1   **Moose browsing, understorey structure, and plant species**

2   **composition across spruce budworm-induced forest edges**

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22   **Abstract**

23   **Question**: To what extent do forest edges created by an insect outbreak influence patterns

24   of moose browsing severity, understorey structure, and species composition?

25   **Location**: Balsam fir-dominated boreal forest in Cape Breton Highlands National Park,

26   Nova Scotia, CA.

27   **Methods**: We sampled understorey vegetation (moose browsing damage, sapling density,

28   plant composition, diversity) in contiguous 1 m^2 quadrats along six 120 m transects across

29   the forested edges of insect outbreak areas. Patterns of each response variable across the

30   disturbed area-forest gradient were determined using generalized additive mixed models.

31   Randomization tests and wavelet analyses were used to estimate the extent of edge/forest

32   influence and location of abrupt change along the edge-to-interior gradient, respectively.

33   **Results**: Most saplings in the disturbed area were severely browsed and shorter than those

34   in adjacent intact forest. Although moose preferred to browse on tall saplings, shorter

35   saplings were severely browsed in the disturbed area. Compared to the forest, the

36   disturbed area was characterized by more shade-intolerant species, increased graminoid

37   cover, and reduced bryophyte cover. Distance of edge influence did not extend into the

38   forest for almost all response variables. Abrupt changes in understorey vegetation

39   occurred at various distances on both sides of the edge.

40   **Conclusions**: Severe moose browsing in the disturbed area is preventing forest

41   regeneration, resulting in the persistence of forest edges that would typically disappear

42   after the collapse of an insect outbreak. Different assessments of the forest edge revealed

43   different results; locations of abrupt change in understorey vegetation occurred even

44   where plant communities were not significantly different than reference forest and

45   disturbed areas. This study reveals that the combined effects of a small insect defoliator

46   and a large ungulate can substantially affect landscape dynamics.

47   **Introduction**

48   Forest edges play important ecological roles by mediating species interactions

49   (Fagan et al. 1999) and by influencing habitat selection (Stewart et al. 2013). Plant

50   community responses to forest edges affect processes such as herbivory (Cadenasso &

51   Pickett 2000), which can alter vegetation characteristics over time. Studies on vegetation

52   at natural edges are required for a better understanding of the spatial-temporal role of

53   natural disturbances in landscape dynamics.

54   Although naturally induced forest edges tend to regenerate once the disturbance

55   agent has subsided, herbivory can maintain forest edges by hindering succession in the

56   disturbed area and thus sustain the contrast between adjacent communities (Williams-

57   Linera 1990; Farnsworth & Anderson 2001). Stand-initiating disturbances such as insect

58   outbreaks create favourable habitat for ungulates such as moose (*Alces alces*) by

59   providing forage (Forbes & Theberge 1993; Lautenschlager et al. 1997). When moose

60   populations are high, severe browsing on regenerating saplings can ultimately inhibit

61   forest succession post-disturbance (Smith et al. 2010). Forest edges maintained by

62   herbivory may be common in ecosystems experiencing a loss of ecological integrity due

63   to overabundant herbivore populations in the absence of predators (Terborgh et al. 2001;

64   McLaren et al. 2004).

65   Due to superior forage production post-disturbance, browsing by moose is severe

66   in areas affected by disturbances such as insect epidemics (Brassard et al. 1974; Forbes &

67   Theberge 1993) despite habitat requirements of shelter, optimal snow depth, and cover for

68   predator avoidance (Timmermann & McNicol 1988). High densities of moose in

69   disturbed areas can alter plant structure and composition (De Jager & Pastor 2009)

70   through severe browsing, which damages saplings by suppressing terminal growth

71   (Brandner et al. 1990; Thompson & Curran 1993; Smith et al. 2010). We predict more

72   severe moose browsing and a corresponding decrease in palatable sapling height at forest

73   edges compared to both interior forests and disturbed areas because edges supply cover

74   adjacent to abundant forage.

75   Natural forest edges on northern Cape Breton Island, Nova Scotia, CA were

76   created by an insect outbreak and have been maintained for nearly three decades by a

77   large moose (*Alces alces andersoni*) population that has been inhibiting forest

78   regeneration (Smith et al. 2010). We evaluated patterns of moose browsing severity, and

79   understorey structure, composition and diversity across the edge for differences from the

80   reference forest (edge influence), differences from the reference disturbed area (forest

81   influence), and abrupt changes (edge detection). Our specific objectives include: 1) to

82   assess patterns of moose browsing on saplings of different species and of different

83   heights, particularly where moose browsing habits change in relation to the edge, and 2)

84   to determine the resulting effects of moose browsing and edges on understorey structure,

85   composition and diversity. Our results will help us gain a better understanding of the

86   interplay between natural edge creation and moose browsing, and of the effects on forest

87   regeneration and understorey diversity.

88   **Methods**

89   **Study area**

90   The study was conducted in Cape Breton Highlands National Park (46°50'N,

91   60°30'W), which encompasses 950 km^2 of northern Cape Breton Island, Nova Scotia,

92   CA. Climatic normals (1981 – 2010) from Cheticamp (46°39'N, 60°57'W), which was

93   located 4.5 – 28.5 km from the study sites, indicate mean January and July temperatures

94   of -4.9°C and 18.3°C, respectively, and mean annual precipitation and snowfall of 1375.1

95   mm and 312 cm, respectively (Environment Canada 2014). The region is characterized by

96   a plateau (elevation 350 – 500 m asl) underlain by Precambrian granitic and volcanic

97   bedrock (Webb & Marshall 1999). The boreal land region, which dominates

98   approximately 50% of the park, consists mainly of *Abies balsamea* interspersed with

99   *Picea glauca* and *Betula papyrifera* (Parks Canada 2010). Soils are mostly sandy loam of

100   moderately coarse texture (Neily et al. 2003). Fire and logging are not common.

101   The spruce budworm, a native insect defoliator in the boreal forest, feeds mainly

102   on *Abies balsamea*, but *Picea* species are also suitable hosts. The latest budworm

103   outbreak in the park (1974 - 1984) was considered to be the most severe compared to

104   prior outbreaks in the area (Ostaff & MacLean 1989)**;** park management refrained from

105   using pest control for outbreak suppression. Affected stands experienced mortality of

106   87% *Abies balsamea* (MacLean & Ostaff 1989) and 27% *Picea* spp. (Ostaff & MacLean

107   1989). The population of the western moose sub-species *Alces alces andersoni*,

108   introduced in 1947 and 1948 (Pulsifer & Nette 1995) after the extirpation of native moose

109   (*Alces alces americana*), has since increased dramatically in Cape Breton (2

110   individuals/km^2 in the park in 2011, James Bridgland, personal communication).

111   **Site selection and data collection**

112   Historical aerial photographs of Cape Breton Island taken in 1969 were compared

113 to 2009 photographs to identify areas of forest canopy reduction caused by the 1974 –

114 1984 spruce budworm outbreak. We selected six spruce budworm induced-forest edges

115 across relatively uniform terrain that were at least 100 m away from another edge, road,

116 trail, or water body and where both the disturbed and fir-spruce dominated forest areas

117 extended at least 80 m from the edge. We defined the forest edge as the limit of

118 continuous canopy between the intact forest and the insect disturbed area. At each edge,

119 we established a 120 m long transect perpendicular to and centred on the edge. The

120 distance of 60 m into each ecosystem was chosen to detect edge influence, which usually

121 dissipates within 20 m from the edge in boreal forests (Harper et al. 2015).

122   We collected data from June to August 2012 in contiguous 1 m^2 quadrats along

123 the entire length of the transects. Three plots of five contiguous quadrats (1 m^2) were

124 established at least 100 m away from the edge to sample reference conditions in the insect

125 disturbed and forest areas. Some reference plots were only 70 m away from the edge, and

126 one and two were absent from the disturbed and forest areas, respectively, due to

127 proximity to other edges.

128   In each quadrat, we recorded the height and species of each seedling (height ≤ 10

129 cm) and sapling (height > 10 cm, dbh < 5 cm). Saplings were classified as short,

130 intermediate, or tall (< 50, 50 – 99, or ≥ 100 cm height, respectively). We classified

131 browsing on each sapling based on the presence of live foliage, growth form, and the

132 proportion of browsed stems (Table 1). If we found fewer than five saplings in a 5 m

133 interval of contiguous quadrats, we evaluated browse severity of the next closest saplings

134 up to 5 m from the transect.

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135   We visually estimated the cover of shrubs, herbaceous plants, ferns, bryophytes,

136   graminoids, and fine woody debris (diameter < 5 cm) to the nearest 1% up to 5%, and to

137   the nearest 5% thereafter. We also estimated cover of individual species of shrubs, herbs,

138   and ferns with the exception of the genera *Amelanchier* spp., *Aster* spp. (other than *A.*

139   *acuminatus*), *Oxalis* spp., *Solidago* spp. (other than *S. macrophylla*), and *Dryopteris* spp.

140   Species with growth habits classified as dwarf shrub according to CFIA and NRCan/CFS

141   (2011) were considered part of the herbaceous layer.

Data analysis

143   We calculated the percentages of *Abies balsamea* and *Betula papyrifera* saplings

144   in each browsing class for each 5 m interval along the edge transects and for the reference

145   plots. We determined the percentages of saplings in each of the six browse classes for

146   each height class but excluded *Picea glauca* saplings since none were browsed and *Acer*

147   *rubrum* saplings due to relatively low densities. Species diversity was calculated using the

148   Shannon-Weiner index for different categories of plants and for overall understorey

149   diversity, which included shrubs, herbs, and ferns. Analyses were conducted for

150   individual understorey species with at least 10% frequency on at least three transects.

151   We evaluated general patterns of response variables along the transects (reference

152   data were not included) using generalized additive mixed models (GAMM) in the *mgcv*

153   package (Wood 2011) in R software (R Core Team 2013). Each site was recognized as a

154   random variable; data collected at the same site were not considered independent from

155   one another. We used the binomial, Poisson and Gaussian distributions for browse

156   severity, count data, and other continuous variables, respectively. Response variables

157   were assessed after sequential Bonferroni correction (Holm 1979) for multiple tests.

158   The distance of edge influence (DEI) and the distance of forest influence (DFI)

159   are the distances at or near the edge, over which a given response variable is significantly

160   different from the forest (Harper et al. 2005) and disturbed area references, respectively

161   (Franklin et al. 2015). We quantified DEI and DFI using the randomized test of edge

162   influence with no blocking, which compares the average value at a specific distance from

163   the edge to the reference values using randomizations but does not block by transect

164   (Harper & Macdonald 2011). We considered a significance level of 0.05 using a two-

165   tailed test. To address the issue of multiple testing, DEI and DFI were sets of three or

166   more consecutive distances (or separated by one or two distances) with significant edge

167   or forest influence.

168   To complement the DEI and DFI, we introduce the distance of edge change

169   (DEC), which we define as the set of locations of abrupt change in a response variable.

170   Edge detection studies have previously considered edges as the location of greatest

171   change along a transect (e.g., Brunt & Conley 1990). Whereas DEI/DFI can be visualized

172   as the width of the edge, DEC is the width of the steepest gradient in the response to the

173   edge. The DEC could not be determined for browsing severity because of missing data

174   (quadrats with no saplings).

175   We determined the DEC across the insect disturbed area-forest edge gradient

176   using wavelet analysis in PASSaGE 2.0 (Rosenberg & Anderson 2011). In wavelet

177   analysis, different sizes (scales) of a wavelet template are moved along the transect to

178   quantitatively assess the match of the template to the data (see Dong et al. 2008 for a

179   tutorial). Greater values indicate a strong resemblance of the data to the pattern of the

180   wavelet template at that scale and position. We conducted wavelet analysis on variables

181   with at least 10% frequency using the Haar wavelet, which detects locations of abrupt

182   change with high values of wavelet variance, along each 120 m transect for a maximum

183   scale of 30 m. We assessed position variance, the sum of all values of wavelet variance

184   over all scales, to determine the abruptness of the gradient at each position along the

185   transect (see Batllori et al. 2009 for an example). We tested the significance of peaks in

186   position variance using 999 randomizations. For a conservative estimate of the DEC, we

187   considered significant peaks of at least two consecutive distances on at least two

188   transects. To account for variation in the location of 0 m, we also considered distances

189   with peaks along two transects that were offset by 1 m. DEC was then estimated as the set

190   of three or more consecutive distances (or separated by one or two distances) with

191   significant peaks representing abrupt change.

192   **Results**

193   **Moose browsing severity**

194   Patterns of herbivory were similar between *Abies balsamea* and *Betula papyrifera*

195   with more prevalent moose browsing on the disturbed side of the edge compared to the

196   forest (Fig. 1). A greater proportion of living and unbrowsed *Abies balsamea* saplings

197   were in the forest reference than in the disturbed area reference (Fig. 1a). The proportion

198   of live, unbrowsed *Betula papyrifera* saplings increased from the disturbed area into the

199   forest, yet percentages were significantly higher at the edge compared to the disturbed

200   area reference (Fig. 1b). The proportions of lightly and moderately browsed saplings were

201   generally low and did not reveal any edge or forest influence (Fig. 1c-d). The majority of

202   browsed saplings were severely browsed and stunted. Both *Abies balsamea* and *Betula*

203   *papyrifera* saplings exhibited significant decreases in severe browsing from the disturbed

204   area into the forest (Fig. 1e-f).

205   Evidence of sapling mortality causes varied between species and across the edge

206   gradient (Fig. 1g-j). There were more unbrowsed dead saplings on the forest side of the

207   edge compared to the disturbed side; however, only *Abies balsamea* revealed significant

208   edge and forest influence on the percentage of unbrowsed dead saplings (Fig. 1g-h). *Abies*

209   *balsamea* saplings that experienced mortality following severe browsing were more

210   abundant on the disturbed side of the edge compared to the forest (Fig. 1i).

211   Patterns of browse severity differed among saplings in different height classes as

212   taller saplings were more severely affected by browsing (Fig. 2). The proportion of live

213   unbrowsed saplings was greatest for short saplings, particularly right at the edge (Fig. 2a).

214   The shortest 11 cm tall browsed saplings were found in the disturbed area. Percentages of

215   live unbrowsed saplings of intermediate height were more variable across the gradient

216   (Fig. 2b). No tall saplings were unbrowsed from the disturbed side up to 15 m into the

217   forest, after which very few were unbrowsed (Fig. 2c). Severely browsed saplings of all

218   heights decreased from the disturbed area into the forest (Fig. 2d-f), yet overall

219   percentages were greatest for the tallest saplings (DEI = -1 m, Fig. 2f). More taller

220   saplings were dead compared to shorter ones (Fig. 2g-l).

221   **Understorey structure and composition**

222   *Abies balsamea* sapling height increased from the disturbed area into the forest

223   (Fig. 3a). *Betula papyrifera* was the shortest species at most sampled distances (Fig. 3b).

224   There was no significant DEI, DFI, or DEC for the height of *Picea glauca* saplings,

225   which were more than twice as tall as other saplings in much of the disturbed area (Fig.

226   3c). Total sapling density did not differ significantly across the insect disturbed area-

227   forest gradient due to contrasting patterns between species. Most saplings were *Abies*

228   *balsamea*, which increased from the disturbed area to the forest interior (Fig. 3d). In

229   contrast, *Betula papyrifera* sapling density decreased significantly from the disturbed area

230   to the forest (Fig. 3e). Abrupt changes in sapling density were restricted to the disturbed

231   side of the edge (DEC around -50 m for *Abies balsamea*, throughout the disturbed area

232   for *Betula papyrifera*). *Picea glauca* sapling density did not exhibit any significant

233   pattern (GAMM: p = 0.08; edf = 2.0). Seedlings, the vast majority of which were *Abies*

234   *balsamea*, increased significantly from the disturbed area into the forest with abrupt

235   changes in abundance only in the forest (Fig. 3f). Average seedling density of *Betula*

236   *papyrifera* and *Picea glauca* was very low and did not exhibit significant patterns for

237   either species (GAMM: *Betula papyrifera*: p=0.68; edf=1.0, *Picea glauca*: p=0.28;

238   edf=1.0).

239   Graminoid cover decreased from the disturbed area to the forest, with significant

240   DEC only within the disturbed area (Fig. 4a). In contrast, bryophyte cover increased from

241   the disturbed area up to 35 m into the forest with significant changes at the edge and in

242   the forest (Fig. 4b). Fine woody debris cover increased slightly from the disturbed area

243   into the forest with abrupt changes up to 50 m into the forest (Fig. 4c). Average shrub

244   cover was significantly lower 11-25 m on the forest side of the edge compared to both

245   references but with abrupt changes at the edge and up to 56 m into the adjacent

246   communities (Fig. 4d). Overall herbaceous cover was relatively higher than for shrubs

247   and decreased from the edge to 25 m into the forest, and then steadily increased (Fig. 4e).

248   Fern cover exhibited a similar but stronger non-monotonic pattern (Fig. 4f). Abrupt

249   changes in herb and fern cover matched the patterns determined by the GAMM analysis

250   and were restricted to the forest for fern cover.

251   The majority of shrubs and herbs that exhibited significant patterns across the

252   edge increased in cover from the disturbed area into the forest (*Amelanchier* spp., *Kalmia*

253   *angustifolia*, *Vaccinium angustifolium*, *Clintonia borealis*, *Linnaea borealis*,

254   *Maianthemum canadensis*, *Trientalis borealis*), although the cover of some species

255   decreased (*Rubus idaeus, Aster acuminatus*) (Table 2). The only exotic species, *Rumex*

256   *acetosella*, was exclusively found in the disturbed area.

257   Species diversity of saplings and seedlings did not display significant patterns

258   across the disturbed area-forest gradient (GAMM: saplings: p=0.08; edf=1.0, seedlings:

259   p=0.48; edf=1.0). Total understorey species diversity was significantly lower 16-40 m

260   from the edge into the forest compared to the disturbed area reference but abrupt changes

261   were only found in the disturbed area (Fig. 5a). Herbs accounted for the greatest diversity

262   and followed a very similar pattern but with no significant DEI or DFI (Fig. 5b). Fern

263   diversity was relatively lower than herb diversity with abrupt decreases at the edge and 20

264   m into the forest (Fig. 5c). Shrub diversity was significantly lower in the disturbed area

265   and increased into the forest (Fig. 5d).

266

267   **Summary of DEI, DFI and DEC**

268   Despite contrasting trends in the proportions of variables with DEI and DFI, there

269   was no pattern for DEC along the insect disturbed area-forest gradient (Fig. 6). Overall,

270   maximum DFI extended slightly further from the edge (-35 m) than DEI (25 m). DEC for

271   individual variables (Table 2, Figs. 3-5) was usually confined to either the forest or the

272   disturbed area. Some common understorey forest species (e.g., bryophytes, ferns,

273   *Clintonia borealis, Trientalis borealis*), fine woody debris, and *Abies balsamea* exhibited

274   change mostly on the forest side and other forest species (*Cornus canadensis,*

275   *Maianthemum canadense, Dryopteris* spp., *Pteridium aquilinum*) changed abruptly on

276   both sides. Species that also grow in more open habitats (*Amelanchier* spp.*, Aster*

277   *acuminatus*, *Rubus idaeus, Sorbus americana*), understorey diversity, and *Betula*

278   *papyrifera* showed abrupt changes mostly on the disturbed side. DEC rarely coincided

279   with the pre-determined forest edge, with DEI or with DFI.

280   **Discussion**

281   **Moose browsing and regeneration**

282   We attribute moose preference for forage in the disturbed area to a combination of

283   the lack of predators and food quality. Since moose in northern Cape Breton are not

284   pressured to seek refuge from predators, they can select habitats based on preferred forage

285   rather than protective cover (Massé & Côté 2009). Moose may browse in the disturbed

286   area more than the forest as a result of the higher density of *Betula papyrifera*, a preferred

287   food source for moose (Peek et al. 1976; Lautenschlager et al. 1997; Smith et al. 2010).

288   *Abies balsamea* is an important winter browse species whereas *Betula papyrifera* is a

                                                                                            14

289   substantial dietary component year-round (Peek et al. 1976); therefore browse severity

290   could be greater in the disturbed area because it provides a constant supply of food

291   throughout the year.

292   Moose browse damage was most severe for the tallest saplings, which are

293   considered most vulnerable to moose (Andrén & Angelstam 1993), as they are not

294   concealed by deep snow in winter. However, we found moose browsed saplings as short

295   as 11 cm, a finding that should be considered in studies that have previously ignored

296   saplings shorter than 100 cm (e.g., Danell & Ericson 1986; Andrén & Angelstam 1993).

297   Moose in northern Cape Breton may be foraging on shorter saplings because the ungulate

298   population is relatively high and food may be scarcer.

299   Moose prevented regeneration of palatable species by restricting sapling growth,

300   particularly on the disturbed side of the edge where browsing was most severe. Opposing

301   trends of a decrease in browsing severity and an increase in *Abies balsamea* sapling

302   height from the disturbed area into the forest suggest that saplings experiencing less

303   herbivory pressure had greater opportunities for growth and survival. Other studies

304   revealed that moose browsing suppresses terminal growth of *Abies balsamea*

305   (Risenhoover & Maass 1987; Brandner et al. 1990; Thompson & Curran 1993) and can

306   inhibit individual trees from growing over one metre in height (Thompson et al. 1992;

307   McLaren et al. 2004). *Betula papyrifera*, a shade-intolerant species, was not taller in the

308   disturbed area where growth conditions were favourable. Moose browsing also restricts

309   *Betula* spp. growth (Heikkilä et al. 2003; Persson et al. 2005); hence more severe browse

310   damage in the disturbed area may have limited sapling height causing an insignificant

311   trend in *Betula papyrifera* sapling height.

312   Variation in moose browse severity along the disturbed area-forest gradient could

313   eventually affect overstorey composition. Severely browsed saplings were common in our

314   study area (Smith et al. 2010) and in high moose density areas of Newfoundland (Dodds

315   1960) and Sweden (Andrén & Angelstam 1993). These saplings may not reach their full

316   growth potential and soon die (Bergerud & Manuel 1968), thereby hindering recruitment

317   of preferred species to reproductive-aged trees (McInnes et al. 1992; Heikkilä &

318   Härkönen 1996). Moose browsing has hindered forest succession in clearcut areas by

319   preventing growth of selected sapling species in Fennoscandia (Edenius et al. 2002;

320   Speed et al. 2013) and Russia (Kuznetsov 2002). In Cape Breton, moose preferentially

321   feeding on *Abies balsamea* could prevent the return to the fir-dominated forests that were

322   typical of the past (Brandner et al. 1990; McInnes et al. 1992). Instead, negative effects of

323   herbivory on sapling growth of browsed species could lead to more successful

324   regeneration of *Picea glauca* saplings, which were much healthier and taller than *Abies*

325   *balsamea* and *Betula papyrifera*, as a result of reduced competition (Snyder & Janke

326   1976; Thompson & Curran 1993). As browsing was less severe on the forest side of the

327   edge, changes in canopy composition will be less apparent, leading to greater contrasts in

328   vegetation composition between the severely browsed disturbed area and adjacent intact

329   forest. Severe moose browsing may prolong the existence of forest edges in landscapes

330   affected by other types of disturbances; for example, high moose densities in

331   Fennoscandia could be maintaining forest edges because they select early successional

332   forests post-disturbance (Edenius et al. 2002).

16

Understorey composition

333

334   Moose browsing could indirectly affect understorey composition by altering

335   interspecific competition. The overall decrease in the shrub and herbaceous layers, ferns,

336   and understorey diversity approximately 10-25 m from the edge into the forest

337   corresponded to the area of high seedling density, relatively low browse severity, and

338   increased sapling height. Reduced herbivory could have benefited palatable saplings but

339   consequently kept the abundance of non-dietary herbs, shrubs, and ferns low, as these

340   understorey species experience greater competition for resources with vigorous saplings

341   and seedlings. Densities of unpalatable shrub species were found to be lower inside

342   moose exclosures, where the lack of moose browsing resulted in greater sapling density

343   and consequently more shading (Thompson & Mallik 1989). The zone of change in

344   understorey composition 10-25 m into the forest may be related to an overlap in increased

345   light near the edge of the disturbed area and decreased browsing in the forest.

346   Species diversity was not higher at the edge compared to the adjacent ecosystems,

347   possibly due to the gradual transition between disturbed and forest oriented species.

348   Although greater diversity at other forest edges (Harper et al. 2005) usually results from

349   the edge functioning as an adequate habitat for species found on both sides of the

350   interface (Harris 1988), the opposite effect may have occurred at these insect-induced

351   forest edges. Species that were either disturbed area oriented (e.g. *Rubus ideaus*) or forest

352   oriented (e.g. *Kalmia angustifolia*) were less abundant within 20 m from the edge, which

353   could reflect a distinct contrast in growing conditions between the two ecosystems.

354   In contrast to the forest, the disturbed area was characterized by species that thrive

355   under low canopy cover, such as *Rubus idaeus* (Ricard & Messier 1996). The disturbed

356   area also contained the only exotic species, *Rumex acetosella*, which is an early

357   successional weed (Stopps et al. 2011). Species that were able to grow in shaded as well

358   as open canopy conditions, such as *Cornus canadensis* (Hall & Sibley 1976), did not

359   exhibit edge influence and were ubiquitous across the disturbed area-forest gradient.

360   Therefore, the disturbed area was an attractive growing habitat for fast growing shade-

361   intolerant species, which would have most likely been outcompeted by shade-tolerant

362   species had forest regeneration progressed post-disturbance.

363   **Edge/forest influence and methodological considerations**

364   Weak edge influence on the understorey suggests that vegetation at the edge is

365   relatively similar to the forest reference. Edge influence on understorey vegetation was

366   also not very extensive at forest edges induced by wildfire (Harper et al. 2014) and at

367   anthropogenic edges in the boreal forest, where DEI is usually less than 20 m (Harper et

368   al. 2015). Species experiencing periodic natural disturbance could be more resilient to

369   changes in environmental conditions and therefore less affected by edge creation (Harper

370   et al. 2015).

371   Our findings reveal the challenges associated with defining forest edges, which

372   have been considered the location of greatest change as determined by wavelet analysis

373   (e.g., Camarero et al. 2006). Based on our findings, edges of spruce budworm outbreaks

374   would be difficult to detect using our DEC analysis. The location of DEC was usually

375   very different from our pre-defined edge (as determined visually on site) and from any

376   determination using DEI or DFI. Rather than identifying boundaries as the locations of

18

377   greatest change, an edge could instead be located at the intersection of the proportion of

378   response variables with DEI and DFI. In our study this would be 10 m into the disturbed

379   area, which suggests that there might have been edge degradation since edge creation.

380   Our results also highlight the importance of sampling the entire gradient between the two

381   communities, particularly when studying older edges, which may have shifted over time.

382   **Conclusions**

383   Moose browsing appeared to be maintaining the spruce budworm-forest edges by

384   restricting sapling height and preventing forest regeneration on the disturbed side of the

385   edge. Overall sapling density did not differ significantly across the edge, yet greater

386   density of *Betula papyrifera* saplings in the disturbed area suggests that diet preference

387   may be based on variety rather than quantity. Graminoids and other shade intolerant

388   species capable of thriving in the disturbed area benefitted from the hindrance of forest

389   succession, which could result in moose diet preferences ultimately altering species

390   composition. Consequently, forest previously dominated by *Abies balsamea* may become

391   dominated by unpalatable *Picea glauca*, and grassland expansion may lead to habitat loss

392   for species dependent on closed-canopy forest. The spruce budworm-induced forest edges

393   reveal that naturally created edges, once thought to be typically short-term features of the

394   landscape (Thomas et al. 1979), can persist when affected by ecological processes such as

395   herbivory.

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Figure 1. Mean percentage of *Abies balsamea* saplings (n = 824) and *Betula papyrifera* saplings (n = 315) in individual browse severity classes at each 5 m interval along insect disturbed area-forest edge transects (n = six). Negative and positive distances represent the disturbed and forest sides of edge, respectively (DR = disturbed area reference, FR = forest reference). Standard error bars are included for the reference means but not at other distances for clarity. Trend lines (solid = significant smoothing term, dashed = not significant) represent the fitted generalized additive mixed model with 95% CI (dotted lines), p-values and estimated degrees of freedom (edf). Horizontal lines near the top of the graphs represent significant distance of edge influence (solid line) and of forest influence (dashed line).
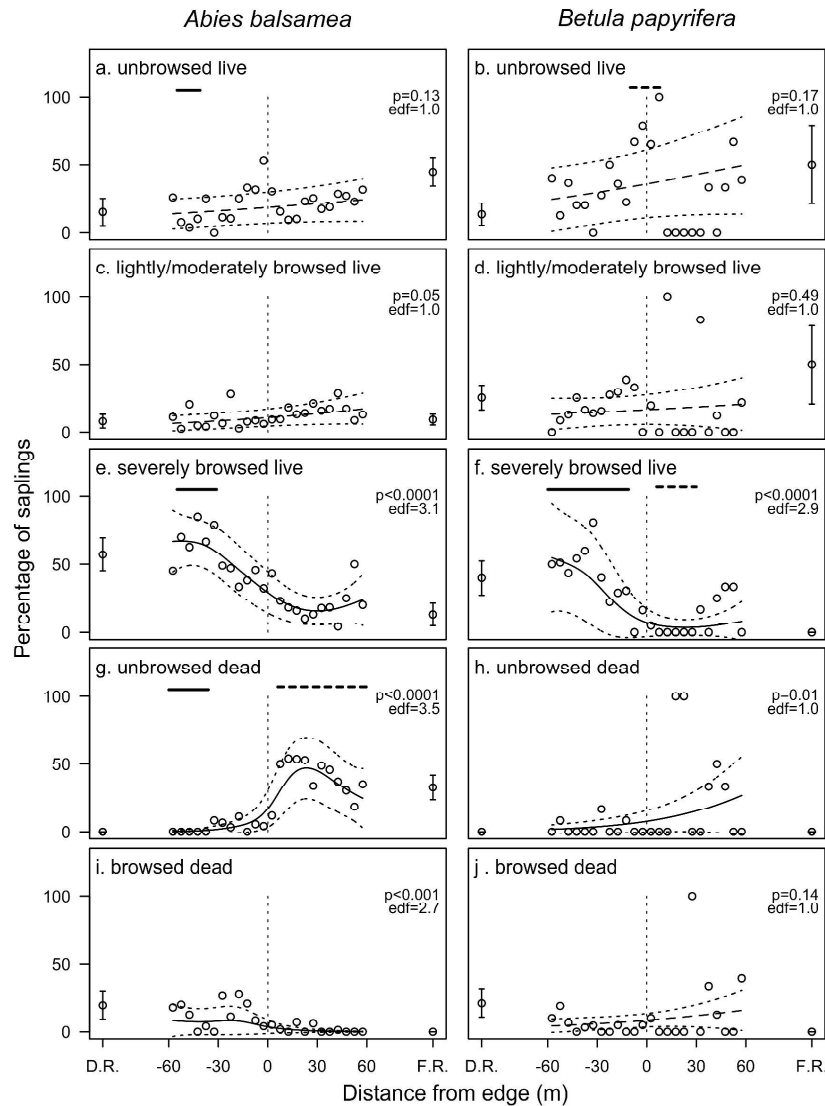
Figure 2. Percentage of *Abies balsamea* and *Betula papyrifera* saplings divided by three height classes (short = < 50 cm, intermediate = 50-99 cm, tall = > 99 cm) in individual browse severity classes along the insect disturbed area-forest edge gradient. See Figure 1 for further details.
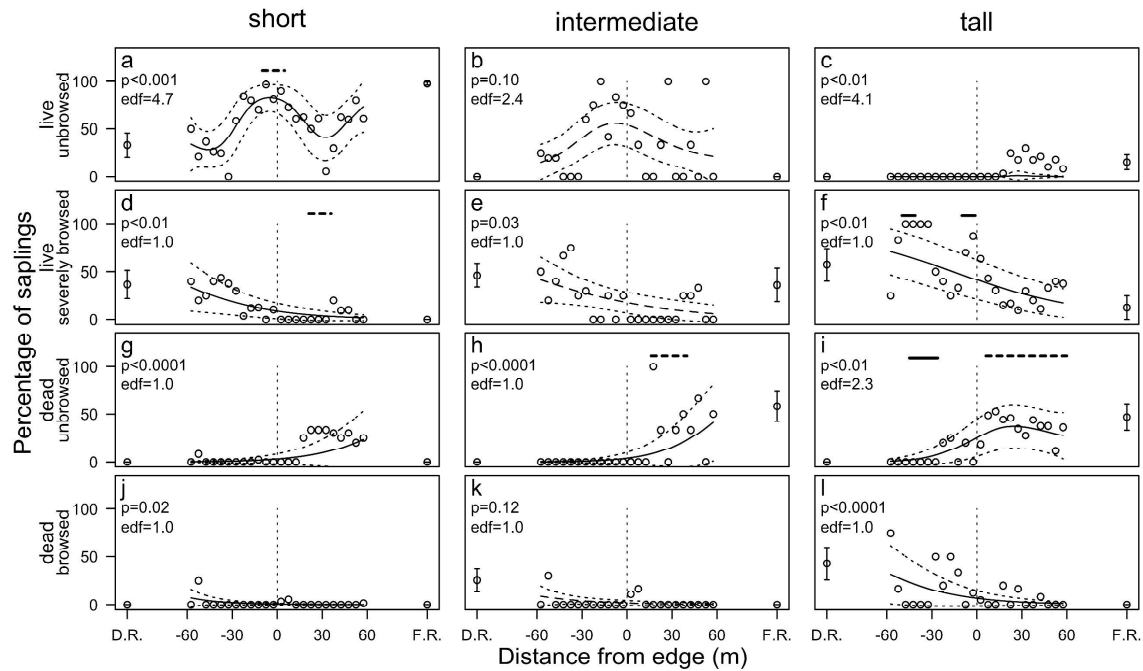
Figure 3. Mean maximum sapling height for (a) *Abies balsamea*, (b) *Betula papyrifera*, and (c) *Picea glauca*; and mean density of (d) *A. balsamea* saplings, (e) *B. papyrifera* saplings, and (f) *A. balsamea* seedlings along the insect disturbed area-forest edge gradient. See Figure 1 for further details; the gray horizontal line near the top of the plots represents significant distance of edge change.
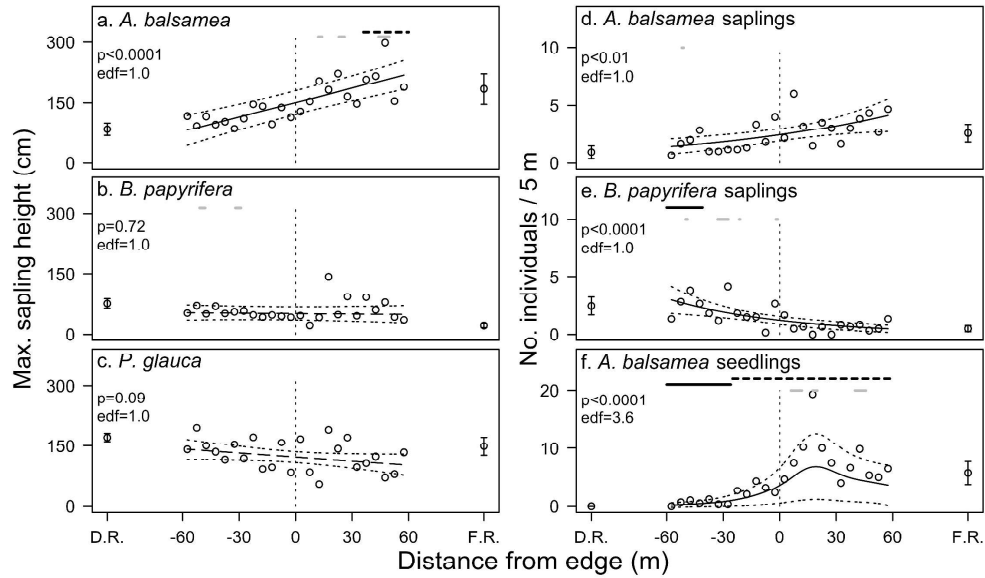
Figure 4. Mean cover of (a) graminoids, (b) bryophytes, (c) fine woody debris, (d) shrub layer species, (e) herbaceous layer species, and (f) fern species along the insect disturbed area-forest edge gradient. See Figures 1 and 3 for further details.
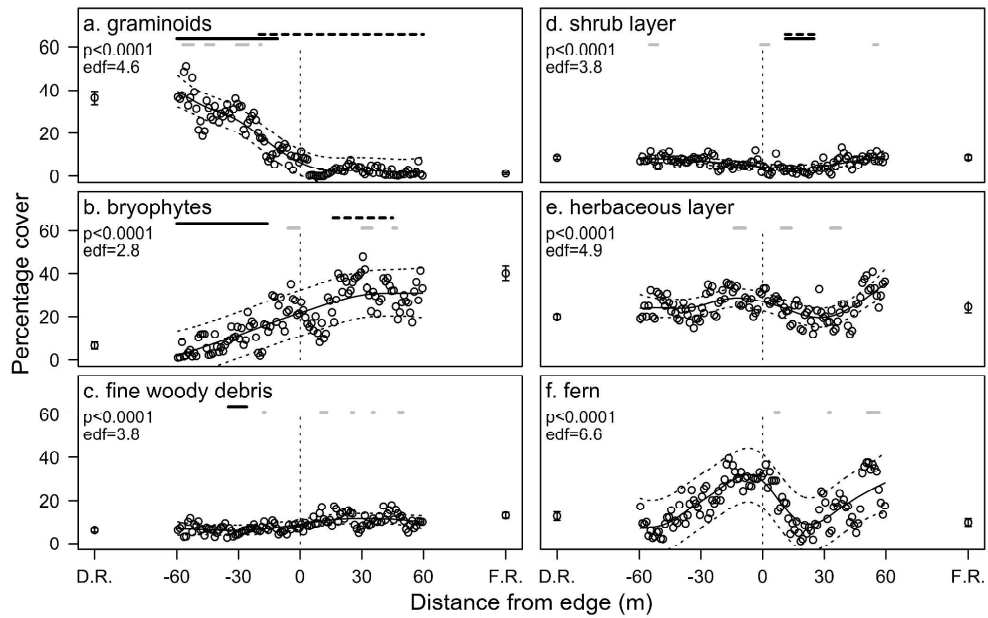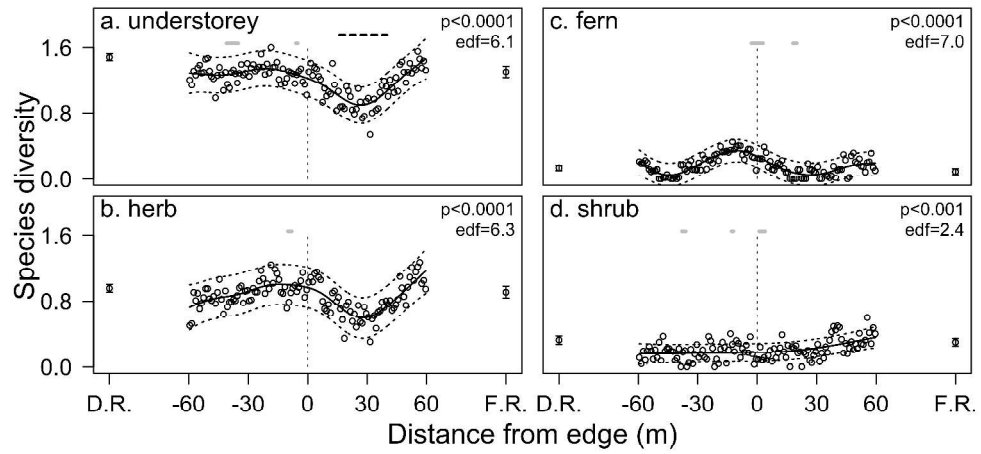
Figure 5. Mean species diversity of (a) understorey plants (shrubs, herbs, and ferns combined), (b) herbs, (c) ferns, and (d) shrubs along the insect disturbed area-forest edge gradient. See Figures 1 and 3 for further details.

Figure 6. Percentage of response variables with significant distance of edge influence, distance of forest influence, and distance of edge change along the insect disturbed area-forest edge gradient. Response variables include percentages of *Abies balsamea* and *Betula papyrifera* saplings in each of six different browse classes; percentages of short, intermediate, and tall saplings in each of six different browse classes; maximum sapling height; sapling and seedling densities; cover of graminoids, bryophytes, fine woody debris, shrub layer (height ≥ 15 cm), herb layer (height < 15cm), ferns, and individual species; and diversity of understorey species, herbs, fern, and shrubs.
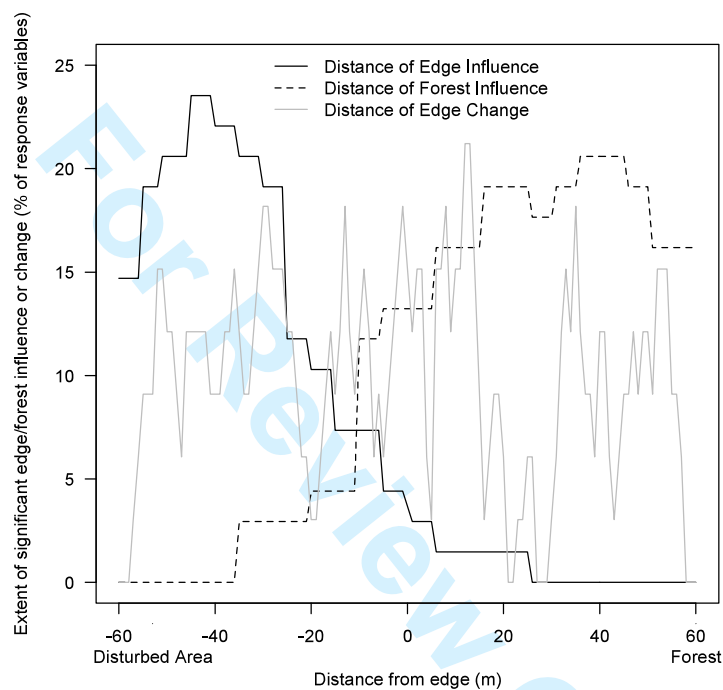
Table 1. Criteria used for determining severity of moose browsing on individual saplings. The classification system was adapted from Smith et al. (2010).

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 (*Abies balsamea*)/ Multiple dead stems (*Betula papyrifera*)	No	No	No	Yes	No	Yes

Table 2. Average cover at the edge (-5 to 5 m), in the forest reference (FR), and in the disturbed area reference (DR); performance of generalized additive mixed model (GAMM) (edf = estimated degrees of freedom of the smoothing term); distance of edge change (DEC); distance of edge influence (DEI); and distance of forest influence (DFI) for individual understorey species. Sample size is n = six transects.

Species	Average cover (%) ± SE			GAMM		DEC (m)	DEI (m)	DFI (m)
	DR	Edge	FR	edf	P			
Shrub layer								
Amelanchier spp.	0.4 ± 0.3	1.4 ± 0.6	1.7 ± 0.4	1.0	0.002	-9 to -6	-40 to -21	ns
Kalmia angustifolia	0.0 ± 0.0	0.0 ± 0.0	3.5 ± 0.7	4.2	<0.001	34 to 35, 40 to 42, 49 to 57	-60 to 10	31 to 60
Rubus idaeus	5.7 ± 0.5	0.5 ± 0.2	0.0 ± 0.0	4.8	<0.001	-56 to -42, -36 to -26, -18 to -17	-60 to -6	-10 to 60
Sorbus americana	0.7 ± 0.3	0.7 ± 0.2	0.5 ± 0.2	1.5	0.078	-16 to -13	ns	ns
Vaccinium angustifolium	0.1 ± 0.1	1.7 ± 0.7	2.4 ± 0.7	1.0	0.046	ns	ns	ns
Herbaceous layer								
Aralia nudicaulis	3.0 ± 0.4	2.6 ± 0.4	2.0 ± 0.3	4.8	<0.001	-16 to -9	ns	ns
Aster acuminatus	1.1 ± 0.3	0.7 ± 0.2	0.2 ± 0.1	1.0	<0.001	-52 to -24	-55 to -16	ns
Clintonia borealis	0.2 ± 0.1	0.6 ± 0.2	2.1 ± 0.5	6.1	<0.001	11 to 13, 17 to 19	ns	6 to 15
Cornus canadensis	9.7 ± 0.9	17.1 ± 1.7	14.1 ± 1.8	4.1	0.052	-30 to -27, -13 to -8, 8 to 15, 32 to 38, 52 to 53	ns	ns
Linnaea borealis	0.0 ± 0.0	1.6 ± 0.3	1.8 ± 0.4	3.5	0.002	ns	ns	-35 to 20, 31 to 60
Maianthemum canadense	1.0 ± 0.2	1.5 ± 0.2	1.5 ± 0.2	4.9	<0.001	-26 to -23, -14 to -13, -4 to 1, 6 to 8, 52 to 54	-40 to -26	-35 to -26
Trientalis borealis	0.03 ± 0.02	0.7 ± 0.1	1.2 ± 0.3	1.0	<0.001	6 to 8, 35 to 41	-60 to -21	1 to 60
Ferns								
Dryopteris sp.	6.3 ± 1.1	2.2 ± 0.7	2.3 ± 0.7	2.9	0.003	-46 to -34, 47 to 54	ns	-10 to -1
Osmundastrum cinnamomeum	0.1 ± 0.1	15.0 ± 2.6	3.7 ± 1.2	6.6	<0.001	2 to 10	-45 to -36	-5 to 15, 36 to 60
Pteridium aquilinum	0.8 ± 0.6	11.8 ± 3.4	2.8 ± 1.1	6.0	<0.001	-16 to -15, 12 to 15	ns	ns
Thelypteris noveboracensis	5.5 ± 1.6	7.2 ± 4.2	0.5 ± 0.3	6.9	<0.001	-4 to -1, 31 to 33	-20 to -6	ns

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