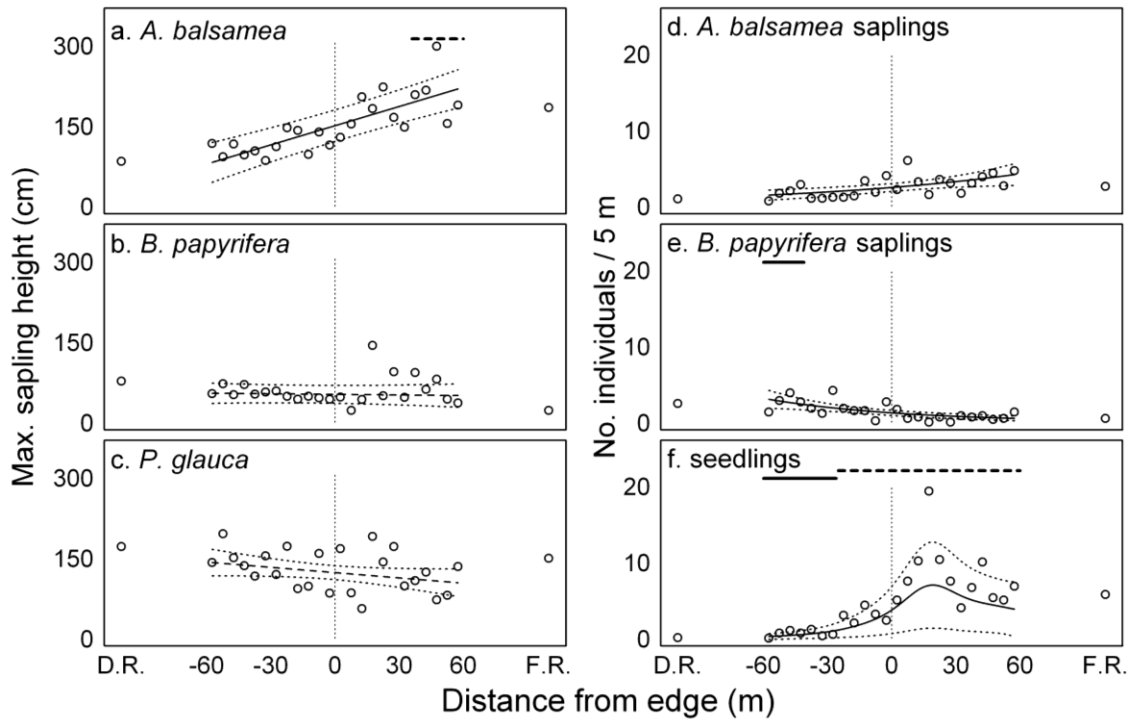


Figure 3-7. Mean maximum sapling height of (a) *Abies balsamea*, (b) *Betula papyrifera*, and (c) *Picea glauca* and mean density of (d) *A. balsamea* saplings, (e) *B. papyrifera* saplings, and (f) seedlings of all species along the insect disturbed area-forest edge. Negative and positive values on the x-axis represent the disturbed and forest sides of edge, respectively (D.R. = disturbed area reference, F.R. = forest reference). Circles indicate mean values from all sites at each 5 m interval along the transect and the trend lines (dashed = $p \geq 0.05$, solid = $p < 0.05$) represent the fitted model with 95% CI (dotted lines). Horizontal lines near the top of the graphs represent significant DEI as compared to the forest (solid line) and disturbed area (dashed line).

Understorey composition

Average cover of graminoids decreased along the disturbed area-forest gradient and was significantly lower up to 10 m from the edge into the disturbed area compared to the disturbed area reference (Figure 3-8a). In contrast to the decreasing pattern of graminoids cover, bryophytes cover increased from the disturbed area into the forest up to approximately 35 m from the edge, at which point cover began to stabilize (Figure 3-8b). Furthermore, bryophytes cover was over six times greater in the forest reference than the disturbed area reference. Despite relatively low values of percentage cover, fine woody debris abundance was significantly lower in the disturbed area compared to the forest (Figure 3-8c). Litter cover did not vary significantly across the edge gradient (Figure 3-8d). Average shrub layer cover was significantly lower at 11 to 25 m on the forest side of the edge compared to both the disturbed area and forest references (Figure 3-8e). Overall herbaceous layer cover was relatively higher than shrub layer cover and decreased from the edge to 25 m into the forest, after which cover then steadily increased (Figure 3-8f). Overall fern cover exhibited a similar pattern to herb cover and was approximately 30% on the disturbed area side of the edge and decreased to 25 m from the edge into the forest before increasing again (Figure 3-8g).

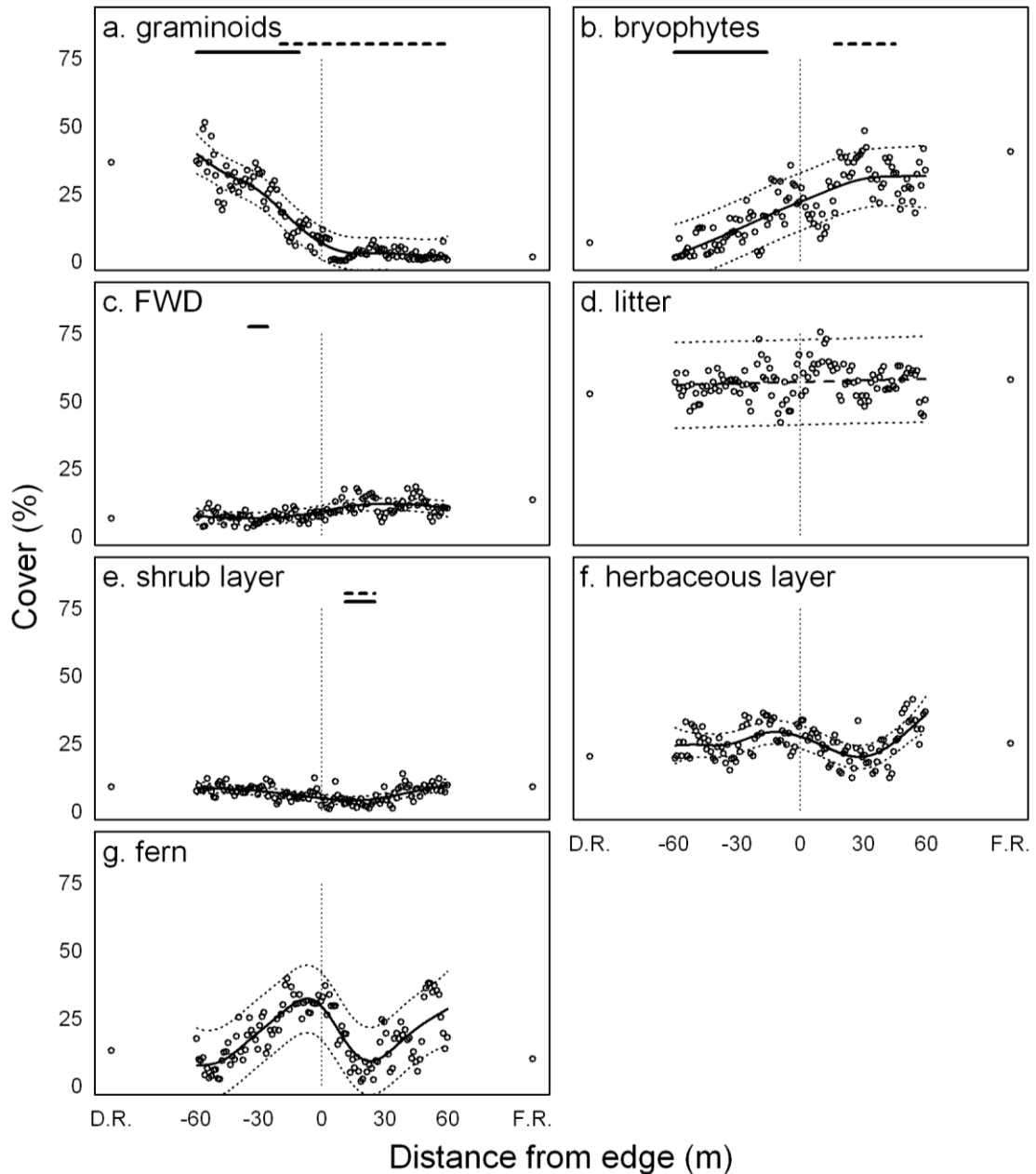


Figure 3-8. Mean percentage cover of (a) graminoids, (b) bryophytes, (c) FWD = fine woody debris, (d) litter, (e) shrub layer species, (f) herbaceous layer species, and (g) fern species along the insect disturbed area-forest edge. Negative and positive values on the x-axis represent the disturbed and forest sides of edge, respectively (D.R. = disturbed area reference, F.R. = forest reference). Circles indicate mean values from all sites at each 1 m distance along the transect and the trend lines (dashed = $p \geq 0.05$, solid = $p < 0.05$) represent the fitted model with 95% CI (dotted lines). Horizontal lines near the top of the graphs represent significant DEI as compared to the forest (solid line) and disturbed area (dashed line).

A total of 16 species of shrubs and 22 species of herbs were identified, none of which were considered endangered. The only exotic species, *Rumex acetosella*, was only found in the disturbed area. The majority of shrubs and herbs that exhibited significant patterns in percentage cover across the edge gradient increased from the disturbed area into the forest (*Amelanchier* spp., *Kalmia angustifolia*, *Vaccinium angustifolium*, *Clintonia borealis*, *Coptis trifolia*, *Epigaea repens*, *Gaultheria hispidula*, *Linnaea borealis*, *Maianthemum canadensis*, *Trientalis borealis*) although cover of some species decreased (*Rubus idaeus*, *Aster acuminatus*, other *Aster* spp., *Solidago macrophylla*).

Of the four ferns identified, cover of three species varied significantly across the insect disturbed area to forest interior (Table 3-2). Percent coverage of *Thelypteris noveboracensis* and *Osmundastrum cinnamomeum* fluctuated across the edge gradient; however, the latter species was relatively more prevalent in the forest compared to the former species. *Pteridium aquilinum* was most abundant on the disturbed area side of the edge. Meanwhile, *Dryopteris* spp. cover fluctuated less than patterns for the other three fern species, despite a slight decrease in cover on the forest side of the edge.

Among individual species of shrubs, herbs, and ferns, only *Kalmia angustifolia* had a significant distance of edge influence when compared to the forest reference (Table 3-2). The extent of edge influence compared to the disturbed area reference was greatest for *Rubus idaeus* and *Solidago macrophylla* (DEI = -10 to 60 m, Table 3-2).

Maianthemum canadense was the only species that had significantly lower cover at a specific distance (26 to 35 m from edge into the disturbed area) compared to both

reference ecosystems. Of the fern species, *Dryopteris* spp. cover only exhibited a negative edge response when compared to the disturbed area reference, while *Thelypteris noveboracensis* cover resulted in a negative edge response compared to the forest reference.

Table 3-2. Average cover, generalized additive mixed model results, and distance of edge influence for individual understorey species. Estimated degrees of freedom = 1 when pattern is linear and higher values correlate positively with more non-linear curves. Bolded p-values indicate significance at the 0.05 significance level after sequential Bonferroni correction. Distance of edge influence (DEI) is distance from the edge over which edge influence is statistically significant compared with the forest or disturbed area reference. For average cover at each distance, see Appendix 3-B.

Species	Average cover (%) ± SE			Generalized Additive Mixed Model		Distance of Edge Influence (m)	
	Disturbed area reference	Edge (-5 to 5 m)	Forest reference	Estimated degrees of freedom	p-value	Forest reference	Disturbed area reference
Shrub layer							
<i>Amelanchier</i> spp.	0.44 ± 0.25	1.4 ± 0.55	1.7 ± 0.36	1.00	0.0015	-40 to -21	ns
<i>Kalmia angustifolia</i>	0.0 ± 0.0	0.0 ± 0.0	3.5 ± 0.7	4.16	< 0.0001	-60 to 10	31 to 60
<i>Rubus idaeus</i>	5.7 ± 0.51	0.53 ± 0.22	0.0 ± 0.0	4.80	< 0.0001	-60 to -6	-10 to 60
<i>Sorbus americana</i>	0.7 ± 0.34	0.7 ± 0.23	0.53 ± 0.22	1.48	0.0777	ns	ns
<i>Vaccinium angustifolium</i>	0.12 ± 0.08	1.7 ± 0.7	2.4 ± 0.7	1.00	0.0462	ns	ns
Herbaceous layer							
<i>Aralia nudicaulis</i>	3.0 ± 0.41	2.6 ± 0.35	2.0 ± 0.34	4.81	< 0.0001	ns	ns
<i>Aster acuminatus</i>	1.1 ± 0.26	0.7 ± 0.23	0.23 ± 0.11	1.00	< 0.0001	-55 to -16	ns
<i>Aster</i> spp. (other than <i>A. acuminatus</i>)	1.7 ± 0.45	0.0 ± 0.0	0.0 ± 0.0	1.00	0.00971	ns	ns
<i>Clintonia borealis</i>	0.15 ± 0.07	0.6 ± 0.18	2.1 ± 0.53	6.08	< 0.0001	ns	6 to 15

Species	Average cover \pm S.E. (%)			Generalized Additive Mixed Model		Distance of Edge Influence (m)	
	Disturbed area reference	Edge (-5 to 5 m)	Forest reference	Estimated degrees of freedom	p-value	Forest reference	Disturbed area reference
<i>Coptis trifolia</i>	0.52 \pm 0.14	1.1 \pm 0.25	0.25 \pm 0.06	5.49	< 0.0001	ns	ns
<i>Cornus canadensis</i>	9.7 \pm 0.9	17.1 \pm 1.7	14.1 \pm 1.8	4.07	0.0517	ns	ns
<i>Epigaea repens</i>	0.0 \pm 0.0	0.07 \pm 0.07	0.20 \pm 0.10	2.41	0.0149	ns	ns
<i>Gaultheria hispidula</i>	0.01 \pm 0.02	0.08 \pm 0.05	0.53 \pm 0.16	4.67	< 0.0001	ns	46 to 60
<i>Linnaea borealis</i>	0.0 \pm 0.0	1.6 \pm 0.26	1.8 \pm 0.42	3.53	0.00156	ns	-35 to 20, 31 to 60
<i>Maianthemum canadensis</i>	1.0 \pm 0.18	1.5 \pm 0.24	1.5 \pm 0.18	4.94	0.000699	-40 to -26	-35 to -26
<i>Mitchella repens</i>	0.0 \pm 0.0	0.40 \pm 0.24	0.0 \pm 0.0	2.09	0.0634	ns	ns
<i>Oxalis</i> spp.	0.36 \pm 0.11	0.03 \pm 0.02	0.28 \pm 0.08	1.00	0.294	ns	ns
<i>Solidago macrophylla</i>	2.0 \pm 0.48	0.03 \pm 0.02	0.07 \pm 0.05	2.10	< 0.0001	ns	-10 to 55
<i>Trientalis borealis</i>	0.03 \pm 0.02	0.7 \pm 0.14	1.2 \pm 0.26	1.00	< 0.0001	-60 to -21	1 to 60
Ferns							
<i>Dryopteris</i> sp.	6.3 \pm 1.1	2.2 \pm 0.7	2.3 \pm 0.7	2.91	0.00321	ns	-10 to -1
<i>Osmundastrum cinnamomeum</i>	0.11 \pm 0.07	15.0 \pm 2.6	3.7 \pm 1.2	6.60	< 0.0001	-45 to -36	-5 to 15, 36 to 60
<i>Pteridium aquilinum</i>	0.8 \pm 0.55	11.8 \pm 3.4	2.8 \pm 1.1	5.99	< 0.0001	ns	ns
<i>Thelypteris noveboracensis</i>	5.5 \pm 1.6	7.2 \pm 4.2	0.47 \pm 0.30	6.93	< 0.0001	-20 to -6	ns

Sapling and seedling diversities did not display significant spatial patterns across the edge gradient and seedling diversity was quite low, especially on the disturbed area side of the edge. Total understory species diversity was significantly lower 16 to 40 m from the edge into the forest compared to the disturbed area reference (Figure 3-9a). Herbs accounted for the greatest amount of diversity and followed a very similar pattern to total understory diversity (Figure 3-9b). Although fern diversity was relatively lower than herb diversity, the pattern across the gradient was similar with a decrease of approximately 20 m from the edge into the forest (Figure 3-9c). Shrub diversity was significantly lower in the disturbed area and increased into the forest (Figure 3-9d).

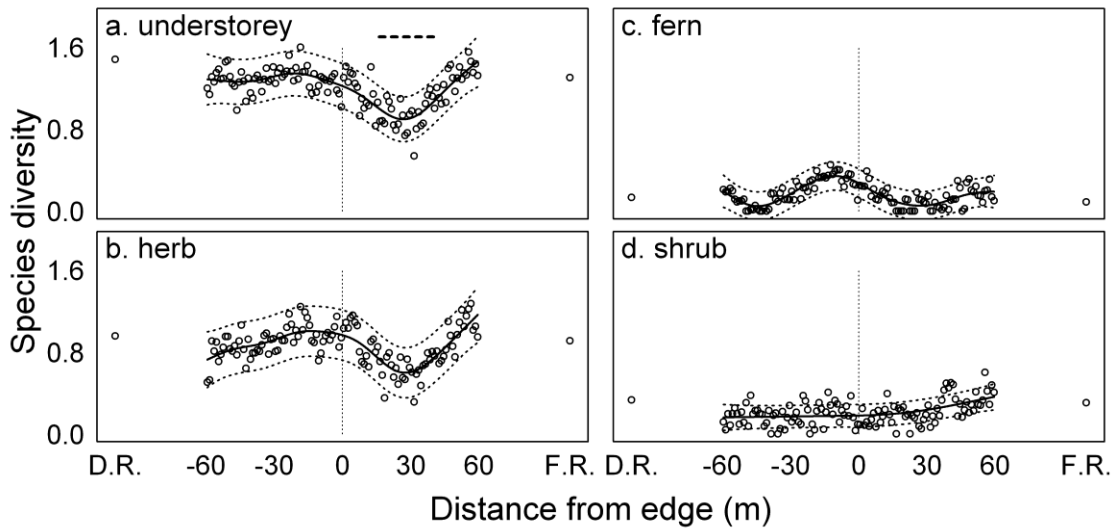


Figure 3-9. Mean species diversity of (a) understory plants (shrubs, herbs, and ferns combined), (b) herbs, (c) ferns, and (d) shrubs along the insect disturbed area-forest edge. Negative and positive values on the x-axis represent the disturbed and forest sides of edge, respectively (D.R. = disturbed area reference, F.R. = forest reference). Circles indicate mean values from all sites at each 1 m interval along the transect and the trend lines (solid = $p < 0.05$) represent the fitted model with 95% CI (dotted lines). Dashed horizontal line near the top of the graph represents significant DEI as compared to the disturbed area.

4. Discussion

My results suggest that the preference for moose browse on the disturbed side of the edge caused a reduction in sapling growth and an increase in shade-intolerant species. In the following sections, I describe the potential function of the edge in relation to moose activity and then explain the spatial patterns and extents of edge influence for moose browse severity classes. The influence of browsing on regeneration is subsequently addressed and followed by an explanation of the implications of understorey composition patterns on ecosystem dynamics.

Moose pellet cover and browse

Significantly higher moose pellet cover at the edge suggests that moose may be using the forest edge to travel between abundant food supply in the disturbed area and adequate thermal cover in the forest. Moose in other parts of Nova Scotia prefer areas that contain excellent food supplies rather than those with extensive shelter (Telfer 1967), but moose abundance may be highest at the spruce budworm-induced forest edge because it is located in between both resources. Moose may use different plant communities for specific purposes just as elk and deer use clear-cut openings only to feed but then return to the forest to ruminate (Lyon & Jensen 1980). Moose prefer dense conifer cover for bedding sites (Telfer 1967; Van Ballenberghe & Peek 1971; Peek et al. 1976) and may retreat to shaded forest cover when temperatures are high because they are vulnerable to heat stress (Renecker & Hudson 1990). Prior studies have indicated that moose use clearcut-forest edges (Mastenbrook & Cumming 1989) and logging roads (Van

Ballenberghe & Peek 1971) as travel corridors hence spruce budworm-forest edges may provide a similar function.

The lack of significant difference in browsing intensity between *Abies balsamea* and *Betula papyrifera* suggests that moose did not prefer one species over the other. Higher percentages of unbrowsed *Betula papyrifera* at the edge compared to the disturbed area reference, a finding that was not shared with *Abies balsamea*, could be attributed to relatively lower *Betula papyrifera* height at the edge. Moose preferred to feed on saplings greater than 50 cm in height and the maximum *Betula papyrifera* sapling height at the edge ranged from 42.5 cm to 46.8 cm. Negative effects of herbivory on sapling growth of both browsed species could lead to more successful regeneration of unpalatable *Picea glauca*. Even though Smith et al. (2010) concluded that *Betula papyrifera* was more severely browsed than *Abies balsamea* in the insect disturbed areas of the Cape Breton Highlands, sampling occurred in more remote insect disturbed areas hence other ecological factors could have influenced food preferences at their study sites.

Moose preference for forage in the disturbed area was more likely related to food quality than food quantity. While other studies found a negative correlation between palatable sapling density and moose browse damage (Bergerud & Manuel 1968; Thompson 1988; Brandner et al. 1990; Andrén & Angelstam 1993), similar trends were only observed for *Abies balsamea* at spruce budworm-induced forest edges. Total sapling density did not vary significantly across the edge gradient, yet the disturbed area contained a greater amount of *Betula papyrifera* saplings compared to the forest. Prior research indicates that *Betula papyrifera* is the preferred food source for moose (Pimlott 1963; Peek et al. 1976; Lautenschlager et al. 1997; Smith et al. 2010), hence moose may

be foraging in the disturbed area rather than the forest as a result of higher *Betula papyrifera* sapling density. Furthermore, *Abies balsamea* is mainly an important winter browse species and *Betula papyrifera* tends to be a substantial dietary component year-round (Peek et al. 1976) so browse severity could be greater in the disturbed area because it provides a more constant supply of food throughout the year. Moose herbivory of conifers has been found to be prevalent in areas with increased density of palatable deciduous tree species (Brassard et al. 1974; Heikkilä & Härkönen 1996) and *Abies balsamea* can be a less important dietary component when various other species are present (Peek 1974). Consequently, the disturbed area may be a more attractive feeding site for moose due to a greater variety of palatable species.

The difference in browse severity along the disturbed area-forest gradient could also be attributed to variations in the nutritional quality of forage. Analysis of nutrition quality was beyond the scope of this study, however Bergerud & Manuel (1968) concluded that moose in Newfoundland selected *Abies balsamea* saplings with high protein content. Furthermore, early successional stands can contain more nutritious forage compared to older stands (Cowan et al. 1950). Thompson et al. (1989) demonstrated that twigs in commercially thinned stands were greater in length, weight, and diameter with higher concentrations of crude fats, crude protein, as well as some nutrients compared to those from unthinned stands.

Moose browse damage was most severe for the tallest saplings, which are considered most vulnerable to moose (Andrén & Angelstam 1993). Shorter saplings may be less affected by browse because they may be concealed by deep snow in winter. Even though taller saplings were preferred, moose browsed saplings as short as 11 cm in

height, a finding which should be considered when creating future sampling designs related to moose browsing. Other researchers have evaluated browse in restricted height classes often known as “browse zones” which ignore saplings shorter than 100 cm (e.g., Danell & Ericson 1986; Andrén & Angelstam 1993) or 50 cm (Basquill & Thompson 1996). Although moose in northern Cape Breton may be foraging on shorter species because the ungulate population is relatively high, an initial trial survey of browse damage in the study area may be useful for researchers to determine optimal height classes of interest because browse activity varies by location and depends on moose density.

At the majority of the distances from the edge, most of the browsed saplings were considered severely browsed. This supports results of Smith et al. (2010), who used a very similar browse damage classification system and also found that the severe browse class represented the greatest proportion of saplings. Similar findings were represented in high moose density areas of Newfoundland, where 84% of trees were heavily browsed and the remainder was of moderately or lightly browsed (Dodds 1960). Saplings severely affected by browsing may have difficulty surviving, may not reach their full growth potential, or may eventually die. Bergerud & Manuel (1968) discovered that over half of trees with 75% of growth removed by simulated browsing died but less than 2% of trees with 10 – 50% of growth removed died within two years. Living *Abies balsamea* should be able to recover within two years if browsing were to cease completely (Bergerud & Manuel 1968); however, in the absence of active population control, moose will continue to occupy the Cape Breton Highlands and browse on saplings even if the population decreases naturally.

In addition to the direct consequences of heavy browsing on individual saplings, indirect effects of browsing could potentially alter the entire ecosystem. Secondary effects of severe browsing in boreal forest include a decline in nitrogen mineralization, microbial activity, as well as the availability of soil nutrients (Pastor et al. 1993). Changes in tree composition can result in negative effects on the ground layer as greater abundance of *Picea* may reduce litter quality and quantity (Pastor et al. 1993). Furthermore, indirect effects of understorey *Abies balsamea* removal, such as a shift from feathermoss seedbed types to those dominated by competing grasses, may result in decreased *Abies balsamea* germination potential (Gosse et al. 2011). Therefore, moose are not only having direct effects on individual plants by modifying growth forms or inducing mortality but they are also causing indirect effects through alterations in habitat characteristics and plant interactions.

Other variables that influence spatial patterns of moose browse activity and movement, including predation, proximity to water, and snow characteristics, were beyond the scope of this study but also influence spatial patterns of moose browse activity and movement. The lack of predators in northern Cape Breton could contribute to higher browse activity in the disturbed area since moose are not pressured to seek refuge and therefore select habitats based on increased forage abundance rather than protective cover (Massé & Côté 2009). Moose frequent aquatic ecosystems in the summer not only to feed on aquatic vegetation, but also to reduce insect irritation (Flook 1959) or to cool off (Kelsall & Telfer 1974), hence proximity to water influences moose behaviour.

Moose retreat to dense forest stands in periods of increased snow hardness (Peek et al. 1976) and rapid snow accumulation (Van Ballenberghe & Peek 1971). Snow levels

less than 75 cm do not seem to affect moose movement (Berg & Phillips 1974; Hamilton et al. 1980; Mastenbrook & Cumming 1989) but snow depths greater than 75 cm seem to deter moose (Peek 1963; Telfer 1970; Krefting 1974; Hundertmark et al. 1990). For the Cape Breton Highlands, 2012 climate data revealed that average snow depths were over 60 cm for only two months of the year (February and March; Parks Canada, unpublished), hence moose may have continued to use the open areas in months of relatively lower snow depth. Unfortunately, snow data were not collected along the spruce budworm induced forest edge and timing of browsing was not calculated, but perhaps saplings in the forest were browsed in months of deep snow cover or periods of increased snow hardness.

Regeneration

Moose appeared to be preventing forest regeneration by restricting sapling growth, particularly on the insect disturbed side of the edge where browsing was most severe. While *Abies balsamea* maximum sapling height increased from the disturbed area into the forest interior, browse severity decreased therefore suggesting that saplings relieved from herbivory pressure had greater opportunities for growth and survival. Other studies revealed that moose browsing suppresses terminal growth of *Abies balsamea* (Bergerud & Manuel 1968; Risenhoover & Maass 1987; Brandner et al. 1990; Thompson & Curran 1993) and can inhibit individual trees from growing over one metre in height (Thompson et al. 1992; McLaren et al. 2004).

In contrast to *Abies balsamea*, maximum *Betula papyrifera* sapling height did not vary significantly across the insect disturbed area-forest edge. Since *B. papyrifera* is a

shade-intolerant species, it was expected to be taller in the disturbed area where growth conditions were favourable. However, moose browsing can restrict *Betula* spp. growth (Bergerud & Manuel 1968; Thompson et al. 1992; Andren & Angelstam 1993; Thompson & Curran 1993; Persson et al. 2005) hence more severe browse damage in the disturbed area may be limiting sapling height causing an insignificant difference in *Betula papyrifera* sapling height across the insect disturbed area-forest gradient. *Picea glauca* was probably the tallest species in the disturbed area because it is unpalatable to moose and therefore was not browsed.

Understorey composition

Moose browsing could be indirectly affecting understorey composition by altering species competition. The overall decrease in shrub layer cover, herbaceous layer cover, fern cover, and understorey diversity approximately 10 – 25 m from the edge into the forest corresponded to high seedling density, relatively low browse severity, and increased sapling height. Reduced herbivory could benefit palatable saplings but consequently decrease the viability of non-dietary herbs, shrubs, and ferns as these understorey species experience greater competition for resources with vigorous saplings and seedlings. In a moose exclosure study, Thompson & Mallik (1989) concluded that densities of unpalatable shrub species were higher outside the exclosures, where moose browsing reduced sapling density and consequently affected the amount of shading received by shrubs. Therefore, the lower abundance of shrubs, herbs, and ferns on the forest side of the edge could be indirectly caused by reduced herbivory and patterns of understorey cover could alter if browse severity changed.

In addition to understorey species abundance, different levels of moose browse severity could eventually affect overstorey composition along the disturbed area-forest gradient. The spruce budworm-forest edge was an intermediate zone of transition between high moose browse severity in the disturbed area and relatively low moose browse in the forest. Future forest composition may be determined by moose, which have the ability to prevent recruitment of preferred species to reproductive-aged trees (McInnes et al. 1992; Heikkilä & Härkönen 1996; Gosse et al. 2011) and to thereby alter the upper canopy in the long term (Didion et al. 2009). Because moose were preferentially feeding on *Abies balsamea*, the fir component of the ecosystem could decrease and therefore eventually prevent the return to the fir-dominated forests that were typical of the past (Brandner et al. 1990; McInnes et al. 1992). *Picea glauca* saplings were much healthier than *Abies balsamea* and *Betula papyrifera* hence *P. glauca* density will most likely increase as a result of reduced competition (Snyder & Janke 1976; Thompson & Curran 1993; Connor 1999), especially on the disturbed side of the edge where palatable species were most affected by browsing. Since browsing was less severe on the forest side of the edge, changes in canopy composition will be less apparent. Consequently, contrasts in vegetation composition between the severely browsed disturbed area and adjacent intact forest may increase.

The dominance of graminoids cover on the disturbed side of the edge area could further prevent forest regeneration and help maintain the forest edge. *Calamagrostis canadensis* was a main component of the graminoid cover in the spruce budworm disturbed areas (Smith et al. 2010). This particular species has the ability to delay thawing of the soil and to decrease mean summer soil temperatures by 3.8°C, which

could potentially slow conifer seedling growth (Hogg & Lieffers 1991). Furthermore, high abundance of *Calamagrostis canadensis* can also result in a smothering mulch layer that ultimately inhibits *Betula papyrifera* as well as *Picea glauca* seedling establishment (Cater & Chapin 2000). Nutrient input from large herbivore carcasses and waste products benefits graminoid cover (McKendrick et al. 1980). Consequently, a positive feedback loop can occur as the prevention of seedling establishment and presence of moose can contribute to more extensive graminoids cover (Smith et al. 2010).

Overall litter cover did not vary significantly across the spruce budworm-induced forest edge most likely because of the contrasting patterns of different litter types. While litter on the forest side of the edge was mainly composed of leaf matter, litter on the disturbed area side of the edge was characterized by thick, insulating dead grass matter. The effects of these two litter types on soil conditions and plant growth could be investigated in the future.

Species diversity was not higher at the edge compared to the adjacent ecosystems, possibly due to the gradual transition between disturbed oriented species and forest oriented species. Greater diversity at other forest edges (Harper et al. 2005) usually results from the edge functioning as an adequate habitat for species found on both sides of the interface (Harris 1988), but the opposite effect may have occurred at the insect-induced forest edges. Species that were either disturbed area oriented (e.g. *Rubus ideaus*) or forest oriented (e.g. *Kalmia angustifolia*) were less abundant within 20 m from the edge, which could reflect a distinct contrast in growing conditions between the two ecosystems.

In contrast to the forest, the disturbed area was characterized by species that thrive under low canopy cover, such as *Rubus idaeus* (Ricard & Messier 1996). The disturbed area also contained the only exotic species, *Rumex acetosella*, which is an early successional weed (Stopps et al. 2011). Species that were able to grow in shaded as well as open canopy conditions, such as *Cornus canadensis* (Hall & Sibley 1976), did not exhibit edge influence and were ubiquitous across the disturbed area-forest gradient. Therefore, the disturbed area was an attractive growing habitat for fast growing shade-intolerant species, which would have most likely been outcompeted by shade-tolerant species had forest regeneration progressed post-disturbance.

5. Conclusions and implications

Moose browsing appeared to be maintaining the spruce budworm-forest edges in Cape Breton Highlands National Park by restricting sapling height and preventing forest regeneration. While moose used the forest edge as a travel corridor, these ungulates selected the disturbed side of the edge as a preferred browsing area. Overall sapling density did not differ significantly across the edge, yet greater density of *Betula papyrifera* saplings in the disturbed area suggests that diet preference may be based on quality and variety rather than quantity. Severely browsed saplings may eventually die or may not reach their full growth potential hence sapling mortality caused by browsing may increase, particularly in the disturbed area. Graminoids and other shade intolerant species capable of thriving in the disturbed area were benefitting from the hindrance of forest succession and moose diet preferences could ultimately alter species composition.

Consequently, forest previously dominated by *Abies balsamea* may become dominated by

unpalatable *Picea glauca*, and grassland expansion may lead to habitat loss for species dependent on closed-canopy forest. The spruce budworm-induced forest edges in Cape Breton Highlands National Park are unique because naturally created edges are usually short-term features of the landscape (Thomas et al. 1979), yet the natural process of herbivory is responsible for their continued existence.

6. Literature cited

- Andren, H. & Angelstam, P. 1993. Moose browsing on Scots pine in relation to stand size and distance to forest edge. *Journal of Applied Ecology* 30: 133-142.
- Bangs, E.E. & Bailey, T.N. 1980. Interrelationships of weather, fire, and moose on the Kenai National moose range, Alaska. *Alces* 16: 255-274.
- Basquill, S. & Thompson, R.G. 1996. *Moose (Alces alces) browse availability and utilization in Cape Breton Highlands National Park*. Parks Canada [report no. 010], Halifax, NS, Canada.
- Berg, W.E. & Phillips, R.L. 1974. Habitat use by moose in northwestern Minnesota with reference to other heavily willowed areas. *Naturaliste canadien* 101: 101-118.
- Bergerud, A.T. & Manuel, F. 1968. Moose damage to balsam fir-white birch forests in central Newfoundland. *The Journal of Wildlife Management* 32: 729-746.
- Brandner, T.A., Peterson, R.O. & Risenhoover, K.L. 1990. Balsam fir on Isle Royale: Effects of moose herbivory and population density. *Ecology* 71: 155-164.
- Brassard, J.M., Audy, E., Crete, M. & Grenier, P. 1974. Distribution and winter habitat of moose in Quebec. *Naturaliste canadien* 101: 67-80.
- Cater, T.C. & Chapin III, F.S. 2000. Differential effects of competition or microenvironment on boreal tree seedling establishment after fire. *Ecology* 81: 1086-1099.
- CFIA and NRCan/CFS. 2011+. Plants of Canada Database. Canadian Food Inspection Agency and Canadian Forest Service of Natural Resources Canada, Ottawa, ON. Retrieved from: <http://www.plantsofcanada.info.gc.ca/> on 10 February 2012.

- Connor, K.J. 1999. *Changes in structure of a boreal forest community following intense herbivory by moose*. M.Sc. thesis, University of New Brunswick, Fredericton, NB, Canada.
- Cowan, I.M., Hoar, W.S. & Hatter, J. 1950. The effect of forest succession upon the quantity and upon the nutritive values of woody plants used as food by moose. *Canadian Journal of Research* 28d: 249-271.
- Danell, K. & Ericson, L. 1986. Foraging by moose on two species of birch when these occur in different proportions. *Holarctic Ecology* 9: 79-83.
- Didion, M., Kupferschmid, A.D. & Bugmann, H. 2009. Long-term effects of ungulate browsing on forest composition and structure. *Forest Ecology and Management* 258: S44-S55.
- Dodds, D.G. 1960. Food competition and range relationships of moose and snowshoe hare in Newfoundland. *The Journal of Wildlife Management* 24: 52-60.
- Environment Canada. 2013. Canadian climate normals or averages 1971-2000. National Climate Data and Information Archive. Retrieved from www.climate.weatheroffice.gc.ca on 30 March 2013.
- Flook, D.R. 1959. Moose using water as refuge from flies. *Journal of Mammalogy* 40: 455.
- Forbes, G.J. & Theberge, J.B. 1993. Multiple landscape scales and winter distribution of moose, *Alces alces*, in a forest ecotone. *Canadian Field Naturalist* 107: 201-207.
- Gosse, J, Hermanutz, L, McLaren, B., Deering, P. & Knight, T. 2011. Degradation of boreal forests by non-native herbivores in Newfoundland's National Parks: recommendations for ecosystem restoration. *Natural Areas Journal* 31: 331-339.
- Hall, I.V. & Sibley, J.D. 1976. The biology of Canadian weeds. 20. *Cornus canadensis* L. *Canadian Journal of Plant Science* 56: 885-892.
- Hamilton, G.D., Drysdale, P.D. & Euler, D.L. 1980. Moose winter browsing patterns on clear-cuttings in northern Ontario. *Canadian Journal of Zoology* 58: 1412-1416.
- Harper, K.A. & Macdonald, S.E. 2011. Quantifying distance of edge influence: a comparison of methods and a new randomization method. *Ecosphere* 2: art94.

- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J.Q., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. & Esseen, P.A. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19: 768-782.
- Harris, L.D. 1988. Edge effects and conservation of biotic diversity. *Conservation Biology* 2: 330-332.
- Heikkilä, R. & Härkönen, S. 1996. Moose browsing in young Scots pine stands in relation to forest management. *Forest Ecology and Management* 88: 179-186.
- Hogg, E.H. & Lieffers, V.J. 1991. The impact of *Calamagrostis canadensis* on soil thermal regimes after logging in northern Alberta. *Canadian Journal of Forest Research* 21: 387-394.
- Hundertmark, K.J., Eberhardt, W.L. & Ball, R.E. 1990. Winter habitat use by moose in southeastern Alaska: Implications for forest management. *Alces* 26: 108-114.
- Kelsall, J.P., & Telfer, E.S. 1974. Biogeography of moose with particular reference to western North America. *Naturaliste canadien* 101: 117-130.
- Krefting, L.W. 1974. Moose distribution and habitat selection in north central North America. *Naturaliste canadien* 101: 81-100.
- Lautenschlager, R.A., Crawford, H.S., Stokes, M.R. & Stone, T.L. 1997. Forest disturbance type differentially affects seasonal moose forage. *Alces* 33: 49-73.
- LeResche, R.E., Bishop, R.H. & Coady, J.W. 1974. Distribution and habitats of moose in Alaska. *Naturaliste canadien* 101: 143-178.
- Lyon, L.J. & Jensen, C.E. 1980. Management implications of elk and deer use of clear-cuts in Montana. *The Journal of Wildlife Management* 44: 352-362.
- Massé, A. & Côté, S.D. 2009. Habitat selection of a large herbivore at high density and without predation: trade-off between forage and cover? *Journal of Mammalogy* 90: 961-970.
- Mastenbrook, B. & Cumming, H. 1989. Use of residual strips of timber by moose within cutovers in northwestern Ontario. *Alces* 25: 146-155.
- Matlack, G.E. & Litvaitis, J.A. 1999. Forest edges. In Hunter, M.L. Jr. (ed.) *Maintaining biodiversity in forest ecosystems*, pp. 210-233. Cambridge University Press, Cambridge, UK.

- McInnes, P.F., Naiman, R.J., Pastor, J. & Cohen, Y. 1992. Effects of moose browsing on vegetation and litter of the boreal forest, Isle Royale, Michigan, USA. *Ecology* 73: 2059-2075.
- McKendrick, J.D., Batzli, G.O., Everett, K.R. & Swanson, J.C. 1980. Some effects of mammalian herbivores and fertilization on tundra soils and vegetation. *Arctic and Alpine Research* 12: 565-578.
- McLaren, B.E., Robert, B.A., Djan-Chékar, N. & Lewis, K.P. 2004. Effects of overabundant moose on the Newfoundland landscape. *Alces* 40: 45-59.
- Neily, P.D., Quigley, E., Benjamin, L., Stewart, B. & Duke, T. 2003. *Ecological land classification for Nova Scotia (Volume 1 – Mapping Nova Scotia's Terrestrial Ecosystems)*. Nova Scotia Department of Natural Resources, Halifax, NS, Canada.
- Parks Canada. 2010. *Cape Breton Highlands National Park of Canada management plan*. Parks Canada, Ingonish Beach, NS, Canada.
- Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F. & Cohen, Y. 1993. Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology* 74: 467-480.
- Peek, J.M. 1963. Appraisal of a moose range in southwestern Montana. *Journal of Range Management* 16: 227-231.
- Peek, J.M. 1974. A review of moose food habits studies in North America. *Naturaliste canadien* 101: 195-215.
- Peek, J.M., Urich, D.L. & Mackie, R.J. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. *Wildlife Monographs* 48: 3-65
- Persson, I. -L., Danell, K. & Bergström. 2005. Different moose densities and accompanied changes in tree morphology and browse production. *Ecological Applications* 15: 1296-1305.
- Pimlott, D.H. 1963. Influence of deer and moose on boreal forest vegetation in two areas of eastern Canada. *Transactions of the International Union of Game Biologists*, 6: 105-116.
- R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

- Renecker, L.A. & Hudson, R.J. 1990. Behavioral and thermoregulatory responses of moose to high ambient temperatures and insect harassment in aspen-dominated forests. *Alces* 26: 66-72.
- Ricard, J.P. & Messier, C. 1996. Abundance, growth and allometry of red raspberry (*Rubus idaeus* L) along a natural light gradient in a northern hardwood forest. *Forest Ecology and Management* 81: 153-160.
- Risenhoover, K.L. & Maass, S.A. 1987. The influence of moose on the composition and structure of Isle Royale forests. *Canadian Journal of Forest Research* 17: 357-364.
- Smith, C. 2007. The Impact of Moose on Forest Regeneration Following Disturbance by Spruce Budworm in the Cape Breton Highlands, Nova Scotia, Canada. MES Thesis, Dalhousie University, Halifax, Nova Scotia, Canada.
- Smith, C., Beazley, K., Duinker, P. & Harper, K.A. 2010. The impact of moose (*Alces alces andersoni*) on forest regeneration following a severe spruce budworm outbreak in the Cape Breton Highlands, Nova Scotia, Canada. *Alces* 46: 135-150.
- Snyder, J.D. & Janke, R.A. 1976. Impact of moose browsing on boreal-type forests of Isle Royale National Park. *American Midland Naturalist* 95: 79-92.
- Stopp, G.J., White, S.N., Clements, D.R. & Upadhyaya, M.K. 2011. The biology of Canadian weeds. 149. *Rumex acetosella* L. *Canadian Journal of Plant Science* 91: 1037-1052.
- Telfer, E.S. 1967. Comparison of a deer yard and a moose yard in Nova Scotia. *Canadian Journal of Zoology* 45: 485-490.
- Telfer, E.S. 1970. Relationships between logging and big game in eastern Canada. *Pulp Paper Magazine of Canada* 71: 69-74.
- Thomas, J.W., Maser, C. & Rodiek, J.E. 1979. Edges. In Thomas, J.W. (ed.) *Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington*, pp. 48-59. U.S. Department of Agriculture Forest Service, Portland, OR, USA.
- Thompson, I.D. 1988. Moose damage to pre-commercially thinned balsam fir stands in Newfoundland. *Alces* 24: 56-61.
- Thompson, I.D. & Curran, W.J. 1993. A re-examination of moose damage to balsam fir-white birch forests in central Newfoundland: 27 years later. *Canadian Journal of Forest Research* 23: 1388-1395.

- Thompson, I.D. & Mallik, A.U. 1989. Moose browsing and allelopathic effects of *Kalmia angustifolia* on balsam fir regeneration in central Newfoundland. *Canadian Journal of Forest Research* 19: 524-526.
- Thompson, I.D., McQueen, R.E., Reichardt, P.B., Trenholm, D.G. & Curran, W.J. 1989. *Oecologia* 81: 506-509.
- Thompson, I.D., Curran, W.J., Hancock, J.A. & Butler, C.E. 1992. Influence of moose browsing on successional forest growth on black spruce sites in Newfoundland. *Forest Ecology and Management* 47: 29-37.
- Timmermann, H.R. & McNicol, J.G. 1988. Moose habitat needs. *The Forestry Chronicle* 64: 238-245.
- Van Ballenberghe, V. & Peek, J.M. 1971. Radiotelemetry studies of moose in northeastern Minnesota. *The Journal of Wildlife Management* 35: 63-71.
- Webb, K.T. & Marshall, I.B. 1999. *Ecoregions and ecodistricts of Nova Scotia*. Agriculture and Agri-Food Canada, Truro, NS, and Environment Canada, Hull, QC, Canada.
- Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society (B)* 73: 3-36.
- Yee, T.W. & Mitchell, N.D. 1991. Generalized additive models in plant ecology. *Journal of Vegetation Science* 2: 587-602.

Appendix 3-A: Secondary and tertiary response variables with significant distance of edge influence (DEI) compared to the disturbed area reference and/or forest reference.

Response variable	DEI (m) for disturbed reference	DEI (m) for forest reference
Tertiary responses		
Overall moose pellet cover	-10 to 5	-10 to 5
Proportion of browse class for all <i>Abies balsamea</i> saplings		
Live unbrowsed	ns	-55 to -41
Lightly browsed	41 to 50	ns
Severely browsed	ns	-55 to -31
Dead unbrowsed	6 to 60	-60 to -36
Proportion of browse class for all <i>Betula papyrifera</i> saplings		
Live unbrowsed	-10 to 10	ns
Severely browsed	6 to 30	-60 to -11
Proportion of browse class for all short saplings		
Live unbrowsed	-10 to 5	ns
Moderately browsed	ns	-55 to -46
Severely browsed	21 to 35	ns
Proportion of browse class for all intermediate height saplings		
Dead unbrowsed	16 to 40	ns
Proportion of browse class for all tall saplings		
Lightly browsed	41 to 50	ns
Severely browsed	ns	-50 to -41, -10 to -1
Dead unbrowsed	6 to 60	-45 to -26
Vegetation Structure		
Maximum sapling height		
All species combined	16 to 60	-45 to -26
<i>Abies balsamea</i>	36 to 60	ns
Sapling density		
<i>Betula papyrifera</i>	ns	-55 to -41
<i>Picea glauca</i>	ns	11 to 20
Seedling density		
<i>Abies balsamea</i>	-26 to 60	-60 to -26
All species combined	-26 to 60	-60 to -26
Vegetation Composition		
Overall understorey cover		
Overall bryophytes cover	16 to 45	-60 to -16
Overall fern cover	ns	ns
Overall fine woody debris cover	ns	-35 to -26
Overall grass cover	-20 to 60	-60 to -11
Overall herb cover	ns	ns
Overall shrub cover	11 to 25	11 to 25

Response variable	DEI (m) compared to disturbed area reference	DEI (m) compared to forest reference
Individual shrub species		
<i>Amelanchier</i> spp.	ns	-40 to -21
<i>Kalmia angustifolia</i>	31 to 60	-60 to 10
<i>Rubus idaeus</i>	-10 to 60	-60 to -6
Individual herb species		
<i>Aster acuminatus</i>	ns	-55 to -16
<i>Clintonia borealis</i>	6 to 15	ns
<i>Gaultheria hispidula</i>	46 to 60	ns
<i>Linnaea borealis</i>	-35 to 20, 31 to 60	ns
<i>Maianthemum canadense</i>	-35 to -26	-40 to -26
<i>Trientalis borealis</i>	1 to 60	-60 to -21
<i>Solidago macrophylla</i>	-10 to 55	ns
Individual fern species		
<i>Dryopteris</i> spp.	-10 to -1	ns
<i>Osmundastrum cinnamomeum</i>	-5 to 15, 36 to 60	-45 to -36
<i>Thelypteris noveboracensis</i>	ns	-20 to -6
Species diversity		
Understorey (including shrubs, herbs, ferns)	16 to 40	ns

Appendix 3-B: Secondary and tertiary response variables and corresponding mean values (\pm standard error) from all sites at individual distances from insect disturbed area-forest edge. Negative and positive distances represent the disturbed side and forest side of the edge, respectively (D.R. = disturbed area reference and F.R. = forest reference).

	Distance from insect disturbed area-forest edge (m)												
	D.R.	-57.5	-52.5	-47.5	-42.5	-37.5	-32.5	-27.5	-22.5	-17.5	-12.5	-7.5	-2.5
Percentage of all <i>A. balsamea</i> saplings													
Unbrowsed live	15.0 \pm 10.0	25.7 \pm 19.4	7.5 \pm 7.5	3.9 \pm 3.9	10.0 \pm 10.0	25.0 \pm 17.1	0 \pm 0	11.1 \pm 11.1	10.3 \pm 4.7	25.0 \pm 8.3	33.1 \pm 12.3	31.7 \pm 9.2	53.2 \pm 13.5
Lightly browsed	1.3 \pm 1.3	8.6 \pm 8.6	0 \pm 0	7.7 \pm 7.7	5.0 \pm 5.0	0 \pm 0	8.3 \pm 8.3	0 \pm 0	5.8 \pm 4.2	2.8 \pm 2.8	3.7 \pm 3.7	1.7 \pm 1.7	0 \pm 0
Moderately browsed	7.0 \pm 5.2	2.9 \pm 2.9	2.5 \pm 2.5	13.2 \pm 5.7	0 \pm 0	4.2 \pm 4.2	4.2 \pm 4.2	6.7 \pm 6.7	22.5 \pm 16.0	0 \pm 0	4.2 \pm 2.7	7.2 \pm 5.5	6.3 \pm 6.3
Severely browsed	57.3 \pm 12.2	45.0 \pm 22.9	70.0 \pm 20.0	62.8 \pm 8.6	85.0 \pm 15.0	66.7 \pm 17.9	79.2 \pm 8.0	48.9 \pm 21.6	63.6 \pm 17.6	25.0 \pm 9.6	27.0 \pm 16.0	40.0 \pm 13.9	28.1 \pm 12.6
Unbrowsed dead	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	0 \pm 0	8.3 \pm 8.3	6.7 \pm 6.7	3.3 \pm 3.3	11.1 \pm 11.1	0 \pm 0	5.6 \pm 5.6	4.2 \pm 4.2
Browsed dead	19.5 \pm 10.4	17.9 \pm 14.6	20.0 \pm 20.0	12.5 \pm 12.5	0 \pm 0	4.2 \pm 4.2	0 \pm 0	26.7 \pm 19.4	11.1 \pm 11.1	27.8 \pm 16.5	20.8 \pm 16.4	8.3 \pm 5.7	4.2 \pm 4.2
Percentage of all <i>B. papyrifera</i> saplings													
Unbrowsed live	13.3 \pm 8.2	40.0 \pm 24.5	12.5 \pm 8.5	36.7 \pm 20.0	20.0 \pm 20.0	20.0 \pm 20.0	0 \pm 0	27.4 \pm 13.6	50.0 \pm 25.5	36.0 \pm 22.3	22.2 \pm 16.5	66.7 \pm 33.3	78.8 \pm 19.2
Lightly browsed	12.6 \pm 6.5	0 \pm 0	0 \pm 0	10.0 \pm 6.7	20.0 \pm 20.0	0 \pm 0	0 \pm 0	5.1 \pm 5.1	11.1 \pm 11.1	5.0 \pm 5.0	27.8 \pm 15.9	16.7 \pm 16.7	0 \pm 0
Moderately browsed	13.2 \pm 7.7	0 \pm 0	8.9 \pm 5.7	3.3 \pm 3.3	5.7 \pm 5.7	16.7 \pm 10.5	14.3 \pm 14.3	10.7 \pm 8.2	16.7 \pm 9.6	25.0 \pm 19.4	11.1 \pm 7.0	16.7 \pm 16.7	0 \pm 0
Severely browsed	39.9 \pm 12.6	50.0 \pm 22.4	51.2 \pm 18.3	43.3 \pm 19.4	54.3 \pm 22.8	60.0 \pm 19.4	81.0 \pm 19.1	40.1 \pm 15.5	22.2 \pm 22.2	29.0 \pm 18.5	30.6 \pm 16.3	0 \pm 0	16.3 \pm 8.3

	Distance from insect disturbed area-forest edge (m)												
	D.R.	-57.5	-52.5	-47.5	-42.5	-37.5	-32.5	-27.5	-22.5	-17.5	-12.5	-7.5	-2.5
Unbrowsed dead	0 ± 0	0 ± 0	8.3 ± 8.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	16.7 ± 16.7	0 ± 0	0 ± 0	8.3 ± 8.3	0 ± 0	0 ± 0
Browsed dead	21.0 ± 10.4	10.0 ± 10.0	19.1 ± 10.1	6.7 ± 6.7	0.0 ± 0.0	3.3 ± 3.3	4.8 ± 4.8	0 ± 0	0 ± 0	5.0 ± 5.0	0 ± 0	0 ± 0	5.0 ± 4.0
Percentage of short (11 - 49 cm in height) saplings													
Unbrowsed live	33.2 ± 12.5	50.0 ± 22.4	21.7 ± 10.1	36.6 ± 20.3	26.7 ± 19.4	25.0 ± 25.0	0 ± 0	58.5 ± 20.1	84.3 ± 7.9	80.0 ± 10.5	70.2 ± 15.4	96.7 ± 3.3	81.3 ± 10.1
Lightly browsed	23.5 ± 11.2	0 ± 0	0 ± 0	4.2 ± 4.2	13.3 ± 13.3	4.2 ± 4.2	8.3 ± 8.3	6.5 ± 6.5	8.3 ± 8.3	4.0 ± 4.0	14.8 ± 11.1	3.3 ± 3.3	0 ± 0
Moderately browsed	6.7 ± 6.7	10.0 ± 10.0	25.0 ± 11.2	34.2 ± 20.8	20.0 ± 20.0	27.1 ± 15.7	54.2 ± 4.2	5.0 ± 5.0	3.7 ± 3.7	4.0 ± 4.0	0.0 ± 0.0	0.0 ± 0.0	83.3 ± 83.3
Severely browsed	36.7 ± 14.7	40.0 ± 24.5	20.0 ± 16.3	25.0 ± 17.1	40.0 ± 24.5	43.8 ± 21.4	37.5 ± 12.5	30.0 ± 20.0	3.7 ± 3.7	12.0 ± 9.7	12.5 ± 12.5	0 ± 0	10.4 ± 8.2
Unbrowsed dead	0 ± 0	0 ± 0	8.3 ± 8.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	2.5 ± 2.5	0 ± 0	0 ± 0
Browsed dead	0 ± 0	0 ± 0	25.0 ± 17.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Percentage of intermediate (50 – 99 cm in height) saplings													
Unbrowsed live	0 ± 0	6.3 ± 6.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	8.3 ± 8.3	0 ± 0	0 ± 0	0 ± 0	5.0 ± 5.0	0 ± 0
Lightly browsed	11.1 ± 8.5	18.8 ± 18.8	0 ± 0	3.3 ± 3.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	13.9 ± 9.0	5.6 ± 5.6	10.0 ± 6.1	5.0 ± 5.0	0 ± 0
Moderately browsed	10.6 ± 4.0	0 ± 0	4.0 ± 4.0	20.0 ± 20.0	0 ± 0	5.6 ± 5.6	0 ± 0	6.7 ± 6.7	20.8 ± 16.4	5.6 ± 5.6	16.7 ± 7.0	10.0 ± 6.1	5.0 ± 5.0
Severely browsed	52.8 ± 11.6	61.7 ± 21.7	78.7 ± 13.7	65.3 ± 18.3	100.0 ± 0.0	82.8 ± 8.6	89.3 ± 6.9	62.2 ± 12.2	56.9 ± 13.7	68.1 ± 12.3	58.3 ± 20.1	70.0 ± 18.4	45.0 ± 20.0

	Distance from insect disturbed area-forest edge (m)												
	D.R.	-57.5	-52.5	-47.5	-42.5	-37.5	-32.5	-27.5	-22.5	-17.5	-12.5	-7.5	-2.5
Unbrowsed dead	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	6.7 ± 6.7	13.9 ± 9.0	0 ± 0	11.1 ± 11.1	0 ± 0	0 ± 0	20.0 ± 20.0
Browsed dead	25.6 ± 1.2	13.3 ± 8.2	17.3 ± 12.9	11.3 ± 7.9	0 ± 0	11.7 ± 8.3	4.0 ± 4.0	8.9 ± 5.9	8.3 ± 8.3	9.7 ± 6.2	15.0 ± 10.0	10.0 ± 6.1	30.0 ± 20.0
Percentage of tall (> 99 cm in height) saplings													
Unbrowsed live	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.00	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Lightly browsed	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Moderately browsed	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.00	0 ± 0	20.0 ± 20.0	0 ± 0	33.3 ± 33.3	10.0 ± 10.0	0 ± 0
Severely browsed	57.1 ± 17.0	25.0 ± 25.0	83.3 ± 16.7	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0	50.0 ± 50.0	40.0 ± 24.5	25.0 ± 25.0	33.3 ± 33.3	70.0 ± 20.0	87.5 ± 12.5
Unbrowsed dead	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.00	0 ± 0	20.0 ± 20.0	25.0 ± 25.0	0 ± 0	20.0 ± 20.0	0 ± 0
Browsed dead	42.9 ± 17.0	75.0 ± 25.0	16.7 ± 16.7	0 ± 0	0 ± 0	0 ± 0	0.00	50.0 ± 50.0	20.0 ± 20.0	50.0 ± 28.9	33.3 ± 33.3	0 ± 0	12.5 ± 12.5
Maximum sapling height (cm)													
All species	123.3 ± 13.3	142.2 ± 14.7	124.3 ± 19.2	142.2 ± 15.3	123.5 ± 19.8	125.7 ± 15.6	126.3 ± 17.8	121.8 ± 15.4	174.7 ± 7.0	158.5 ± 10.3	120.5 ± 15.0	151.8 ± 12.0	119.7 ± 21.7
<i>A. balsamea</i>	83.6 ± 15.4	116.6 ± 31.4	91.8 ± 15.2	115.8 ± 24.6	95.5 ± 34.5	102.7 ± 22.1	85.0 ± 14.9	110.6 ± 20.3	146.2 ± 21.3	141.2 ± 20.2	96.3 ± 14.9	138.2 ± 17.2	113.8 ± 24.1
<i>B. papyrifera</i>	76.5 ± 12.0	53.0 ± 5.5	71.3 ± 21.2	51.0 ± 16.2	70.0 ± 20.4	52.0 ± 12.4	56.0 ± 17.1	58.2 ± 8.9	48.3 ± 12.5	42.6 ± 16.9	48.2 ± 11.7	45.0 ± 17.0	42.5 ± 13.6
<i>P. glauca</i>	171.0 ± 10.4	141.0 ± 15.0	195.0	150.3 ± 24.2	135.0 ± 19.0	116.0 ± 20.5	153.7 ± 26.3	119.0 ± 33.0	171.5 ± 20.5	92.7 ± 39.5	97.0 ± 40.2	158.0	84.0 ± 6.8

	Distance from insect disturbed area-forest edge (m)												
	D.R.	-57.5	-52.5	-47.5	-42.5	-37.5	-32.5	-27.5	-22.5	-17.5	-12.5	-7.5	-2.5
Sapling density (# of individuals / 5 m)													
All species	3.5 ± 1.2	2.5 ± 0.9	4.7 ± 1.3	7.3 ± 2.6	5.7 ± 2.5	3.2 ± 0.9	2.3 ± 1.2	5.5 ± 1.9	3.0 ± 1.7	3.0 ± 1.1	5.0 ± 1.3	2.2 ± 1.0	7.2 ± 1.9
<i>A. balsamea</i>	0.9 ± 0.6	0.7 ± 0.3	1.7 ± 0.8	2.0 ± 1.2	2.8 ± 1.9	1.0 ± 0.4	1.0 ± 0.6	1.2 ± 0.8	1.2 ± 0.8	1.3 ± 0.6	3.3 ± 0.8	1.8 ± 0.9	4.0 ± 0.9
<i>B. papyrifera</i>	2.5 ± 0.8	1.3 ± 0.5	2.8 ± 1.0	3.8 ± 1.3	2.7 ± 1.1	1.8 ± 1.0	1.2 ± 0.8	4.2 ± 2.09	1.8 ± 1.0	1.5 ± 0.8	1.5 ± 0.4	0.2 ± 0.2	2.7 ± 1.6
<i>P. glauca</i>	0.1 ± 0.1	0.5 ± 0.5	0.2 ± 0.2	1.5 ± 1.2	0.2 ± 0.2	0.3 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0 ± 0	0.2 ± 0.2	0.2 ± 0.2	0.2 ± 0.2	0.5 ± 0.3
Seedling density (# of individuals / 5 m)													
All species	0.1 ± 0.1	0 ± 0	0.7 ± 0.5	1.0 ± 0.8	0.7 ± 0.7	1.2 ± 1.2	0.3 ± 0.2	0.5 ± 0.3	3.0 ± 1.3	2.0 ± 1.2	4.3 ± 3.2	3.2 ± 1.7	2.3 ± 1.6
<i>A. balsamea</i>	0 ± 0	0 ± 0	0.7 ± 0.5	1.0 ± 0.8	0.5 ± 0.5	1.2 ± 1.2	0.3 ± 0.2	0.3 ± 0.2	2.7 ± 1.3	2.0 ± 1.2	4.3 ± 3.2	3.2 ± 1.7	2.3 ± 1.6
<i>B. papyrifera</i>	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>P. glauca</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0.2 ± 0.2	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Overall cover (%)													
Graminoids	36.4 ± 3.2	41.9 ± 5.8	37.1 ± 4.4	24.4 ± 4.2	29.4 ± 4.2	29.1 ± 5.2	31.4 ± 5.5	26.1 ± 5.2	26.1 ± 4.3	13.5 ± 2.8	9.7 ± 2.6	11.7 ± 3.5	7.4 ± 2.6
Bryophytes	6.6 ± 1.6	2.8 ± 1.3	2.8 ± 0.6	10.3 ± 3.0	5.1 ± 2.3	5.7 ± 1.7	12.2 ± 4.6	12.5 ± 4.0	12.8 ± 3.8	10.2 ± 3.2	23.6 ± 5.9	20.8 ± 5.7	26.7 ± 5.9
Fine woody debris	6.2 ± 0.9	5.6 ± 0.8	8.8 ± 1.3	6.9 ± 1.1	5.6 ± 0.7	6.7 ± 1.1	4.9 ± 0.9	5.7 ± 0.6	7.2 ± 1.1	7.4 ± 1.1	7.9 ± 1.1	6.0 ± 0.8	7.6 ± 1.2

	Distance from insect disturbed area-forest edge (m)												
	D.R.	-57.5	-52.5	-47.5	-42.5	-37.5	-32.5	-27.5	-22.5	-17.5	-12.5	-7.5	-2.5
Litter	52.2 ± 2.5	55.2 ± 3.9	52.8 ± 4.5	51.3 ± 4.3	56.0 ± 4.8	57.3 ± 5.0	56.4 ± 5.4	56.3 ± 5.2	53.5 ± 5.0	64.0 ± 4.0	54.8 ± 3.9	48.5 ± 4.6	57.3 ± 4.3
Moose pellet	0.3 ± 0.1	0.5 ± 0.2	0.8 ± 0.3	1.1 ± 0.4	0.5 ± 0.2	0.8 ± 0.3	0.4 ± 0.2	0.4 ± 0.2	0.3 ± 0.2	0.6 ± 0.2	0.7 ± 0.3	0.9 ± 0.3	0.9 ± 0.4
Shrub layer	8.6 ± 0.8	7.6 ± 1.1	7.2 ± 1.2	9.7 ± 1.7	6.8 ± 1.0	7.3 ± 0.8	7.8 ± 1.1	8.2 ± 1.4	5.9 ± 1.6	5.7 ± 1.5	4.6 ± 1.2	5.3 ± 1.0	6.8 ± 1.9
Herb layer	19.9 ± 1.2	21.8 ± 2.8	26.8 ± 3.1	27.8 ± 3.2	21.5 ± 2.0	22.3 ± 2.3	19.0 ± 2.3	28.6 ± 3.4	25.8 ± 2.9	33.3 ± 2.3	30.0 ± 3.7	27.2 ± 3.4	25.5 ± 2.6
Fern	12.7 ± 2.0	9.8 ± 2.9	4.6 ± 1.0	7.5 ± 2.9	12.2 ± 3.7	15.6 ± 4.7	18.7 ± 6.0	19.9 ± 5.6	20.7 ± 6.2	32.0 ± 6.3	32.6 ± 6.0	27.8 ± 5.4	30.9 ± 4.1
Shrub layer species cover (%)													
<i>Amelanchier</i> spp.	0.4 ± 0.3	0.6 ± 0.5	0.1 ± 0.1	2.5 ± 1.2	0.5 ± 0.4	0.1 ± 0.1	0.3 ± 0.2	0.1 ± 0.1	0.4 ± 0.2	0.5 ± 0.2	0.2 ± 0.2	1.3 ± 0.5	2.5 ± 1.1
<i>Kalmia angustifolia</i>	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	1.2 ± 0.9	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0	0.0 ± 0.0
<i>Kalmia polifolia</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Myrica gale</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Nemopanthus mucronatus</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Prunus pensylvanica</i>	0.03 ± 0.03	0 ± 0	0 ± 0	0.03 ± 0.03	0 ± 0	0 ± 0	0.03 ± 0.03	0.03 ± 0.03	0 ± 0	0.1 ± 0.1	0 ± 0	0.30 ± 0.03	0.1 ± 0.1
<i>Rhododendron canadense</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Rhododendron groenlandicum</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0

	Distance from insect disturbed area-forest edge (m)												
	D.R.	-57.5	-52.5	-47.5	-42.5	-37.5	-32.5	-27.5	-22.5	-17.5	-12.5	-7.5	-2.5
<i>Ribes glandulosum</i>	0.04 ± 0.02	0.4 ± 0.2	0.4 ± 0.2	0.2 ± 0.2	0 ± 0	0.03 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Rosa nitida</i>	0.5 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Rubus idaeus</i>	5.7 ± 0.5	6.5 ± 1.2	5.1 ± 0.8	6.6 ± 1.3	5.4 ± 0.9	6.7 ± 1.0	6.6 ± 1.0	5.7 ± 1.3	2.4 ± 0.5	4.8 ± 1.5	2.4 ± 0.8	2.1 ± 0.7	1.0 ± 0.4
<i>Rubus pubescens</i>	0.5 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Sambucus racemosa</i>	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Sorbus americana</i>	0.7 ± 0.3	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.4 ± 0.2	0.3 ± 0.2	0.6 ± 0.4	0.7 ± 0.3	0.4 ± 0.2	0.4 ± 0.2	1.4 ± 0.4	0.5 ± 0.2	0.8 ± 0.3
<i>Vaccinium angustifolium</i>	0.1 ± 0.1	0.2 ± 0.2	1.6 ± 0.9	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	1.9 ± 1.2	0 ± 0	0.4 ± 0.2	0.8 ± 0.5	2.3 ± 1.3
<i>Viburnum nudum</i>	0.5 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0.3 ± 0.3	0.4 ± 0.2	0.2 ± 0.2	0 ± 0	0.6 ± 0.4	0.2 ± 0.2	0.2 ± 0.2	0.5 ± 0.2	0.1 ± 0.1
Herbaceous layer species cover (%)													
<i>Anaphalis margaritacea</i>	0.1 ± 0.1	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0.2 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Aralia nudicaulis</i>	3.0 ± 0.4	1.6 ± 0.4	4.9 ± 0.8	3.2 ± 0.6	3.5 ± 0.8	5.2 ± 1.5	3.3 ± 0.9	3.2 ± 0.6	3.6 ± 0.7	5.6 ^a ± 0.7	3.3 ± 0.6	3.6 ± 1.1	2.3 ± 0.3
<i>Aster acuminatus</i>	1.1 ± 0.3	1.2 ± 0.3	2.5 ± 0.6	2.4 ± 0.5	1.8 ± 0.4	1.7 ± 0.4	2.1 ± 0.6	2.8 ± 0.8	2.0 ± 0.4	1.7 ± 0.4	1.1 ± 0.3	1.2 ± 0.3	0.5 ± 0.2
<i>Aster</i> spp. (except <i>A. acuminatus</i>)	1.7 ± 0.5	0.1 ± 0.1	0 ± 0	1.7 ± 1.1	0.8 ± 0.4	0 ± 0	0.3 ± 0.2	0 ± 0	0.1 ± 0.1	0.4 ± 0.2	0.1 ± 0.1	0 ± 0	0 ± 0

	Distance from insect disturbed area-forest edge (m)												
	D.R.	-57.5	-52.5	-47.5	-42.5	-37.5	-32.5	-27.5	-22.5	-17.5	-12.5	-7.5	-2.5
<i>Clintonia borealis</i>	0.2 ± 0.1	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.2	0 ± 0	0.2 ± 0.1	0 ± 0	1.5 ± 0.8	0.8 ± 0.3	0.8 ± 0.4	1.2 ± 0.3	1.1 ± 0.4	0.3 ± 0.2
<i>Coptis trifolia</i>	0.5 ± 0.1	0.3 ± 0.1	0.2 ± 0.2	0.2 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.7 ± 0.4	1.0 ± 0.4	0.3 ± 0.2	0.3 ± 0.1	0.7 ± 0.2	0.9 ± 0.4	0.9 ± 0.4
<i>Cornus canadensis</i>	9.7 ± 0.9	16.1 ± 2.8	14.7 ± 2.0	16.8 ± 3.0	12.2 ± 2.2	9.8 ± 1.9	10.5 ± 2.2	17.5 ± 2.6	13.4 ± 2.5	18.7 ± 2.6	20.8 ± 3.7	17.0 ± 2.8	16.7 ± 2.7
<i>Cypripedium acaule</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Epigaea repens</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Gaultheria hispidula</i>	0.01 ± 0.02	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0.5 ± 0.3	0.3 ± 0.1	0.6 ± 0.3	0.1 ± 0.1	0 ± 0	0.1 ± 0.1
<i>Linnaea borealis</i>	0 ± 0	0.1 ± 0.1	2.4 ± 1.2	0.8 ± 0.7	0.4 ± 0.3	1.7 ± 0.8	1.4 ± 0.5	1.2 ± 0.4	1.6 ± 0.6	3.0 ± 0.8	1.1 ± 0.3	1.7 ± 0.6	1.4 ± 0.4
<i>Maianthemum canadense</i>	1.0 ± 0.2	0.9 ± 0.2	0.9 ± 0.3	0.7 ± 0.2	0.9 ± 0.2	0.4 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	1.5 ± 0.4	1.2 ± 0.3	0.8 ± 0.3	0.5 ± 0.1	1.7 ± 0.4
<i>Mitchella repens</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.1	0 ± 0	0.8 ± 0.4	0 ± 0	0 ± 0	0 ± 0	0.4 ± 0.3
<i>Oxalis</i> spp.	0.4 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.03 ± 0.03	0.4 ± 0.2	0.4 ± 0.2	0.2 ± 0.2	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0 ± 0
<i>Rubus chamaemorus</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0.2 ± 0.2	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	1.0 ± 0.5	0.8 ± 0.3
<i>Rumex acetosella</i>	0.4 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	1.8 ± 0.8	0.3 ± 0.2	0.1 ± 0.1	0.2 ± 0.1	0.7 ± 0.5	0 ± 0	0 ± 0	0 ± 0
<i>Smilacina trifolia</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Solidago macrophylla</i>	2.0 ± 0.5	1.5 ± 0.6	0.6 ± 0.4	1.2 ± 0.6	1.1 ± 0.7	1.5 ± 0.8	0.03 ± 0.03	0.4 ± 0.2	1.1 ± 0.5	0.5 ± 0.2	0.3 ± 0.2	0.03 ± 0.03	0.0 ± 0.0

	Distance from insect disturbed area-forest edge (m)												
	D.R.	-57.5	-52.5	-47.5	-42.5	-37.5	-32.5	-27.5	-22.5	-17.5	-12.5	-7.5	-2.5
<i>Solidago</i> spp. (except <i>S.</i> <i>macrophylla</i>)	0 ± 0	0 ± 0	0.1 ± 0.1	0.03 ± 0.03	0.03 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.3 ± 0.2	0 ± 0	0 ± 0
<i>Trientalis borealis</i>	0.03 ± 0.02	0.1 ± 0.1	0 ± 0	0.03 ± 0.03	0 ± 0	0.03 ± 0.03	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.2 ± 0.1	0.1 ± 0.1	0.3 ± 0.1	0.2 ± 0.1
<i>Vaccinium</i> <i>oxycoccos</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Veronica officinalis</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Fern species cover (%)													
<i>Dryopteris</i> spp.	6.3 ± 1.1	3.4 ± 0.6	3.5 ± 0.8	1.9 ± 0.6	4.0 ± 1.2	6.4 ± 1.7	2.6 ± 0.7	4.0 ± 0.8	2.1 ± 0.6	3.3 ± 1.0	1.9 ± 0.6	0.5 ± 0.2	1.0 ± 0.5
<i>Osmundastrum</i> <i>cinnamomeum</i>	0.1 ± 0.1	0.03 ± 0.03	0.2 ± 0.2	0.5 ± 0.4	0 ± 0	0.1 ± 0.1	1.4 ± 1.2	2.7 ± 1.1	2.7 ± 1.5	6.2 ± 2.1	11.3 ± 3.3	6.5 ± 1.9	12.7 ± 3.5
<i>Pteridium aquilinum</i>	0.8 ± 0.5	2.7 ± 1.1	0.8 ± 0.4	0 ± 0	0.03 ± 0.03	2.0 ± 1.2	9.0 ± 3.8	11.5 ± 5.2	10.3 ± 4.5	13.0 ± 5.5	6.5 ± 2.6	7.0 ± 2.6	12.9 ± 5.4
<i>Thelypteris</i> <i>noveboracensis</i>	5.5 ± 1.6	4.0 ± 2.0	0.3 ± 0.2	5.2 ± 2.9	8.2 ± 3.8	7.5 ± 4.2	6.2 ± 2.7	4.5 ± 2.1	7.5 ± 2.9	13.5 ± 3.1	14.8 ± 3.6	14.9 ± 3.9	13.2 ± 4.2
	Distance from insect-disturbed area forest edge (m)												
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	F.R.
Percentage of all <i>A. balsamea</i> saplings													
Unbrowsed live	30.3 ± 15.1	15.3 ± 10.0	9.3 ± 4.3	9.9 ± 4.9	22.8 ± 11.9	25.2 ± 14.3	17.2 ± 10.6	18.6 ± 10.6	28.5 ± 14.1	27.0 ± 12.1	22.6 ± 14.5	31.6 ± 11.1	44.7 ± 10.4
Lightly browsed	4.8 ± 4.8	3.4 ± 2.2	10.2 ± 6.9	2.4 ± 2.4	4.4 ± 2.9	2.1 ± 2.1	2.8 ± 2.8	6.1 ± 3.9	20.5 ± 12.3	10.9 ± 5.0	4.0 ± 4.0	11.7 ± 8.3	6.2 ± 3.2

	Distance from insect-disturbed area forest edge (m)												F.R.
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	
Moderately browsed	4.8 ± 4.8	6.4 ± 4.0	8.3 ± 5.4	11.1 ± 8.2	10.0 ± 8.2	19.4 ± 16.3	13.3 ± 9.9	11.4 ± 8.3	8.3 ± 8.3	6.7 ± 6.7	5.0 ± 5.0	1.7 ± 1.7	3.3 ± 3.3
Severely browsed	43.1 ± 16.9	23.1 ± 9.3	18.2 ± 8.2	15.9 ± 11.2	10.0 ± 10.0	13.2 ± 10.9	17.8 ± 11.8	18.2 ± 12.7	4.3 ± 2.9	25.0 ± 17.1	50.0 ± 20.9	20.1 ± 9.6	13.1 ± 8.2
Unbrowsed dead	11.9 ± 9.3	50.0 ± 18.4	54.0 ± 18.5	53.6 ± 18.6	52.8 ± 16.9	33.8 ± 17.5	48.9 ± 18.6	45.7 ± 12.3	37.0 ± 16.7	30.5 ± 11.4	18.4 ± 13.6	35.0 ± 17.5	32.8 ± 9.1
Browsed dead	5.2 ± 3.3	1.9 ± 1.9	0 ± 0	7.1 ± 7.1	0 ± 0	6.3 ± 6.3	0 ± 0	0 ± 0	1.4 ± 1.4	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Percentage of all <i>B. papyrifera</i> saplings													
Unbrowsed live	65.0 ± 18.7	100.0	0.0	0.0	0 ± 0	0 ± 0	0 ± 0	33.3 ± 33.3	0 ± 0	33.3 ± 33.3	66.7 ± 33.3	38.9 ± 30.9	50.0 ± 28.9
Lightly browsed	0 ± 0	0.0	0.0	0.0	0 ± 0	0 ± 0	33.3 ± 33.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	16.7 ± 16.7	50.0 ± 28.9
Moderately browsed	20.0 ± 20.0	0 ± 0	100.0	0.0	0 ± 0	0 ± 0	50.0 ± 50.0	0 ± 0	12.5 ± 12.5	0 ± 0	0 ± 0	5.6 ± 5.6	0 ± 0
Severely browsed	5.0 ± 5.0	0.0	0.0	0.0	0 ± 0	0 ± 0	16.7 ± 16.7	0 ± 0	25.0 ± 25.0	33.3 ± 33.3	33.3 ± 33.3	0 ± 0	0 ± 0
Unbrowsed dead	0 ± 0	0.0	0.0	100.0	100.0 ± 0.0	0 ± 0	0 ± 0	33.3 ± 33.3	50.0 ± 50.0	33.3 ± 33.3	0 ± 0	0 ± 0	0 ± 0
Browsed dead	10.0 ± 10.0	0.0	0.0	0.0	0 ± 0	100.0 ± 50.0	0 ± 0	33.3 ± 33.3	12.5 ± 12.5	0 ± 0	0 ± 0	38.9 ± 30.9	0 ± 0
Percentage of all short (11 – 49 cm in height) saplings													
Unbrowsed live	90.0 ± 10.0	72.8 ± 19.5	60.7 ± 39.3	62.5 ± 23.9	50.0 ± 28.9	61.1 ± 30.9	5.6 ± 5.6	30.0 ± 20.0	62.5 ± 23.9	60.0 ± 18.7	80.0 ± 20.0	60.9 ± 24.3	97.7 ± 1.6
Lightly browsed	6.7 ± 6.7	11.7 ± 11.7	11.3 ± 11.3	12.5 ± 12.5	11.1 ± 11.1	5.6 ± 5.6	27.8 ± 27.8	0 ± 0	3.1 ± 3.1	0 ± 0	0 ± 0	9.4 ± 9.4	2.3 ± 1.6
Moderately browsed	0 ± 0	10.0 ± 10.0	28.0 ± 28.0	0 ± 0	5.6 ± 5.6	0 ± 0	3.3 ± 3.3	20.0 ± 20.0	0 ± 0	0 ± 0	0 ± 0	3.1 ± 3.1	0 ± 0
Severely browsed	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	20.0 ± 20.0	9.4 ± 9.4	10.0 ± 10.0	0 ± 0	0 ± 0	0 ± 0

	Distance from insect-disturbed area forest edge (m)												F.R.
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	
Unbrowsed dead	0 ± 0	0 ± 0	0 ± 0	25.0 ± 25.0	33.3 ± 33.3	33.3 ± 33.3	33.3 ± 33.3	30.0 ± 20.0	25.0 ± 25.0	30.0 ± 20.0	20.0 ± 20.0	25.0 ± 25.0	0 ± 0
Browsed dead	3.3 ± 3.3	5.6 ± 5.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	1.6 ± 1.6	0 ± 0
Percentage of intermediate (50 – 99 cm in height) saplings													
Unbrowsed live	4.0 ± 4.0	15.6 ± 11.8	33.3 ± 33.3	0 ± 0	6.7 ± 6.7	20.0 ± 20.0	0 ± 0	0 ± 0	0 ± 0	30.0 ± 20.0	20.0 ± 20.0	12.5 ± 12.5	0 ± 0
Lightly browsed	0 ± 0	0 ± 0	0 ± 0	0 ± 0	6.7 ± 6.7	0 ± 0	0 ± 0	0 ± 0	66.7 ± 33.3	10.0 ± 10.0	0 ± 0	0 ± 0	5.6 ± 5.6
Moderately browsed	5.0 ± 5.0	15.6 ± 11.8	0 ± 0	0 ± 0	10.0 ± 10.0	20.0 ± 20.0	20.0 ± 20.0	10.0 ± 10.0	11.1 ± 11.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0
Severely browsed	67.0 ± 18.4	31.3 ± 18.8	33.3 ± 33.3	40.0 ± 24.5	10.0 ± 10.0	26.7 ± 19.4	20.0 ± 20.0	26.7 ± 19.4	0 ± 0	40.0 ± 24.5	60.0 ± 24.5	50.0 ± 28.9	36.1 ± 17.4
Unbrowsed dead	20.0 ± 20.0	37.5 ± 23.9	33.3 ± 33.3	60.0 ± 24.5	66.7 ± 21.1	20.0 ± 20.0	60.0 ± 24.5	56.7 ± 19.4	11.1 ± 11.1	20.0 ± 20.0	20.0 ± 20.0	25.0 ± 14.4	58.3 ± 16.0
Browsed dead	4.0 ± 4.0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	13.3 ± 13.3	0 ± 0	6.7 ± 6.7	11.1 ± 11.1	0 ± 0	0 ± 0	12.5 ± 12.5	0 ± 0
Percentage of tall (> 99 cm in height) saplings													
Unbrowsed live	0 ± 0	0 ± 0	0 ± 0	3.3 ± 3.3	25.0 ± 17.1	18.1 ± 12.6	30.0 ± 20.0	18.1 ± 13.7	21.7 ± 14.2	10.4 ± 6.8	18.3 ± 13.0	8.3 ± 8.3	15.6 ± 8.1
Lightly browsed	0 ± 0	8.3 ± 8.3	11.1 ± 11.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	11.1 ± 8.2	13.1 ± 8.1	8.3 ± 4.2	10.0 ± 10.0	15.3 ± 12.3	18.8 ± 13.2
Moderately browsed	13.3 ± 13.3	0 ± 0	5.6 ± 5.6	17.5 ± 12.3	12.5 ± 12.5	20.8 ± 16.4	12.5 ± 9.7	7.0 ± 4.6	8.3 ± 8.3	10.4 ± 10.4	20.0 ± 20.0	2.8 ± 2.8	6.3 ± 6.3
Severely browsed	63.3 ± 22.6	43.1 ± 15.6	30.6 ± 16.3	15.0 ± 15.0	16.7 ± 16.7	9.7 ± 9.7	30.0 ± 20.0	20.0 ± 16.3	11.1 ± 8.2	33.3 ± 21.1	40.0 ± 24.5	37.5 ± 20.2	12.5 ± 12.5
Unbrowsed dead	18.3 ± 14.5	48.6 ± 18.3	52.8 ± 18.5	44.2 ± 20.7	45.8 ± 18.7	34.7 ± 16.5	27.5 ± 19.5	43.8 ± 16.3	37.5 ± 18.0	37.5 ± 14.1	11.7 ± 7.3	36.1 ± 17.4	46.9 ± 13.7
Browsed dead	5.0 ± 5.0	0 ± 0	0 ± 0	20.0 ± 20.0	0 ± 0	16.7 ± 16.7	0 ± 0	0 ± 0	8.3 ± 8.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0

	Distance from insect-disturbed area forest edge (m)												
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	F.R.
Maximum sapling height (cm)													
All species	141.3	153.2	203.8	198.7	221.7	175.2	150.5	207.5	216.2	298.2	144.2	188.5	206.3
	± 24.4	± 12.4	± 50.2	± 21.6	± 38.7	± 15.9	± 15.0	± 43.3	± 47.8	± 88.0	± 15.0	± 28.4	± 27.6
<i>A. balsamea</i>	128.0	153.2	203.8	181.7	222.3	165.3	147.2	207.5	216.2	298.2	154.0	188.5	183.8
	± 26.4	± 12.4	± 50.2	± 28.6	± 38.5	± 17.7	± 16.8	± 43.3	± 47.8	± 88.0	± 13.9	± 28.4	± 37.8
<i>B. papyrifera</i>	46.8 ±	22.0 ±	42.0	143.0	49.0 ±	94.0	46.0 ±	92.7 ±	61.0 ±	80.0 ±	42.7 ±	35.7 ±	21.8 ±
	10.4	9.5			12.8		13.0	43.6	20.0	42.3	21.1	12.8	5.0
<i>P. glauca</i>	167.0	84.5 ±	55.0	190.0	142.3	171.0	97.5 ±	107.5	123.5	71.5 ±	80.0 ±	133.5	149.0
		61.5			± 18.3	± 0.0	19.5	± 49.5	± 10.5	37.5	15.0	± 10.5	± 22.5
Sapling density (# of individuals / 5 m)													
All species	4.0 ±	6.8 ±	4.3 ±	1.5 ±	4.3 ±	3.5 ±	2.8 ±	3.8 ±	4.8 ±	5.3 ±	3.7 ±	6.3 ±	5.8 ±
	0.7	3.6	2.8	0.4	1.4	1.3	0.9	1.7	2.6	1.2	1.1	2.1	1.4
<i>A. balsamea</i>	2.2 ±	6.0 ±	3.7	1.5 ±	3.5 ±	3.0 ±	1.7 ±	3.0 ±	3.8 ±	4.3 ±	2.7 ±	4.7 ±	2.6 ±
	0.7	3.3	±1.7	0.4	1.1	1.4	1.0	1.2	2.1	1.1	1.7	1.7	0.7
<i>B. papyrifera</i>	1.7 ±	0.5 ±	0.7 ±	0 ± 0	0.7 ±	0 ± 0	0.8 ±	0.7 ±	0.8 ±	0.3 ±	0.5 ±	1.3 ±	0.5 ±
	0.4	0.3	0.7		0.3		0.5	0.5	0.7	0.2	0.3	1.00	0.3
<i>P. glauca</i>	0.2 ±	0.3 ±	0 ± 0	0 ± 0	0.2 ±	0.5 ±	0.3 ±	0.2 ±	0.2 ±	0.7 ±	0.5 ±	0.3 ±	2.7 ±
	0.2	0.2			0.2	0.3	0.3	0.2	0.2	0.4	0.3	0.2	1.6
Seedling density (# of individuals / 5 m)													
All species	5.0 ±	7.5 ±	10.2 ±	19.3 ±	10.3 ±	7.5 ±	4.0 ±	6.7 ±	10.0 ±	5.3 ±	5.0 ±	6.8 ±	5.8 ±
	1.8	2.7	6.4	16.4	7.0	3.8	2.5	5.2	3.0	1.8	4.3	3.8	2.0
<i>A. balsamea</i>	4.7 ±	7.5 ±	10.2 ±	19.3 ±	10.0 ±	7.5 ±	4.0 ±	6.7 ±	9.8 ±	5.3 ±	5.0 ±	6.5 ±	5.8 ±
	2.0	2.7	6.4	16.4	6.7	3.8	2.5	5.2	3.0	1.8	4.3	3.9	2.0
<i>B. papyrifera</i>	0.2 ±	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
	0.2												
<i>P. glauca</i>	0.2 ±	0 ± 0	0 ± 0	0 ± 0	0.3 ±	0 ± 0	0 ± 0	0 ± 0	0.2 ±	0 ± 0	0 ± 0	0.3 ±	0 ± 0
	0.2				0.3				0.2			0.3	
Overall cover (%)													
Graminoids	7.3 ±	0.1 ±	0.7 ±	3.1 ±	4.5 ±	4.2 ±	2.5 ±	3.2 ±	1.5 ±	0.5 ±	1.5 ±	2.2 ±	1.2 ±
	3.3	0.1	0.3	0.9	1.8	1.7	1.2	1.2	0.7	0.2	0.6	1.2	0.5

	Distance from insect-disturbed area forest edge (m)												
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	F.R.
Bryophytes	20.3 ± 3.9	14.3 ± 2.6	19.1 ± 4.2	29.1 ± 5.5	33.9 ± 5.6	38.4 ± 6.3	35.2 ± 5.9	27.6 ± 4.9	35.8 ± 5.7	24.9 ± 5.6	24.6 ± 4.7	34.1 ± 5.0	40.1 ± 3.3
Fine woody debris	8.1 ± 1.3	10.7 ± 2.0	11.8 ± 1.7	13.1 ± 2.2	14.1 ± 1.7	8.2 ± 1.5	9.5 ± 1.4	10.9 ± 2.0	15.1 ± 2.9	13.1 ± 2.5	8.3 ± 1.5	9.2 ± 1.0	13.0 ± 1.4
Litter	58.0 ± 4.1	64.7 ± 4.5	66.8 ± 5.5	57.5 ± 5.5	59.8 ± 5.7	53.2 ± 6.1	52.9 ± 5.9	58.6 ± 5.5	54.8 ± 5.9	59.0 ± 5.4	60.3 ± 5.6	49.8 ± 4.6	57.6 ± 3.2
Moose pellet	1.5 ± 0.4	0.7 ± 0.4	0.9 ± 0.4	0.6 ± 0.2	1.0 ± 0.6	1.9 ± 0.9	1.5 ± 0.7	1.1 ± 0.5	0.03 ± 0.03	0.4 ± 0.2	1.6 ± 0.6	0.5 ± 0.2	0.2 ± 0.1
Shrub layer	2.3 ± 0.7	5.7 ± 2.4	2.6 ± 0.7	2.7 ± 0.5	1.7 ± 0.4	4.8 ± 1.6	3.5 ± 1.3	9.0 ± 2.3	6.7 ± 1.7	7.4 ± 2.0	8.7 ± 1.7	8.8 ± 1.4	8.7 ± 1.1
Herb layer	29.3 ± 2.2	26.8 ± 3.9	20.4 ± 3.9	21.2 ± 4.2	19.2 ± 5.2	22.5 ± 5.3	18.3 ± 4.2	21.2 ± 3.6	17.3 ± 3.3	30.9 ± 4.3	35.8 ± 2.8	31.2 ± 3.4	24.6 ± 2.8
Fern	31.5 ± 5.1	22.3 ± 4.2	12.7 ± 3.3	5.0 ± 1.7	5.7 ± 1.5	16.1 ± 4.4	11.7 ± 3.7	19.7 ± 4.9	12.9 ± 4.0	19.7 ± 4.0	36.2 ± 5.0	21.6 ± 3.8	9.7 ± 1.8
Shrub layer species cover (%)													
<i>Amelanchier</i> spp.	0.2 ± 0.1	1.3 ± 0.4	0.5 ± 0.3	0.6 ± 0.2	0.4 ± 0.2	2.9 ± 1.1	1.8 ± 0.9	1.4 ± 0.5	2.0 ± 0.6	0.8 ± 0.4	1.3 ± 0.4	1.6 ± 0.4	1.7 ± 0.4
<i>Nemopanthus mucronatus</i>	0.03 ± 0.03	0 ± 0	0.1 ± 0.1	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Kalmia angustifolia</i>	0 ± 0	0 ± 0	0.5 ± 0.2	0.8 ± 0.3	0.3 ± 0.2	1.4 ± 0.6	1.1 ± 0.7	3.1 ± 1.0	2.9 ± 0.9	4.7 ± 1.6	4.7 ± 1.4	2.5 ± 0.6	3.5 ± 0.7
<i>Kalmia polifolia</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Myrica gale</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Prunus pensylvanica</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Rhododendron canadense</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.2 ± 0.2	0 ± 0	0 ± 0	0.2 ± 0.1	0.3 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0

	Distance from insect-disturbed area forest edge (m)												F.R.
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	
<i>Rhododendron groenlandicum</i>	0 ± 0	0 ± 0	0.03 ± 0.03	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0.2 ± 0.2	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Ribes glandulosum</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Rosa nitida</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Rubus idaeus</i>	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Rubus pubescens</i>	0.03 ± 0.03	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.03	0 ± 0
<i>Sambucus racemosa</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0.2 ± 0.2	0.2 ± 0.2	0 ± 0
<i>Sorbus americana</i>	0.5 ± 0.4	1.0 ± 0.6	0.5 ± 0.2	0.6 ± 0.3	0.6 ± 0.3	0.4 ± 0.3	0.2 ± 0.2	1.2 ± 0.4	0.3 ± 0.2	0.6 ± 0.2	0.9 ± 0.3	0.7 ± 0.3	0.5 ± 0.2
<i>Vaccinium angustifolium</i>	1.1 ± 0.4	3.0 ± 1.9	0.4 ± 0.2	0.1 ± 0.1	0.2 ± 0.1	0 ± 0	0.4 ± 0.2	2.6 ± 1.0	0.4 ± 0.2	0.8 ± 0.4	1.0 ± 0.4	2.3 ± 1.1	2.4 ± 0.7
<i>Viburnum nudum</i>	0.2 ± 0.1	0.2 ± 0.2	0.7 ± 0.4	0.4 ± 0.2	0.2 ± 0.1	0.03 ± 0.03	0.03 ± 0.03	0.1 ± 0.1	0.1 ± 0.1	0 ± 0	0.2 ± 0.1	0.7 ± 0.3	0.3 ± 0.1
Herbaceous layer species cover (%)													
<i>Anaphalis margaritacea</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Aralia nudicaulis</i>	2.8 ± 0.6	2.2 ± 0.4	2.3 ± 0.7	1.7 ± 0.5	0.7 ^b ± 0.3	0.8 ± 0.3	0.9 ± 0.4	1.5 ± 0.4	1.1 ± 0.3	3.1 ± 0.7	3.6 ± 0.6	1.8 ± 0.3	2.0 ± 0.3
<i>Aster acuminatus</i>	0.9 ± 0.4	0.6 ± 0.3	0.4 ± 0.2	0.7 ± 0.5	1.8 ± 1.1	0.7 ± 0.4	0.2 ± 0.1	0.1 ^b ± 0.1	0.3 ± 0.2	0.3 ± 0.2	0.3 ± 0.2	0.2 ± 0.1	0.2 ± 0.1
<i>Aster</i> spp. (except <i>A. acuminatus</i>)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0.1 ± 0.1	0.3 ± 0.2	0 ± 0
<i>Clintonia borealis</i>	1.0 ± 0.3	1.5 ± 0.5	1.8 ± 0.5	1.5 ± 0.7	1.1 ± 0.4	1.2 ± 0.4	0.3 ± 0.2	0.03 ± 0.03	0.5 ± 0.3	2.0 ± 0.7	0.7 ± 0.3	2.2 ± 0.7	2.1 ± 0.5

	Distance from insect-disturbed area forest edge (m)												F.R.
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	
<i>Coptis trifolia</i>	1.2 ± 0.4	1.3 ± 0.6	0.6 ± 0.3	0.5 ± 0.2	0.3 ± 0.1	0.5 ± 0.2	0.4 ± 0.2	0.5 ± 0.3	0.9 ± 0.4	1.3 ± 0.6	0.8 ± 0.3	1.7 ± 0.6	0.3 ± 0.1
<i>Cornus canadensis</i>	17.5 ± 2.0	16.8 ± 2.6	12.4 ± 2.6	14.0 ± 3.7	12.1 ± 3.8	16.6 ± 4.4	14.1 ± 3.9	13.9 ± 3.3	9.9 ± 2.6	20.3 ± 3.2	22.7 ^b ± 3.1	17.2 ± 2.7	14.1 ± 1.8
<i>Cypripedium acaule</i>	0 ± 0	0 ± 0	0.1 ± 0.1	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Epigaea repens</i>	0.1 ± 0.1	1.2 ± 0.6	0 ± 0	0 ± 0	0.3 ± 0.2	0.4 ± 0.2	0 ± 0	0.1 ± 0.1	0 ± 0	0.2 ± 0.1	0.03 ± 0.03	0.1 ± 0.1	0.2 ± 0.1
<i>Gaultheria hispidula</i>	0.1 ± 0.1	0.2 ± 0.1	0.4 ± 0.2	0.2 ± 0.1	0.1 ± 0.1	0.1 ± 0.1	0.3 ± 0.2	1.1 ± 0.5	0.7 ± 0.3	0.6 ^b ± 0.2	1.3 ^b ± 0.5	2.0 ^b ± 0.6	0.5 ± 0.2
<i>Linnaea borealis</i>	1.8 ± 0.3	2.0 ± 0.8	1.0 ± 0.5	1.2 ± 0.4	0.6 ± 0.2	1.0 ± 0.4	0.6 ± 0.3	1.8 ± 0.6	2.2 ± 0.6	1.6 ± 0.5	3.2 ± 1.1	2.4 ± 0.6	1.8 ± 0.4
<i>Maianthemum canadense</i>	1.3 ± 0.3	0.6 ± 0.2	0.6 ± 0.2	0.5 ± 0.2	0.6 ± 0.3	1.1 ± 0.3	1.0 ± 0.2	0.8 ± 0.2	0.8 ± 0.3	1.2 ± 0.3	1.9 ± 0.4	1.1 ± 0.3	1.5 ± 0.3
<i>Mitchella repens</i>	0.4 ± 0.3	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Oxalis</i> spp.	0.1 ± 0.1	0.2 ± 0.1	0.3 ± 0.1	0.2 ± 0.1	0.4 ± 0.2	0.03 ± 0.03	0.2 ± 0.1	0.1 ± 0.1	0.03 ± 0.03	0.1 ± 0.1	0.03 ± 0.03	0.1 ± 0.1	0.3 ± 0.1
<i>Rubus chamaemorus</i>	0.7 ± 0.5	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Rumex acetosella</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Smilacina trifolia</i>	0 ± 0	0 ± 0	0.1 ± 0.1	0.7 ± 0.4	1.0 ± 0.6	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.03 ± 0.03	0 ± 0
<i>Solidago macrophylla</i>	0.1 ± 0.1	0.03 ± 0.03	0.1 ± 0.1	0.1 ± 0.1	0.03 ± 0.03	0 ± 0	0.1 ± 0.1	0 ± 0	0.03 ± 0.03	0 ± 0	0.1 ± 0.1	0.1 ± 0.1	0.1 ± 0.1
<i>Solidago</i> spp. (except <i>S. macroph.</i>)	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0
<i>Trientalis borealis</i>	1.1 ± 0.2	0.6 ± 0.2	0.2 ± 0.1	0.3 ± 0.1	0.3 ± 0.1	0.4 ± 0.1	0.5 ± 0.2	1.0 ± 0.3	0.9 ± 0.3	0.7 ± 0.2	1.2 ± 0.2	0.8 ± 0.2	1.2 ± 0.3

	Distance from insect-disturbed area forest edge (m)												F.R.
	2.5	7.5	12.5	17.5	22.5	27.5	32.5	37.5	42.5	47.5	52.5	57.5	
<i>Vaccinium oxycoccos</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.6 ± 0.4	1.1 ± 0.6	0.02 ± 0.02
<i>Veronica officinalis</i>	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0 ± 0	0.02 ± 0.02
Fern species cover (%)													
<i>Dryopteris spp.</i>	3.4 ± 1.2	4.7 ± 1.7	1.1 ± 0.4	1.5 ± 0.6	2.9 ± 1.2	1.7 ± 0.8	1.7 ± 0.5	1.6 ± 0.5	2.7 ± 1.6	4.0 ± 1.7	7.5 ± 2.7	3.9 ± 1.8	2.3 ± 0.7
<i>Osmundastrum cinnamomeum</i>	17.3 ± 3.7	12.2 ± 3.5	4.9 ± 1.9	3.2 ± 1.7	2.5 ± 1.2	6.0 ± 2.2	3.8 ± 1.7	7.4 ± 2.9	4.5 ± 1.9	11.8 ± 3.1	12.1 ± 3.7	9.8 ± 3.6	3.7 ± 1.2
<i>Pteridium aquilinum</i>	10.6 ± 4.2	5.4 ± 2.2	4.8 ± 2.0	0.1 ± 0.1	0.03 ± 0.03	2.3 ± 1.2	0.8 ± 0.8	0 ± 0	0.2 ± 0.2	3.1 ± 1.9	4.8 ± 2.5	3.9 ± 1.5	2.8 ± 1.1
<i>Thelypteris noveboracensis</i>	1.2 ± 0.4	1.2 ± 0.9	1.8 ± 1.2	0 ± 0	0.1 ± 0.1	5.4 ± 2.7	5.3 ± 3.0	10.9 ± 4.5	5.5 ± 2.6	1.5 ± 1.2	11.7 ± 4.7	4.0 ± 1.8	0.5 ± 0.3

Appendix 3-C: Generalized additive mixed model results for individual secondary and tertiary response variables.

Variables are grouped according to family of tests that were analyzed collectively. Estimated degrees of freedom = 1 when pattern is linear and higher values correlate positively with more non-linear curves. Bolded p-values indicate significance at the 0.05 significance level after sequential Bonferroni correction.

Response variable	p-value	Estimated degrees of freedom	R ² adj
Moose pellet cover	0.12	1	0.00167
% of unbrowsed live AB saplings	0.13	1	0.0059
% of lightly browsed AB saplings	0.03	1	0.0244
% of moderately browsed AB saplings	0.27	1	-0.00445
% of severely browsed AB saplings	< 0.0001	3.115	0.227
% of unbrowsed dead AB saplings	< 0.0001	3.46	0.296
% of browsed dead AB saplings	< 0.001	2.67	0.052
% of unbrowsed live BP saplings	0.17	1	-0.0166
% of lightly browsed BP saplings	0.07	1	-0.0245
% of moderately browsed BP saplings	0.87	1	-0.0123
% of severely browsed BP saplings	< 0.0001	2.879	0.17
% of unbrowsed dead BP saplings	0.01	1	0.042
% of browsed dead BP saplings	0.14	1	0.021
% of short unbrowsed live saplings	< 0.001	4.678	0.214
% of short lightly browsed live saplings	0.85	1	-0.00948
% of short moderately browsed live saplings	0.02	1	0.0545
% of short severely browsed live saplings	< 0.001	1	0.126
% of short unbrowsed dead saplings	< 0.0001	1	0.102
% of short browsed dead saplings	0.02	1	0.0433
% of int. unbrowsed live saplings	0.10	2.417	0.116
% of int. lightly browsed live saplings	0.08	1	-0.00837
% of int. moderately browsed live saplings	0.16	1	0.0203
% of int. severely browsed live saplings	0.03	1	0.0877
% of int. unbrowsed dead saplings	< 0.00011		0.194
% of int. browsed dead saplings	0.12	1	0.0291
% of tall unbrowsed live saplings	< 0.001	4.077	-0.027
% of tall lightly browsed live saplings	< 0.001	1	0.078
% of tall moderately browsed live saplings	0.16	1	-0.000154
% of tall severely browsed live saplings	< 0.001	1	0.114
% of tall unbrowsed dead saplings	0.01	2.306	0.128

Response variable	p-value	Estimated degrees of freedom	R ² adj
% of tall browsed dead saplings	< 0.0001	1	0.0969
Max. sapling height (all species)	< 0.0001	1	0.117
Max. sapling height (AB)	< 0.0001	1	0.187
Max. sapling height (BP)	0.72	1	-0.0133
Max. sapling height (PG)	0.09	1	0.0384
Sapling density (all species)	0.87	1	-0.00685
Sapling density (AB)	< 0.01	1	0.053
Sapling density (BP)	< 0.0001	1	0.1039
Sapling density (PG)	0.08	1.97	0.00047
Seedling density (all species)	< 0.0001	3.60	0.0756
Seedling density (AB)	< 0.0001	3.58	0.075
Seedling density (BP)	0.68	1	-0.0069
Seedling density (PG)	0.28	1	-0.0001
Graminoids cover	< 0.0001	4.632	0.344
Bryophytes cover	< 0.0001	2.811	0.132
Fine woody debris cover	< 0.0001	3.789	0.0641
Litter cover	0.35	1	-0.000779
Shrub layer cover	< 0.0001	3.771	0.0489
Herb layer cover	< 0.0001	4.947	0.0364
Fern cover	< 0.0001	6.594	0.0926
Sapling diversity	0.08	1	0.003
Seedling diversity	0.48	1	-0.000705
Understorey diversity	< 0.0001	6.135	0.0968
Shrub diversity	< 0.001	2.362	0.0258
Herb diversity	< 0.0001	6.252	0.0759
Fern diversity	< 0.0001	6.969	0.0967

Chapter 4: Conclusion

1. Summary and ecological implications of insect disturbed area-forest edge characteristics

The varying patterns and extents of edge influence for individual responses to edge creation emphasize the complexity of forest edges. The spruce budworm-induced forest edges in Cape Breton Highlands National Park were structural zones of transition approximately 10 m wide between disturbed area and intact forest. The disturbed side of the edge was characterized by lower values of canopy cover, stem density, tree height, and overall structural diversity compared to the forest side of the edge. Even though decomposition rate did not vary significantly across the disturbed area-forest gradient, more recently decayed deadwood was found on the forest side of the edge, which most likely resulted from self-thinning. A greater abundance of logs on the disturbed side of the edge probably formed from snags falling to the ground after insect-caused tree mortality.

While naturally created edges tend to regenerate after the disturbance agent has subsided, the forest edges in Cape Breton were rather unique because they were maintained by moose browse. Moose browse activity decreased from the disturbed area into the forest and the majority of saplings were severely browsed. Browsing may be influencing species composition as spruce, one of the three main tree species in the study area, was never browsed and therefore appeared much healthier than browsed saplings that were suffering from abnormal growth forms. Furthermore, relatively high cover of graminoids in the disturbed area may prevent overall seedling germination. The distinct

structural and compositional contrast between disturbed area and forest remains, a characteristic that is usually lost at regenerating edges over time (Harper et al. 2005).

Moose browsing may ultimately affect the cyclic pattern of the spruce budworm outbreak in the Cape Breton Highlands. For instance, the lack of regeneration in previously disturbed areas may delay the insect population from reaching outbreak levels due to the absence of continuous tracts of mature host trees. Alternatively, the next outbreak may result in less damage than prior outbreaks due to a lower number of adequate host trees. Even if herbivory pressure is reduced, forests may become less vulnerable to spruce budworm outbreaks because mortality rates are lower in stands comprised mainly of *Picea* and in immature stands of *Abies* (MacLean 1980). Furthermore, the spruce budworm, which normally feeds on mature *Abies balsamea*, may instead alter its feeding behavior to target the less preferred unpalatable food source of *Picea* spp.. Predictions of future spruce budworm epidemics are difficult because they cannot be based solely on assessments of past outbreaks in the area (Blais 1968). The indirect effect of moose herbivory on forest succession will most likely make predictions even more challenging.

2. Comparison of the extent of edge influence among different responses to edge creation.

Overall, distance of edge influence was greater when variables were compared to the disturbed area reference as opposed to the forest reference (Figure 4-1). When compared to the forest reference, edge influence did not even extend past 0 m into the forest for any of the primary response variables (Figure 4-1a). Meanwhile, significant

edge effects resulting directly from edge creation extended up to 40 m into the disturbed area when compared to the disturbed area reference (Figure 4-1b). A sampling design that considers the relationship between the edge and both adjacent ecosystems reveals greater insight into the influence of edge creation on ecological processes across the entire disturbed area-forest gradient. Edge movement into the forest since time of edge creation (Gascon et al. 2000) could explain the greater similarity between characteristics at the edge and in the forest reference compared to the disturbed area reference. If the edge is receding and continues to recede, the study area could be at risk for additional forest loss.

Indirect effects to edge creation extended further into the forest than direct effects when compared to the forest reference (Figure 4-1a). Since secondary responses to edge creation are influenced by primary effects on vegetation, the former type of response is hypothesized to begin later, last longer, and occur farther from the edge compared to the latter (Harper et al. 2005). Greater extent of edge influence for understorey variables compared to primary response variables has been noted in prior studies (e.g., Palik & Murphy 1990; Harper & Macdonald 2001) and reflects the ongoing effects of edge creation decades after the insect disturbance ceased.

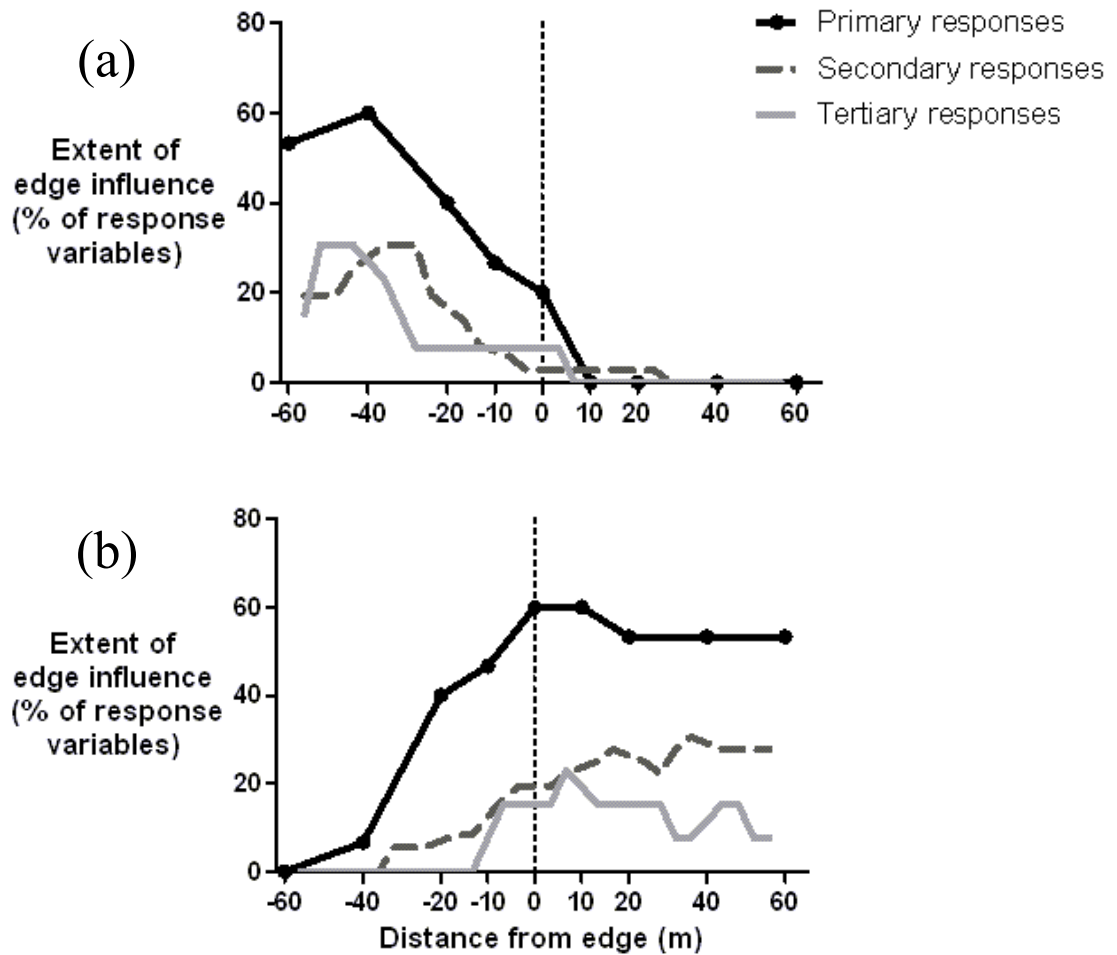


Figure 4-1. Percentage of primary, secondary, and tertiary response variables with significant distance of edge influence compared with the (a) forest reference and (b) disturbed area reference at spruce budworm disturbed area-forest edges. Primary responses include all variables examined in the second chapter, secondary responses include structural and compositional variables examined in the third chapter, and tertiary responses include all moose-related variables. Black circles indicate distances from the edge at which primary response variable data were collected. Data collection for secondary and tertiary responses occurred continuously along the gradient.

3. Methods for assessing edge influence

Differences between findings on edge influence among separate studies may be attributed to inconsistent methods of data analysis. For example, nonparametric analysis

methods usually result in reduced estimates of DEI compared to other methods of analysis (Harper & Macdonald 2011), which may explain the lack of significant edge influence on moose browse activity found in prior studies (Hamilton et al. 1980; Andren & Angelstam 1993). Future research should attempt to determine the most accurate methods of data analysis and collection to facilitate more effective comparisons of results.

Another important concept to consider when interpreting the results gained from this study is that statistical significance may not necessarily imply biological significance. Although RTEI indicated a numerical significant difference between the edge and the reference ecosystems, the effects of these differences on overall forest dynamics are unknown. Therefore, additional research is required to determine the biological impact of RTEI results to ultimately interpret the ecological meaning of DEI for each individual response variable.

4. Research directions

Future studies could address direct effects of moose on vegetation other than browsing, such as trampling or the rubbing of antlers. Trampling by ungulates can uproot vegetation, which causes a loss of insulation and change in species composition (Pegau 1970). Despite being distasteful to moose, *Picea glauca* is heavily selected by moose for scent marking (Bowyer et al. 1994). Consequently, the effects of different moose behaviour on selected species should be addressed when considering the overall impacts of high moose densities on ecosystem dynamics. Furthermore, specific species of invertebrates and fungi may benefit from moose carcasses, pellets, or urine patches, yet the impact of high moose densities on these organisms is unknown.

The future state of the moose population in the Cape Breton Highlands is difficult to predict. As a forest approaches a climax stage, decreases in the quantity and quality of forage cause a decline in the carrying capacity for moose (Cowan et al. 1950; Krefting 1974). Furthermore, time since disturbance plays a role in habitat quality. For example, area disturbed by fire is considered beneficial for moose habitat up to 50 years post-disturbance but moose densities peak 20-25 years following the burn (LeResche et al. 1974). While the last spruce budworm outbreak ceased over three decades ago, moose densities in the Cape Breton Highlands are still relatively high but may eventually decline. Therefore, edge influence on herbivory may vary depending on the disturbance responsible for edge creation as well as ungulate population densities prior to the disturbance.

Future studies could evaluate moose browse activity at other types of natural edges and over longer time periods. The overall value of a disturbed area to moose habitat depends on various abiotic variables (soil conditions, temperature, moisture), the severity and duration of the disturbance, as well as the size of the created open area (LeResche et al. 1974). In addition to different edge types, future research could address the relationship between edge function and temporal dynamics pertaining to seasonal and annual changes in species palatability and availability. Dietary preferences change depending on the season and year (Peek et al. 1976), so studies designed to evaluate moose browse activity constantly throughout the year would provide us with a better understanding of edge influence on herbivory.

Even though long-term implications of herbivory can take a long time to detect, research could be invested into monitoring forest succession in the Cape Breton

Highlands because the interplay between the insect outbreak and moose herbivory on the island is relatively unique. Cape Breton Highlands National Park currently maintains two moose exclosures that are being used to evaluate forest regeneration in the absence of browsing pressure. Perhaps it would be useful to test browsing pressure with densities of low, moderate, and high ungulate densities as moose exclosures represent extreme and arguably unrealistic conditions. Moreover, future studies could establish exclosures across forest edges to investigate browse activity across ecosystem boundaries and monitor the structural development of the moose-browsed forest edges over time.

5. Literature cited

- Andren, H. & Angelstam, P. 1993. Moose browsing on Scots pine in relation to stand size and distance to forest edge. *Journal of Applied Ecology* 30: 133-142.
- Blais, J.R. 1968. Regional variation in susceptibility of eastern North American forests to budworm attack based on history of outbreaks. *The Forestry Chronicle* 44: 17-23.
- Bowyer, R.T., Van Ballenberghe, V. & Rock, K.R. 1994. Scent marking by Alaskan moose – Characteristics and spatial distribution of rubbed trees. *Canadian Journal of Zoology* 72: 2186-2192.
- Cowan, I.M., Hoar, W.S. & Hatter, J. 1950. The effect of forest succession upon the quantity and upon the nutritive values of woody plants used as food by moose. *Canadian Journal of Research* 28: 249-271.
- Hamilton, G.D., Drysdale, P.D. & Euler, D.L. 1980. Moose winter browsing patterns on clear-cuttings in northern Ontario. *Canadian Journal of Zoology* 58: 1412-1416.
- Harper, K.A. & Macdonald, S.E. 2001. Structure and composition of riparian boreal forest: new methods for analyzing edge influence. *Ecology* 82: 649-659.
- Harper, K.A. & Macdonald, S.E. 2011. Quantifying distance of edge influence: a comparison of methods and a new randomization method. *Ecosphere* 2: art94.

- Harper, K.A., Macdonald, S.E., Burton, P.J., Chen, J.Q., Brosofske, K.D., Saunders, S.C., Euskirchen, E.S., Roberts, D., Jaiteh, M.S. & Esseen, P.A. 2005. Edge influence on forest structure and composition in fragmented landscapes. *Conservation Biology* 19: 768-782.
- Krefting, L.W. 1974. Moose distribution and habitat selection in north central North America. *Naturaliste canadien* 101: 81-100.
- LeResche, R.E., Bishop, R.H. & Coady, J.W. 1974. Distribution and habitats of moose in Alaska. *Naturaliste canadien* 101: 143-178.
- MacLean, D.A. 1980. Vulnerability of fir-spruce stands during uncontrolled spruce budworm outbreaks: A review and discussion. *The Forestry Chronicle* 56: 213-221.
- Palik, B.J. & Murphy, P.G. 1990. Disturbance versus edge effects in sugar-maple/beech forest fragments. *Forest Ecology and Management* 32: 187-202.
- Peek, J.M., Urich, D.L. & Mackie, R.J. 1976. Moose habitat selection and relationships to forest management in northeastern Minnesota. *Wildlife Monographs* 48: 3-65
- Pegau, R.E. 1970. Effect of reindeer trampling and grazing on lichens. *Journal of Range Management* 23: 95-97.