THE IMPACT OF MOOSE (*ALCES ALCES ANDERSONI*) ON FOREST REGENERATION FOLLOWING A SEVERE SPRUCE BUDWORM OUTBREAK IN THE CAPE BRETON HIGHLANDS, NOVA SCOTIA, CANADA

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ABSTRACT: Two interacting disturbances such as stand-level defoliation by spruce budworm (*Choristoneura fumiferana*) and subsequent herbivory by moose (*Alces alces*) may affect landscapes differently than if they occurred in isolation. We studied moose (*A. a. andersoni)* browsing on sites disturbed approximately 25 years ago by a severe spruce budworm outbreak in a region historically dominated by balsam fir (*Abies balsamea*) forest on northern Cape Breton Island, Nova Scotia, Canada. Our objectives were to 1) describe the impact of a large resident moose population on post-budworm regeneration of balsam fir and white birch (*Betula papyrifera*), and 2) to examine the interplay between moose abundance, site conditions, and variation in post-budworm forest regeneration. Fifty-eight randomly located sites were sampled for composition and structural characteristics, moose browse severity, moose pellet group density, and site conditions. We used univariate general linear modelling (GLM) and multivariate redundancy analysis (RDA) to examine relationships between moose abundance as indicated by pellet-groups, site conditions, and post-budworm regeneration. Approximately 65% of all balsam fir and white birch saplings tallied were severely browsed by moose, exhibiting stunted, abnormal growth forms. Both the GLM and the RDA indicated that moose abundance was the best predictor of variation in the density of post-budworm regeneration of balsam fir and white birch. Site conditions were less useful predictors of variation in regeneration. The relationship between moose abundance and regeneration of balsam fir and white birch was positive, suggesting that moose may be more abundant in areas where regeneration is more dense. Sustained, severe browsing in areas regenerating after spruce budworm outbreak may significantly inhibit future forest development and alter the well documented spruce budworm-balsam fir cyclic successional system of northern Cape Breton Island.

Natural disturbances are drivers of change in the composition and structure of forest ecosystems. While classic succession theory predicts cyclic patterns, many recent studies offer an opposing view, suggesting that post-disturbance development may take alternate successional pathways or trajectories in a wide variety of ecosystems (see Dublin et al. 1990, Augustine and Frelich 1998, Frelich and Reich 1999, Payette et al. 2000, Jasinski and Payette 2005). Interactions between disturbances and the resultant impact on landscapes remain poorly studied despite their relative prevalence (Radeloff et al. 2000). Paine et al. (1998) argued that interacting or compounding disturbances carry greater potential ramifications for the long-term transformation of a community than that of large, infrequent disturbances.

The spruce budworm (*Choristoneura fumiferana)*, a native insect defoliator in the spruce-fir forests of eastern Canada, is prone to population explosions that can result in stand-replacing disturbance in balsam fir

(*Abies balsamea*) dominated forests (MacLean 1984). The ability of balsam fir forests to succeed themselves through advanced regeneration has contributed to claims that spruce budworm and balsam fir interact in a cyclic successional system (e.g., Baskerville 1975, MacLean 1984, 1988).

The impacts of moose (*Alces* spp.) browsing on forest ecosystems have been well studied in North America and Scandinavia. These studies have shown that browsing by moose can alter the development of individual trees (Bergerud and Manual 1968, Snyder and Janke 1976, Brandner et al. 1990), alter the compositional and structural make-up of a forest (Risenhoover and Maass 1987, Thompson et al. 1992, Connor et al. 2000), and serve as an important function in the cycling of nutrients within an ecosystem (Pastor and Naiman 1992, Pastor et al. 1993, Pastor and Kjell 2003).

Interactions between an outbreak of spruce budworm and browsing by a significant population of moose may have created a previously undocumented successional pattern in the forest ecosystem of northern Cape Breton Island. Radeloff et al. (2000) studied the effects of disturbance by an outbreak of the jackpine budworm (*Choristenuera pinus pinus*) and subsequent salvage logging and found that these 2 interacting disturbances had together affected the landscape differently than if they had occurred in isolation of each other. Citing examples of interplay among forestry practices, agricultural development, and forest fires in the southern boreal forest, and between climatic conditions and exotic invasive species in San Francisco Bay, among others, Paine et al. (1998) found that the impacts of these "compounded perturbations" were more significant, long-term, and fundamentally different than the impacts of even "large infrequent disturbances" on the host ecosystem.

In this paper we examine the impacts of moose (*Alces alces andersoni*) on regeneration of balsam fir and white birch (*Betula papyrifera*) following an outbreak of spruce budworm on northern Cape Breton Island, Nova Scotia. A large portion of the area affected by spruce budworm outbreaks is not presently following the expected cyclic successional trajectory (Smith 2007). We believe a second, unanticipated disturbance – herbivory by moose – is inhibiting post-budworm successional development. Our research objectives were to 1) describe the impact of moose on post-budworm regeneration of balsam fir and white birch, and 2) examine the interplay between moose abundance, site conditions, and variation in post-budworm forest regeneration. The response of sites disturbed by spruce budworm followed by moose herbivory is of increasing interest to land and resource management agencies in the Atlantic Provinces. Monitoring their succession, or alternatively their regression, will yield insight into interacting population irruptions of spruce budworm and moose and their resultant impact on the boreal forest of northern Cape Breton, with potential relevance for similar interacting disturbances in forests elsewhere.

METHODS

Study area

The study area was between 60º 56´ and 60º 94´ latitude and 46º 61´ and 46º 90´ longitude and encompassed 2 protected areas: 1) Cape Breton Highlands National Park (hereafter referred to as the National Park) a 948 km^2 protected area spanning the Island from the west coast to east, and 2) the provincially designated Pollet's Cove-Aspy Fault Wilderness Area (hereafter referred to as the Wilderness Area), which abuts the northern border of the National Park and extends almost to the northernmost tip of the Island (Fig. 1). Specifically, the study sites were located on the Cape Breton Plateau in areas of the National Park and the Wilderness Area affected by the spruce budworm outbreak of 1974-84 (see Smith 2007).
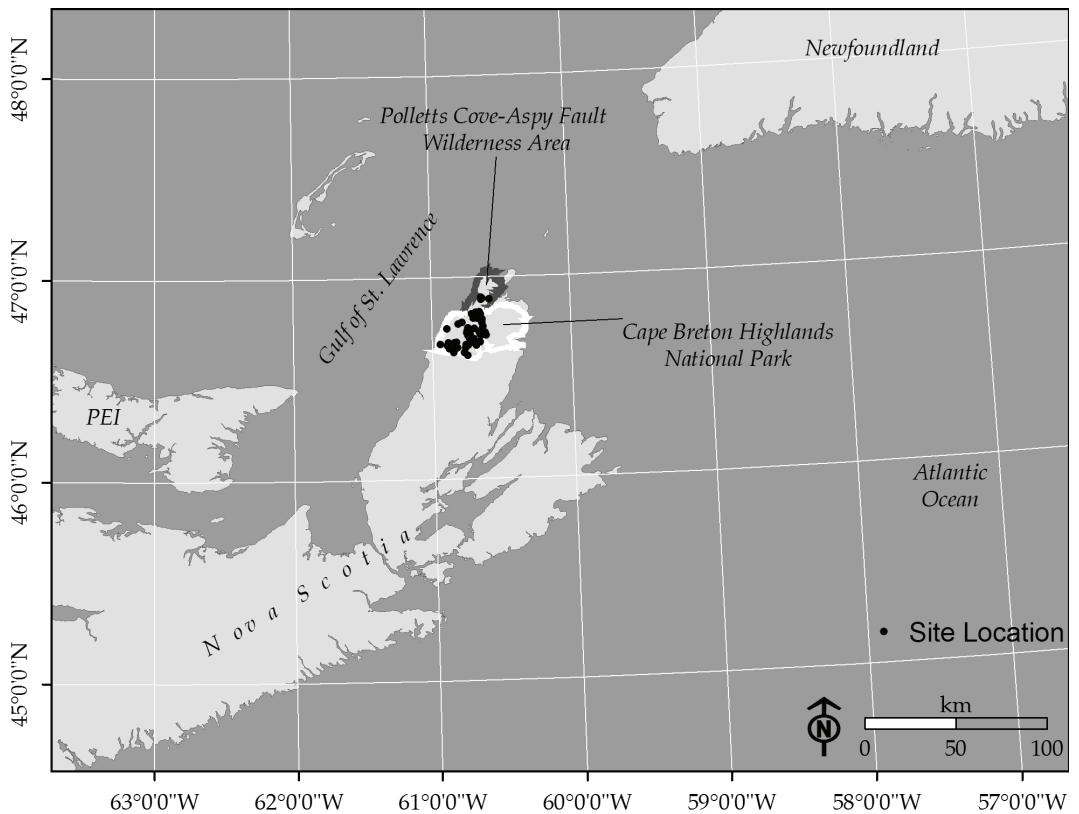
Fig. 1. Study area and site locations in Polletts Cove-Aspy Fault Wildnerness Area and Cape Breton Highlands National Park, Nova Scotia, Canada.

The close proximity of the Atlantic Ocean influences the climate of northern Cape Breton in all seasons. The sharp rise of the plateau from the ocean produces orographic precipitation with a notable gradient from west to east. The plateau region of the highlands is cooler than lower-lying coastal areas. Snowfall accumulations are greater and generally persist well into spring (Bridgland and Millette 1995). The maritime influenced boreal forest, unique in Nova Scotia, is the dominant forest type on the plateau, is close to the southern limit of its range, and has historically been dominated by balsam fir (Fernow 1912, Collins 1951). Black spruce (*Picea mariana*) is also abundant, while white spruce (*P. glauca*), mountain ash (*Sorbus americana*) and red maple (*Acer rubrum*) are less common. A landcover type characterized by barrens, stunted black spruce trees, and lichen-heath communities, locally

referred to as Taiga, is also at elevations >400 m (a.s.l.).

Spruce budworm in northern Cape Breton -- Spruce budworm is an important agent of disturbance in balsam fir-dominated forests. The most recent outbreak (1974-1984) on northern Cape Breton Island was intense, resulting in 87% average mortality in affected stands (Ostaff and MacLean 1989). Balsam fir mortality levels were evenly distributed among diameter classes and were not correlated with site characteristics (MacLean and Ostaff 1989). Despite the severity of the Cape Breton outbreak, it was widely believed that advanced regeneration would facilitate a return to a canopy largely dominated by balsam fir. This expected return would follow stages of secondary succession characterized by a mix of deciduous (primarily white birch) and coniferous (primarily balsam fir with some

spruce [*Picea* spp.]) stands (MacLean 1988, Pardy 1997, Smith 1998).

Moose in northern Cape Breton -- Moose are native to all of Nova Scotia but were extirpated from Cape Breton Island in the early twentieth century, likely due to over-hunting and habitat alteration (Cameron 1958). In 1947 and 1948, 18 moose were transported from Elk Island National Park in Alberta and released in northern Cape Breton (Pulsifer and Nette 1995). These moose were of a different subspecies (*A. a. andersoni*) than those endemic (*A. a. americana*) to Nova Scotia. While initial population growth after re-introduction was slow, the moose population has increased drastically since the 1970s. Mid-winter surveys in recent years suggest that as many as 5000 ($\pm$ 1000) moose inhabit northern Cape Breton, with local mid-winter densities as high as 20 animals/km^2 in some areas (Parks Canada, unpublished data); however, the most recently (2008) compiled estimates suggest the population may be in decline (D. Quann, Cape Breton Highlands National Park, unpublished data). Moose in northern Cape Breton forage heavily on white birch (Basquill and Thompson 1996) during summer, whereas balsam fir is a more important forage of moose in eastern Canada than in other parts of North America (Bergerud and Manuel 1968, Risenhoover and Maass 1987, McInnes et al. 1992, Basquill and Thompson 1996).

Sample site selection

We imposed a 10-ha minimum patch size requirement on potential sites, enabling us to minimize potential edge effects when orienting sampling units. This requirement restricted the observed sites to the western portion of the National Park and the central portion of the Wilderness Area (Fig. 1). Potential sample sites were stratified across a gradient of moose abundance within the study area. Abundance values derived from 4 years of aerial surveys (Parks Canada, unpublished data) were

summed for each survey block (approximately 5 km^2), and classified as either low or high (moose abundance) using an arbitrary cut-off of an average abundance rating of 9 moose per survey block ($\leq$ 9 moose/survey block = low abundance, >9 moose/survey block = high abundance). Abundance ratings were derived from sightings, tracks, and other moose sign. A subjectively ranked sightability factor was included in the calculation of abundance scores to account for differences in tree cover and other variables affecting overall ability to see moose or moose sign.

We used gridded random tessellation sampling to randomly select 15 sample sites from the varied number of possibilities for 4 different site types. Site types were determined from spectral signatures derived from a supervised classification of a SPOT 5 MS 10 satellite scene of the post-budworm landscape. The spectral signatures were identified as predominant from photographic analysis of sites associated with each spectral signature and refined using field verification and statistical analysis. The final classified and filtered image resulted in 4 classes identified by their seemingly predominant characteristics: grassland (GRASS), snag (SNAG), downed wood (BLOWDOWN), and browsed deciduous (BROWSED DECIDUOUS). Access issues and misclassifications altered the intended sample size so that final sample sizes ranged from 13-18 sites per class, for a total of 58 sites (see Smith 2007 for further description).

Field measurements

We sampled trees ($\geq$2.0 m in height), saplings (<2.0 m and $\geq$0.5 m in height) and seedlings (<0.5 m in height) using a series of 4 parallel, rectangular plots placed at 5 m intervals. Plots were 4 m x 50 m for trees and snags (4 x 200 m^2 = 800 m^2 total), and 2 m x 50 m for saplings and seedlings (4 x 100 m^2 = 400 m^2 total). Start-points and orientation of plots were pre-determined and designed to maximize randomization and minimize

potential edge effects.

The density of live and dead woody species was recorded. All live individuals were classified subjectively according to browsing severity: unbrowsed, lightly browsed, moderately browsed, severely browsed, and dead. Unbrowsed individuals exhibited no evidence of moose browsing. Dead individuals had no living parts; we assumed that dead saplings exhibiting signs of severe browsing suffered mortality as a direct result of that browsing. While no dead saplings devoid of evidence of severe browsing were encountered, it is possible that some individuals perished as a result of several cumulative factors. However, in the absence of disease, drought, interspecific competition, or other known stressors, and given the abundance of moose in the region, we concluded that it was a justified assumption.

The browse severity classification was based on growth form, the proportion of stems browsed, and the presence/absence of live foliage (Table 1). While severity classifications have been criticized elsewhere (e.g., McLaren et al. 2004) for being subjective and potentially variable among species, we believe that ours was an efficient method to obtain a relative measure of the proportion of individuals browsed by moose versus those that were unbrowsed or dead. While

the conditional approach taken is admittedly subjective, the simplicity of the method, the low number (3) of species classified, and the ubiquity of severely altered growth forms afforded us confidence in our measure.

Trees were assigned to 1 of 2 height classes (2-4 m, >4 m) and measured for diameter at breast height (dbh). Ground vegetation was sampled using 1-m^2 quadrats placed every 10 m within each of the 4 plots composing one sample site, for a total of 20 per site (20 m^2 total). Herbaceous plants were identified to species, with the exception of *Aster* spp., which were identified to genus. Grasses and sedges were identified to family, with the exception of *Calamagrostis* spp. Lichens and mosses were simply identified as such, with the exception of *Sphagnum* spp., which were identified to genus. Nomenclature followed Zinck (1998).

At each site we measured the continuous variables elevation (ELEV) and slope (SLOPE), and the categorical variable aspect (ASPECT, 8 categories). Additional categorical environmental variables included topography (TOPO, 4 categories), drainage (DRAIN, 2 categories), and soil texture that were obtained from the Nova Scotia Department of Natural Resources (NSDNR) ecological land classification (Neily et al. 2003). Soil texture was later dropped from the analysis

Table 1. Criteria and decision making used in the browse severity classification used to assess impact of moose browsing on forest regeneration, Cape Breton Highlands, Nova Scotia.

Question	Unbrowsed	Lightly browsed	Moderately browsed	Severely browsed	Dead
Live foliage?	Yes	Yes	Yes	Yes	No
Evidence of browse?	No	Yes	Yes	Yes	N/A
Growth form altered?	No	No	Yes - some evidence	Yes - drastic alteration	N/A
Multiple dead stems? (white birch, mountain ash)	No	No	No	Yes	N/A
Cylindrical and dense? (balsam fir)	No	No	No	Yes	N/A
Proportion of stems browsed?	None	< 1/3	> 1/3, < 2/3	>2/3	N/A

N/A = not applicable

because it was homogeneous across all sample sites. Moose feces, deposited as pellets in winter and non-pelletized clumps in summer, were recorded within the 2 x 50 m portion of the plot. Non-pelletized fecal deposits and pellet groups consisting of >30 pellets were counted (Neff 1968). The predictor variable (PELLET), used here as a surrogate for moose abundance, represents the density of moose fecal deposits found within the total area of each sample site (800 m^2).

Data analyses

We used both univariate and multivariate modeling approaches to examine the relationship between environmental variables and post-budworm regeneration of balsam fir and white birch. For the dependent variable in the univariate analysis, we developed a Regeneration Index - an additive measure of post-budworm regeneration success (white birch (wB) and balsam fir (bF)) on each site. Our regeneration index is the sum of the densities of trees (t), saplings (s), and seedlings (sd) weighted by their growth form:

Regeneration Index = 3wB(t) +3bF(t) + 2wB(s) + 2bF(s) + wB(sd) + bF(sd).

We then used the PROC GENMOD function in SAS version 9.1 (Littell et al. 1996, SAS Institute 2003) to fit a generalized linear model (GLM) to the response variable Regeneration Index. Goodness-of-fit statistics indicated that a model fit to the gamma distribution of the 'Regeneration Index' using the log-link function was most appropriate. We confirmed this with a visual inspection of a histogram. The gamma distribution is a continuous probability distribution arising from the Poisson process and may take a variety of shapes. The link function is a mathematical transformation embedded in the model used to normalize the distribution of errors. In the case of the gamma distribution, the log-link is recommended (McCullagh and Nelder 1989).

To fit the model, we tested the significance of individual model terms using Chi-Square probability values from likelihood ratio tests (Type III analyses; α = 0.05) that are independent of the order in which variables are entered into the model (Johnstone n.d.). Significant predictor variables were used as a base model to which additional model terms were added individually to test whether they improved the model fit. Models were ranked using Akaike's Information Criterion (AIC), a part of the information-theoretic approach to model selection (Burnham and Anderson 1998). The AIC formula is:

$$-2(\text{log likelihood}) + 2(p)$$

where p is the number of parameters in the model. Differences between models (Δ_i) of >10 AIC units or more from the model with the lowest AIC value indicate strong support that the model is not the best. Differences of <2 AIC units are considered small and suggest that identification of a best model between the two is not pragmatic (Burnham and Anderson 1998).

To examine the multivariate relationship between environmental variables and post-budworm regeneration of balsam fir and white birch, we conducted constrained ordinations for each of white birch and balsam fir using redundancy analysis (RDA; Rao 1964). The multivariate species variables were the densities of white birch and balsam fir in various stages of growth, including seedling density and the densities of saplings within 4 browse severity classes (unbrowsed, lightly browsed, moderately browsed, severely browsed) excluding dead individuals. We also included trees in the 2-4 m height class as post-budworm regeneration, believing them to be young enough to have germinated and grown in years following the spruce budworm outbreak; trees >4 m in height were identified as potential budworm survivors and were not regarded as post-budworm regeneration.

Redundancy analysis is a technique akin to a multiple regression for all dependent variables simultaneously, combining elements of ordination and regression to detect patterns in response data that can be best explained by the subset of environmental or predictor variables used (ter Braak 1995). The final set of environmental variables was selected in a preliminary RDA using forward selection ($\alpha = 0.10$) and only significant variables from the preliminary analysis were used in the final iteration, as recommended by Lepš and Šmilauer (2003). Significance testing was by Monte Carlo permutation. The redundancy analysis was performed in CANOCO for windows ver. 4.54 (ter Braak and Šmilauer 2002).

Non-parametric Spearman correlations were calculated to examine associations between PELLET and the browse severity classes. Significance testing was performed in SPSS 11.5 (SPSS Inc. 2005).

RESULTS
Moose browse severity

Evidence of moose browsing was ubiquitous across our study sites. The classification of browse severity showed that few saplings had been browsed by moose, and the vast majority had been severely browsed or were dead as a result of browsing. Greater than two-thirds of all white birch and balsam fir saplings encountered were severely browsed (Fig. 2). The browse classifications for white birch were dominated by the severely browsed and dead categories; more variation existed for balsam fir that had more stems classified as unbrowsed, lightly browsed, and moderately browsed than white birch (Fig. 2). Mountain ash (*Sorbus spp.*) was recorded far more infrequently; 84% were browsed severely
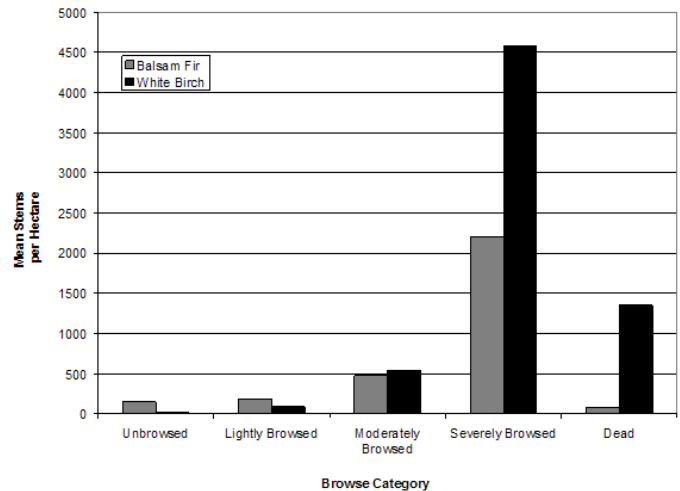

Fig. 2. Mean stem density of balsam fir and white birch and the proportional breakdown among the 5 browse severity classes, Cape Breton Highlands, Nova Scotia.

(not shown) but no dead individuals were encountered at any site.

Predicting variation in post-budworm regeneration

PELLET was the most important variable in the fit of the GLM (Tables 2, 3). Adding subsequent model terms resulted in a slightly improved fit but higher AIC value in most cases (Table 2), with the exception of the PELLET + SLOPE model. Because the difference between the PELLET model and the PELLET + SLOPE model is <2 AIC units, it is not possible to declare either of them best. Therefore, we present additional information for only the PELLET + SLOPE model that had the lowest AIC value (Table 3).

PELLET and SLOPE had similar effect sizes in relation to the density of post-budworm regeneration; the coefficients indicate that for approximately every 1-unit increase in PELLET and SLOPE (1 pellet-group, 1° slope), regeneration increased by 1 unit (1 stem). The subset of predictors fit the gamma distribution of the dependent variable Regeneration Index well (scaled deviance = 1.00) despite known cases of clustering and outliers. The scaled deviance is the measure of the fit of the residuals to the predicted distribution, in

Table 2. Generalized linear model results examining the influence of predictor variables on post-budworm regeneration (models were fit to the gamma distribution of errors using the log link function), Cape Breton Highlands, Nova Scotia. L-Likelihood = Log likelihood for the model, AIC = Akaike's Information Criterion, and Δi = difference between a given model and the model with the lowest AIC in units of AIC. Variables are described in Methods.

Model term	n	L-Likelihood	AIC	Δi
PELLET	58	-355.41	712.82	0.9
PELLET + SLOPE	58	-353.96	**711.92**	**0**
PELLET + ELEV	58	-355.4	714.8	2.88
PELLET + TOPO	58	-355.74	715.48	3.56
PELLET + DRAIN	58	-355.08	714.16	2.24
PELLET + ASPECT	58	-355.76	715.52	3.6
PELLET + SLOPE*ASPECT + SLOPE + ASPECT	58	-355.31	718.7	6.78

this case, the gamma. One (1.00) is a centre point that indicates a good fit; the farther the deviance is from 1.00 in either direction, the poorer the fit.

Results of the multivariate RDA examining the relationship of the environmental variables and PELLET coincided with the GLM indicating that PELLET was the best predictor of variation of post-budworm regeneration. Redundancy analyses explained 27% of variation in balsam fir regeneration and 22% of the variation in white birch regeneration, indicating that factors other than PELLET and the interaction between SLOPE and ASPECT contribute to the variation in post-budworm regeneration.

In the RDA, the first axis accounted for >98% of the explained regeneration-

Table 3. Details for the PELLET + SLOPE model used to assess impact of moose browsing on forest regeneration, Cape Breton Highlands, Nova Scotia. Intercept coefficient represents mean regeneration holding other model terms constant. Coefficient = effect size, S.E. = Standard Error, and P-Value is for Chi-Square goodness of fit test. The Scaled Deviance is obtained by df/Deviance; a value closer to 1 indicates a good fit.

Model term	Coefficient	S.E.	P - Value
Intercept	126.23	1.19	–
PELLET	1.08	1.03	**0**
SLOPE	1.01	1.03	0.33
Scaled Deviance = 1.00			

environment relations for both balsam fir and white birch regeneration (Table 4). The variable PELLET and the interaction term SLOPE*ASPECT were significantly related to variation in post-budworm regeneration of both species. The first axis of each RDA analysis explained 27% and 22% of the overall variation (not shown) for balsam fir and white birch, respectively. For balsam fir, interset correlations showed that axis 1 was strongly positively correlated with PELLET, and negatively correlated with all other variables. Interset correlations in the ordination for white birch showed that the first axis was positively correlated with all variables, most strongly with PELLET and the interaction term SLOPE*ASPECT. Axis 2 explained < 1% of the variation in regeneration for both species (not shown).

The Spearman correlations examining the association between PELLET and the 5 sapling browse categories for each of white birch and balsam fir indicated that the relationship between PELLET and the Regeneration Index is likely a function of significant positive associations between moose pellet abundance and the density of severely browsed balsam fir and white birch saplings (Table 5).

DISCUSSION
Moose and post-budworm regeneration
Evidence of sustained, heavy moose

Table 4. Results of constrained ordination (redundancy analysis) analyzing the relationship between predictor variables and variation in post-budworm regeneration of balsam fir and white birch, Cape Breton Highlands, Nova Scotia. Only variables determined to be significant ($\alpha = 0.10$) using a preliminary stepwise selection were included. Eigenvalues for the axes represent the percentage of variation explained by each. The species-environment correlation is a measure of the relationship between each axis and the species data. Also given are the cumulative percentage of the variation explained by the axes and the cumulative percentage of the total species-environment relations. Pearson interset correlations represent the association of each variable with each axis; SLOPE*ASPECT is the interaction between SLOPE and ASPECT.

	Balsam fir		White birch	
	Axis 1	Axis 2	Axis 1	Axis 2
Eigenvalue	0.268	0.003	0.223	0.002
Species-environment correlation	0.576	0.239	0.491	0.305
Cumulative % variation explained	26.8	27.2	22.3	22.5
Cumulative % species-environment	98.4	99.5	98.6	99.6
Interset Correlations				
PELLET	0.48	0.12	0.398	0.142
SLOPE*ASPECT	-0.096	0.052	0.267	-0.146
ASPECT	-0.313	0.131	0.075	-0.226
SLOPE	-0.105	0.075	0.244	0.012

browsing in the form of severely stunted, atypical growth forms was noted on >65% of all white birch and balsam fir saplings. Low runners or shoots emerging from the root collar were often the only live vegetation noted on saplings. Mortality as a result of browsing was much more common for white birch than balsam fir, suggesting a lower tolerance to browsing or possibly reflecting moose preference for white birch. However, as McLaren et al. (2009) concluded, foraging preference is a useful, but not holistic predictor of vegetation responses in the short term, and shade tolerance and the ability to invest in below ground resources will also dictate a species' response to the onset of, or release from, severe browsing by moose. Strong survivorship under intense browsing can also be inferred from our field data for mountain ash which was relatively common on the landscape in a severely browsed condition, yet never recorded as dead.

Our hypothesis regarding the impact of moose on post-budworm regeneration was that the density of post-budworm regen-eration would exhibit a negative relationship with moose abundance. We also anticipated more significant mortality levels. However, we found that where regeneration was most dense, moose were more abundant, and while browsing pressure was extreme, mortality

Table 5. Non-parametric Spearman correlations between PELLET and the sapling browse severity classes, Cape Breton Highlands, Nova Scotia.

	Browse class	Correlation coefficient	P - value
Balsam fir	Unbrowsed	0.065	0.63
	Lightly browsed	-0.034	0.8
	Moderately browsed	0.124	0.35
	Severely browsed	0.493	**0**
	Dead	0.013	0.92
White birch	Unbrowsed	-0.188	0.15
	Lightly browsed	-0.067	0.61
	Moderately browsed	0.171	0.19
	Severely browsed	0.554	**0**
	Dead	0.152	0.25

was not. The positive relationship between moose abundance (PELLET) and the density of post-budworm regeneration is likely a function of: 1) the significant correlation with the density of severely browsed saplings (Table 5), 2) growth form adaptations in response to browsing, and 3) rapid degradation of moose feces by insects and precipitation (as found by Timmerman and Buss 1997).

The significant correlations between PELLET and the density of severely browsed white birch and balsam fir indicate that severely browsed saplings are significantly associated with increased moose abundance while all other browse classification categories are not. Both balsam fir (Brandner et al. 1990, McLaren 1996) and white birch (McLaren et al. 2009) adapt their growth form under browsing pressure. Balsam fir has been shown to adopt exaggerated apically or laterally oriented forms, depending upon the nature of the browsing and access to light (Brandner et al. 1990, McLaren 1996), whereas white birch (among other hardwoods) has been shown to invest more in below-ground-growth (McLaren et al. 2009). While detailed structural data were not collected for saplings, we observed many altered growth forms similar to those described elsewhere (e.g., Brandner et al. 1990, McLaren 1996).

We are not aware of any data regarding rates of decomposition for moose feces in northern Cape Breton, though Neff (1968) reported that the time span required for ungulate pellet decomposition can be as little as several months. Comparing the short amount of time required for decomposition of moose feces in conjunction with the presumably longer period of time required for mortality induced by repeated browsing indicates that mortality occurring beyond the decomposition period would not be reflected in our snapshot of the current situation. We believe the non-significant correlations between PELLET and dead saplings are representative of this.

The cumulative result of these 3 factors

is that sites exhibiting the ultimate impact of sustained, severe moose browsing – a reduction in the densities of preferred browse species as a result of mortality - are not adequately represented by our Regeneration Index. However, the positive relationship between moose abundance and post-budworm regeneration (particularly the ubiquity of severely browsed saplings) describes the relationship between the ecosystem response to the stand initiating disturbance caused by spruce budworm, and the large resident moose population of the northern Cape Breton Highlands.

Site factors as predictors of post-budworm regeneration

With the exceptions of SLOPE in the GLM and the interaction term SLOPE*ASPECT in the RDAs, environmental variables were not important in explaining variation in post-budworm regeneration. An increase in SLOPE was associated with an increase in regeneration; however, only 3 sites had a slope of >10 degrees (none >14), making it difficult to interpret any real significance from this association. While it is possible that site factors are not contributing to variation in regeneration, it is also possible that the landscape-level data we used, derived from an ecological land classification of the entire province of Nova Scotia, was too coarse to detect subtle site conditions that may be contributing to the emergence of varied regeneration. Particularly, site-specific information on soil moisture and site productivity during the growing season may improve understanding of the presence and potential expansion of *Calamagrostis* spp.

Capacity for recovery

Our field data suggest that with sustained high levels of moose browsing, the sparsely treed conditions prevailing in most budworm-affected areas of the National Park and the Wilderness Area are likely to persist. We derive this conclusion by considering several points.

First, the current condition and proportion of both balsam fir and white birch saplings recorded as severely browsed indicates that these individuals will either perish or, at a minimum, not grow to become canopy trees. In addition, a lack of trees having escaped the moose browse zone (0-3 m in height) indicates a diminished and potentially inadequate seed source from continued tree regeneration. An extreme example of this has been noted in Terra Nova National Park, Newfoundland, Canada, where annual seed rain was consistently ~0.0014 seeds/m^2 over 8 years of collection (L. Hermanutz, Memorial University, personal communication). Data on cone production and seed rain in regenerating areas and adjacent sites would be useful in understanding the potential for a return to forested conditions if browsing were reduced. Additionally, the recent establishment of moose exclosures will facilitate an understanding of the effects of the removal of moose browsing pressure, and could provide insight into the capacity for restoration of a balsam fir-dominated canopy. Experimental work allowing for reduced, but not absent, browsing pressure would be of greater interest in understanding current potential resilience within this system, and would allow managers to simulate the effect of a moose population reduction.

The ubiquity of *Calamagrostis* in some sites (Smith 2007) may inhibit future forest development by affecting seedling germination and success. Hogg and Lieffers (1991) reported notable changes in soil thermal regimes under *Calamagrostis* sod, noting mid-summer soil temperatures fully 4.0º C warmer than in open sites. *Calamagrostis* reduces root growth and water and nutrient uptake in spruce seedlings (Grossnickle 1988) and can potentially cause drought stress (MacDonald 1986). Further, Cater and Chapin (2000) found that white birch seedlings were also suppressed under the dense sod of *Calamagrostis*.

In addition, *Calamagrostis* expands rapidly, requiring just a few years to fully colonize sites after canopy removal (Eis 1981). Coomes et al. (2003) noted expanded niche occupation by non-palatable species as a potential cause of a lack of regeneration following deer population reduction in New Zealand. If *Calamagrostis* is contributing to seedling mortality thereby furthering conditions conducive to its expansion, in essence a positive feedback switch (Wilson and Agnew 1992), it may substantially alter future forest development even with reduced moose browsing. Further understanding of the dynamics of sites dominated by *Calamagrostis* would provide insight into the future successional trajectory of the affected areas of the Cape Breton plateau.

The most salient consideration in understanding the future state of these sites is the growth and condition of the moose population on northern Cape Breton Island. In addition to the absence of wolves (*Canis lupus*) and low levels of predation by black bear (*Ursus americanus*), disease and parasites present among moose populations in other regions, including *Parelaphostrongylus tenuis* (brainworm) and *Dermacentor albipictus* (winter tick), appear to exist at low levels in the Cape Breton population. This is likely because there is no significant range overlap with deer, and a function of moose preference for the higher elevations where they exist (Telfer 1967, 1968); it may also reflect lack of formal monitoring (T. Nette, NSDNR, personal communication).

The most recent population estimate (2008) for the study area suggests that the moose population of northern Cape Breton Island is declining (D. Quann, Cape Breton Highlands National Park, unpublished data). Population estimates from 2009 and 2010 will assist in confirming whether this decline is short-term or trending.

An alternate stable state?
The spruce budworm outbreak acting alone would not have resulted in the land-

scape described herein. While Smith (2007) reported moderate densities of regeneration at the sapling stage, the severe levels of browsing and the low densities of trees indicate that the compounding effects of intense herbivory by moose may be giving rise to what Paine et al. (1998) called an "ecological surprise." While not studied to date, it seems likely that the moose population and its herbivory following the spruce budworm outbreak have been above the ecological carrying capacity for this region. Given lower levels of herbivory by moose following the spruce budworm disturbance, we assume the forest would have progressed slowly through the reorganization of nutrients and energy to a mature balsam fir forest, co-inciding with the concept of the budworm-fir cyclic succession model (Baskerville 1975, MacLean 1984, 1988) and model predictions for our study area (Smith 1998).

As browsing by moose has become more severe, it is arguable that the system has been, or will be, pushed beyond a critical threshold or a "catastrophic bifurcation" as described by Scheffer and Carpenter (2003), causing dramatic change in the successional trajectory of budworm affected area. Asselin et al. (2006) suggested only 2 simple criteria for assessing whether an alternate stable state exists: 1) occurrence of the states under the same environmental conditions (Sutherland 1974), and 2) persistence over time (Connell and Sousa 1983, Jasinski and Asselin 2004). Two drastically different states are currently occurring side by side in northern Cape Breton in previously forested areas: forested and non-forested areas. Factors such as a paucity of established trees on many sites and a potential expansion of *Calamagrostis* may perpetuate the observed lack of forest development.

Management implications

This study offers some insight into the current condition of budworm-affected areas in northern Cape Breton, and will assist managers in guiding future research activi-

ties; however, determining whether current conditions threaten ecological integrity as it was understood or simply imply new baseline conditions will be paramount. Understanding the ecology of the disturbed sites is critical to informing decision-making regarding provincially endangered species such as the American marten (*Martes americana*) and the Canada lynx (*Lynx canadensis*), both of which persist currently in small numbers in the area.

By monitoring regeneration on sites with high levels of moose browsing and high abundance of balsam fir and white birch, an understanding of stand-level responses to browsing pressure over time may be gained. In particular, permanent sample plots would provide data to monitor the evolution of these sites over time. Measures of moose population density and abundance with more longevity will be required to understand trends in browse-induced mortality as they relate to landscape pattern.

Given the amount of damage by moose to post-budworm regeneration, it is questionable whether even a drastic reduction in the moose population would prevent further regression of this landscape. The hardy, resilient nature of species such as white birch and balsam fir may be conducive to recovery, however, and as such, active management should not be precluded. We caution strongly that sites sampled in this study are almost certainly in the areas most affected by spruce budworm and being affected most severely by moose. We advocate for further research investigating the impact of moose on sites that were not affected by the spruce budworm during the last outbreak. Our findings indicate northern Cape Breton Island is currently an ecosystem where studying ecological responses to severe, compounding disturbances over time may yield increased knowledge of the dynamics of the spruce-fir forests of eastern Canada.

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