Changes in woody vegetation abundance and diversity after natural disturbances causing different levels of mortality

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Abstract

Questions: How does woody vegetation abundance and diversity differ after natural disturbances causing different levels of mortality?

Location: *Abies balsamea–Betula papyrifera* boreal mixed-wood stands of southeast Quebec, Canada.

Methods: Woody vegetation abundance and diversity were quantified and compared among three disturbance-caused mortality classes, canopy gap, moderate-severity disturbances, and catastrophic fire, using redundancy analysis, a constrained linear ordination technique, and diversity indices.

Results: Substantial changes in canopy tree species abundance and diversity only occurred after catastrophic fire. Shade-tolerant, late-successional conifer species remained dominant after canopy gap and moderate-severity disturbances, whereas shade-intolerant, early-successional colonizers dominated canopy tree regeneration after catastrophic fire. Density and diversity of mid-tolerant and shade-intolerant understory tree and shrub species increased as the impact of disturbance increased. Highest species richness estimates were observed after catastrophic fire, with several species establishing exclusively under these conditions. Relative abundance of canopy tree regeneration was most similar after canopy gap and moderate-severity disturbances. For the sub-canopy tree and shrub community, relative species abundances were most similar after moderate-severity disturbances and catastrophic fire. Vegetation responses to moderate-severity disturbances thus had commonalities with both extremes of the disturbance-caused mortality gradient, but for different regeneration layers.

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Conclusions: Current spatio-temporal parameters of natural disturbances causing varying degrees of mortality promote the development of a complex, multi-cohort forest condition throughout the landscape. The projected increase in time intervals between catastrophic fires may lead to reduced diversity within the system.

Introduction

Variation in level of disturbance-caused mortality is a key factor in determining successional pathways. The range of conditions created by the variety of disturbance agents occurring within boreal mixed-woods allows a number of different species to dominate after disturbance, depending on the amount of mortality caused. Large, severe disturbances cause extensive overstory and understory mortality, and drive succession back to conditions wherein seral species dominate (Turner et al. 1997; Gromtsev 2002). Conversely, canopy gap disturbances affect one to a few overstory trees, and facilitate the regeneration and growth of late-successional species (Kneeshaw & Bergeron 1998). Conditions after moderate-severity disturbances (defined here as an abiotic or biotic disturbance that is intermediate between canopy gap and catastrophic fire in terms of amount of mortality caused) are less predictable. Moderate-severity disturbances have been shown to drive succession back, perpetuate existing conditions, drive change towards an alternate stable state, or drive succession towards old-growth conditions (Frelich & Reich 1999; Bergeron 2000; Reyes & Kneeshaw 2008).
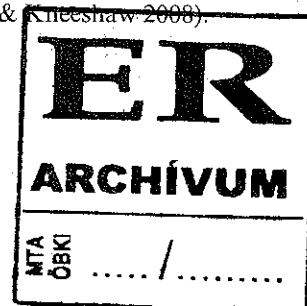
Catastrophic fire has historically been the prominent large, severe disturbance driving stand dynamics in *Abies balsamea–Betula papyrifera* boreal mixed-wood forests of northeastern North America (Bergeron et al. 2001). But with a recent climate-induced decrease in catastrophic fire frequency (Bergeron et al. 1998), other smaller and/or less severe disturbance types, such as those caused by spruce budworm (*Choristoneura fumiferana*) outbreaks, windthrow, and their interactions, can become more important in terms of shaping landscape structure and species distribution patterns. Moderate-severity disturbances, in particular, can cause profound change, as they can affect 10 to 100 s of hectares of forest (Clinton & Baker 2000; Gray et al. 2000; Nagel & Diaci 2006), and can occur relatively frequently in the absence of fire. Spruce budworm outbreak, for example, has occurred on a 20- to 50-year cycle in northeast North America since the end of the Little Ice Age (~1850) (Blais 1983; Bouchard et al. 2006). Note, however, that although being similar in spatial extent to catastrophic fire, unlike catastrophic fire, moderate-severity disturbances leave the regeneration layer relatively intact, and are thus less severe.

Successful establishment occurs where species life-history strategies are compatible with the prevailing establishment or regeneration conditions generated by the disturbance regime (Grime 1977). Different species functional groups often show divergent responses to disturbance (Oliver 1981; Roberts 2004; Kennard & Putz 2005). Early-succession, light-demanding species are usually associated with larger, more severe disturbances, whereas late-succession, shade-tolerant species often dominate the regeneration layer after smaller, less severe disturbances (Frelich 2002; Gromtsev 2002). Species diversity tends to increase after disturbance (Peterson & Pickett 1995), and is also affected by variation in the amount of disturbance-caused mortality (Peltzer et al. 2000). Highest estimates are hypothesized to occur at intermediate levels (Connell 1978; Miller 1982).

Given the variability in species responses, the ability to predict regeneration patterns after different types of natural disturbance causing varying degrees of mortality would significantly contribute to our understanding of boreal mixed-wood stand dynamics; further, although the early/late successional species classification is useful to predict species abundance and diversity after canopy gap versus large, catastrophic disturbances, species responses to moderate-severity disturbances remain unclear. Past research in boreal mixed-woods has focused on either end of the disturbance impact spectrum (e.g., Leemans 1991; Bergeron & Dansereau 1993; Kneeshaw & Bergeron 1998), with little consideration of patterns of recovery across a range of disturbance-caused mortality.

The objectives of our study are to examine and compare woody species regeneration abundance and diversity after natural disturbances causing varying degrees of mortality. Specifically, we aim to: (1) determine if significant changes in relative abundances of the principal canopy species occur after canopy gap, moderate-severity, and large, catastrophic fire disturbances; and (2) examine the variation in woody species diversity in relation to the these disturbance-caused mortality classes.

Study Area

The study was conducted within *A. balsamea–B. papyrifera* boreal mixed-wood stands located in the Chaleur Bay region of the Gaspé Peninsula, Quebec, Canada (48°10′– 48°35′N, 65°45′–66°15′W). Total surface area of the study area is approximately 6480 km². These *A. balsamea–B. papyrifera* stands are a part of a transitional boreal mixed-wood bioclimatic domain bounded by boreal forests to the north and north-temperate deciduous forests to the south. Consequently, the forest canopy consists of a mix of evergreen conifer and broadleaf deciduous species. *A. balsamea*, a shade-tolerant, evergreen conifer species characteristic of late-succession conditions in these forests, and *B. papyrifera*, a shade-intolerant broadleaf deciduous colonizer, dominate the forest landscape. Species of lesser importance include the shade-tolerant *Picea glauca*, *Picea mariana*, and *Thuja occidentalis*, the mid-tolerant *Acer rubrum*, *Betula alleghaniensis*, and *Pinus strobus*, and the shade-intolerant *Populus balsamifera* and *Populus tremuloides*. The general transition of species after catastrophic fire is from a broadleaf deciduous canopy followed by a mixed coniferous–deciduous canopy that can persist for several generations, which transitions to a conifer-dominated climax community in the absence of fire (Bergeron 2000).

Climate for the region is humid continental. Mean minimum daily temperature in January is −15.8°C, while mean daily maximum in July is 22.6°C. Mean annual precipitation is 984 mm, with approximately 79% falling as rain (Environment Canada 2004). General topography is rolling to montane, as the region is within the northern limit of the Appalachian Mountain chain that runs from an

east–northeast to a west–southwest into the USA. Elevations range from 80 to 600 m (mean 285 m a.s.l.). Soils originate from glacial tills, glacio-lacustrine, fluvio-lacustrine, or alteration deposits (Robitaille & Saucier 1998). Soil drainage ranges from imperfect to rapid. Very few lakes are present although several important rivers are interspersed throughout the region.

The current fire cycle, estimated to be between 170 and 250 years (Lauzon et al. 2007), allows many stands to escape catastrophic disturbances for long periods of time. Subsequently, canopy gap and moderate-severity disturbances can have greater impacts on the ensuing regeneration composition if occurring more frequently than fire. Return interval estimates were 30 and 39 years for canopy gap and moderate-severity disturbances, respectively (calculated using methods described in Canham & Loucks 1984; Runkle 1992; Zhang et al. 1999). Return interval estimates were consistent with estimates from associated research undertaken within the eastern boreal mixed-wood region of Quebec, Canada (Bouchard et al. 2006; De Römer et al. 2007).

Methods

Effects of variation in disturbance-caused mortality on regeneration abundance and diversity

Stands were surveyed during the summer of 2004. Relative species composition of the tree canopy can be quite variable among *A. balsamea–B. papyrifera* boreal mixed-wood stands. To isolate differences in regeneration patterns due to variation in disturbance-caused mortality, we selected mature (≥ 89-year-old) *A. balsamea–B. papyrifera* boreal mixed-wood stands having similar relative canopy species composition and density prior to disturbance, general topography, elevation, and soil moisture and drainage regimes (as determined from various Government of Quebec forest inventory and land classification maps). Thus, we sampled from mesic sites having 75:25 conifer to deciduous tree species ratios prior to disturbance, being well stocked, occurring on relatively flat terrain, and having good to rapid drainage. Ground-truthing of sites (quantifying live and dead canopy trees within the disturbed area) verified that conifers represented at least 75% of the tree canopy density prior to disturbance, of which *A. balsamea* accounted for at least 60% of all conifer trees. *B. papyrifera* was the most abundant deciduous species, accounting for at least 60% of all deciduous canopy trees. Sampling

protocols for each disturbance-caused mortality class are described below.

Canopy gap disturbances

Canopy gap disturbances were differentiated from moderate-severity disturbances according to the spatial extent of the mortality caused to the tree canopy. Disturbances affecting between 0.0004 and 0.2 ha of contiguous tree canopy were classified as canopy gap disturbances. One to three transects of variable length (approximately 100 to 400 m) were randomly established within each of five mature *A. balsamea–B. papyrifera* boreal mixed-wood stands (≥ 89 years old) to quantify vegetation regeneration abundance and diversity after canopy gap disturbances. Canopy gaps were caused by a number of disturbance agents (including mortality caused by the spruce budworm, windthrow, and senescence). Canopy gaps wherein the cause of gap formation could not be determined (i.e., no sign or presence of gap makers) were not included in our study. Transects started and ended at least 30 m from the nearest logging road or forest edge, and followed a straight trajectory. A total of 46 gaps were sampled. Various gap characteristics were quantified within each canopy gap that traversed the transect line. Length and width of each gap were measured using the longest north–south distance affected by gap disturbance in conjunction with the longest distance in an east–west direction that traversed the north–south vector. Gap size was determined using the following equation: area = $\pi(\text{length} \times \text{width})/4$ (Runkle 1992). Gap age (i.e., time since disturbance) was determined using annual ring counts measured at ground level from five shade-intolerant *Prunus pensylvanica* or *B. papyrifera* seedlings established within each gap, as it was expected that shade-intolerant species established soon after gap formation. In the absence of these species, timing of release of *A. balsamea* was determined using the same methods, as we assumed that release from suppression of *A. balsamea* occurred within a few years after gap formation (Fraver & White 2005; Metslaid et al. 2005). Tree, sub-canopy tree, and shrub regeneration density (all individuals ≤ 8 cm dbh) was quantified along the north–south vector used to measure gap length, within an area 2 m of each side of the vector. Thus, sampling effort was a function of gap size. Mean gap size was 0.004 ha, ranged from 0.0005 to 0.02 ha, with more than half the gaps smaller than the mean, necessitating the use of a different sampling protocol

from moderate-severity disturbances and cata-
strophic fire described below.

Moderate-severity disturbances

Spruce budworm outbreak, windthrow, and in-
teraction disturbances (defined as a stand affected
by spruce budworm outbreak followed by wind-
throw prior to complete canopy recovery) fall within
our moderate-severity disturbance class when caus-
ing more than 0.2 ha of continuous canopy
mortality. An upper spatial limit was not initially
firmly specified, as moderate-severity disturbances
can be quite extensive, differing with catastrophic
fire primarily in relation to effect on the regenera-
tion layer. Nonetheless, the largest disturbed area
examined was 95 ha (mean = 24 ha, smallest = 0.03
ha). Eleven stands affected by moderate-severity
disturbances were sampled. Three to six, randomly
placed 20×20 m quadrats were examined within
each disturbed stand. A total of 43 quadrats were
sampled. All quadrats were at least 40 m from the
nearest intact forest edge and 30 m from the nearest
logging road, to avoid edge effects. In every quadrat,
regeneration density was determined for all tree,
sub-canopy tree, and shrub species using a nested
plot design: density of seedlings <1-m tall were tal-
lied in a 2×10-m area, those between 1- and 2-m tall,
in a 5×10-m area, and regeneration >2-m tall and
≤ 8 cm dbh, using the entire 20×20-m area. Time
since disturbance was determined with the same
methods used for canopy gap disturbances.

Large catastrophic fire disturbances

Stand-level effects of catastrophic fire can be
highly variable (e.g., Lampainen et al. 2004). Unlike
canopy gap and moderate-severity disturbances,
catastrophic fire can affect stands in young, early
successional stages. Moreover, divergent succes-
sional trajectories have been shown to occur when
stand age differed prior to disturbance (Heinselman
1973; Johnstone & Chapin 2006). To make mean-
ingful comparisons with the other disturbance-
caused mortality classes, we limited our sampling to
severely affected areas (extensive mortality to both
canopy and regeneration layers) that were mature
A. balsamea–B. papyrifera stands prior to a cata-
strophic fire that burned 59 ha of forest in 1988.
Note that we did not account for variation in sever-
ity of catastrophic fire damage to the organic or
mineral soil layers. Given that we sampled 16 years
after fire, most of the differences among sites have

become difficult to detect. Thus, we only ensured
that we sampled in areas wherein >75% mortality
of the pre-fire regeneration layer occurred. This was
verified in the field by determining the age of the re-
generation from annual ring counts at ground level
of ten of the largest seedlings within each quadrat.
Pre-disturbance stand compositions and stand age
classes were determined using Government of Que-
bec forest inventory maps of the region produced
prior to 1988, and were verified in the field with
identification (mostly to species, but at least to con-
ifer versus deciduous) and annual ring counts of
remnant stumps. Tree and shrub regeneration den-
sity was assessed in ten, 20×20-m quadrats using the
moderate-severity disturbance protocol.

Analyses

Effects of variation in disturbance-caused mortality on regeneration abundance and diversity

Canonical ordination analyses were used to ex-
amine the role of variation in disturbance-caused
mortality (canopy gap versus moderate-severity ver-
sus large catastrophic fire) on the response of
regenerating tree, sub-canopy tree, and shrub species,
in terms of absolute densities, with CANOCO 4.02
software (ter Braak & Smilauer 1998). Disturbance
types (spruce budworm outbreak, windthrow, inter-
action, or other) were included in analyses as dummy
variables, to examine responses of vegetation to each
of these factors. An initial run using detrended corre-
spondence analysis (DCA) showed data to have linear
distribution (all gradient lengths were <2.2 standard
deviations for axes 1 to 4). Therefore, redundancy
analysis (RDA), a direct gradient approach, was
used to examine disturbance-caused mortality, dis-
turbance type, and regeneration abundance and
diversity relationships. The forward selection option
was implemented to rank the importance of each
environmental variable, and to remove any environ-
mental variables that did not significantly contribute
to the observed variation. Monte Carlo permutation
tests were used to evaluate the significance of each
environmental variable (at $\alpha = 0.05$ to enter or stay in
model, 200 permutations for each run). While canopy
gap, moderate-severity, and large catastrophic fire
disturbances significantly affected regeneration abun-
dance and diversity (all $P < 0.05$), none of the various
disturbance types had significant effects (all $P > 0.05$).
Thus, only outputs comparing relationships between
each disturbance-caused mortality class and re-

generation composition and abundance are shown. A set of analyses separating regeneration size classes (seedlings < 1-m tall, those between 1- and 2-m tall, and regeneration > 2-m tall and ≤ 8 cm dbh) were also run. Because our results did not appreciably differ from those with regeneration size classes pooled, only results showing pooled size classes are shown. Further, only sites that had undergone disturbances within a few years of one another were included in analyses to ensure that differences in species composition and abundance among disturbance-caused mortality classes were not a result of large discrepancies in time since disturbance. Thus 23, 33, and 10 of the canopy gap, moderate-severity disturbance, and catastrophic fire plots, respectively, were included in this analysis. Times since disturbance for each canopy gap, moderate-severity, and catastrophic fire disturbance were 15, 19, and 16 years, respectively.

Species richness and diversity in relation to variation in disturbance-caused mortality

Differences in species richness (*R*) among severity classes were examined by randomly selecting 10 plots from each of the canopy gap (two plots from each site) and MSD (one plot each from 10 of the 11 sites) classes and analyzing these against the 10 catastrophic fire plots. Species richness (*R*), defined as the total number of tree, sub-canopy tree, and shrub species, and Shannon's diversity index:

$$H' = -\Sigma p_i \ln p_i \qquad (1)$$

were determined for each plot, and compared among disturbance-caused mortality classes using GLM procedures (SPSS 10.0 1999). The Student–Newman–Keuls multiple range test (α = 0.05) was used for *post hoc* comparisons. Data transformation was unnecessary for *R* as data met the parametric assumptions of normality and homogeneity of variances among treatment groups (Zar 1996), whereas *H'* data were ln transformed prior to analyses.

Results

Effects of variation in disturbance-caused mortality on regeneration abundance and diversity

Variation in disturbance-caused mortality resulted in distinct changes in woody species abundance and diversity. Canopy gap and moderate-severity disturbances caused minor changes to the relative abundance and diversity of canopy tree species in relation to pre-disturbance conditions (≥ 75% conifer overstory), whereas substantial changes were observed after catastrophic fire (Fig. 1a and b). Most sub-canopy tree and shrub species increased in abundance after catastrophic fire (Fig. 1c and d). The first two axes in RDA explained 26 and 5% of the total variance in the species data, respectively (Fig. 2). Catastrophic fire was the environmental variable most strongly correlated with axis 1 (canopy gap: *r* = − 0.43, moderate-severity disturbance: *r* = − 0.24, catastrophic fire: *r* = 0.91), while canopy gap and moderate-severity disturbances were more strongly correlated to axis 2 (canopy gap: *r* = 0.63, moderate-severity disturbance: *r* = − 0.69, catastrophic fire: *r* = 0.12). Early-succession, post-fire species segregated to the right along axis 1 whereas late-successional, shade-tolerant species pooled to the left with the canopy gap and moderate-severity disturbances. The second axis mainly differentiated mid- to high-shade-tolerant species (in the upper left quadrant of the ordination diagram) from mid- to low-shade-tolerant species (in the lower half of the ordination diagram) between canopy gap and moderate-severity disturbances.

A. balsamea, a shade-tolerant conifer species, was strongly associated with both canopy gap and moderate-severity disturbances (Fig. 2). *A. balsamea* accounted for 92% and 81% of all seedlings after canopy gap and moderate-severity disturbances, respectively (Fig. 1a and b). *B. papyrifera*, a shade-intolerant deciduous species, dominated the tree regeneration after catastrophic fire, accounting for 54% of all seedlings established (Fig. 1b). Other shade-intolerant and mid-tolerant tree species such as *Pinus strobus*, *Populus balsamifera* and *Populus tremuloides* clustered to the right, along axis 1 in ordination space, and thus were more strongly associated with catastrophic fire.

The shade-intolerant *Corylus cornuta* and *Prunus pensylvanica* dominated the sub-canopy tree and shrub components after catastrophic fire, but were present at only very low densities after canopy gap and moderate-severity disturbances. *Rubus* spp., which are rapidly colonizing, shade-intolerant shrubs, were abundant after both moderate-severity disturbances and catastrophic fire, and absent after canopy gap disturbances. *Salix* spp. established only after catastrophic fire, while the mid-tolerant *Acer rubrum* and the high shade-tolerant *A. pensylvanicum* pooled towards the upper left in ordination space, indicating greater abundance after canopy gap disturbances. *A. spicatum* was able to successfully regenerate under all post-disturbance
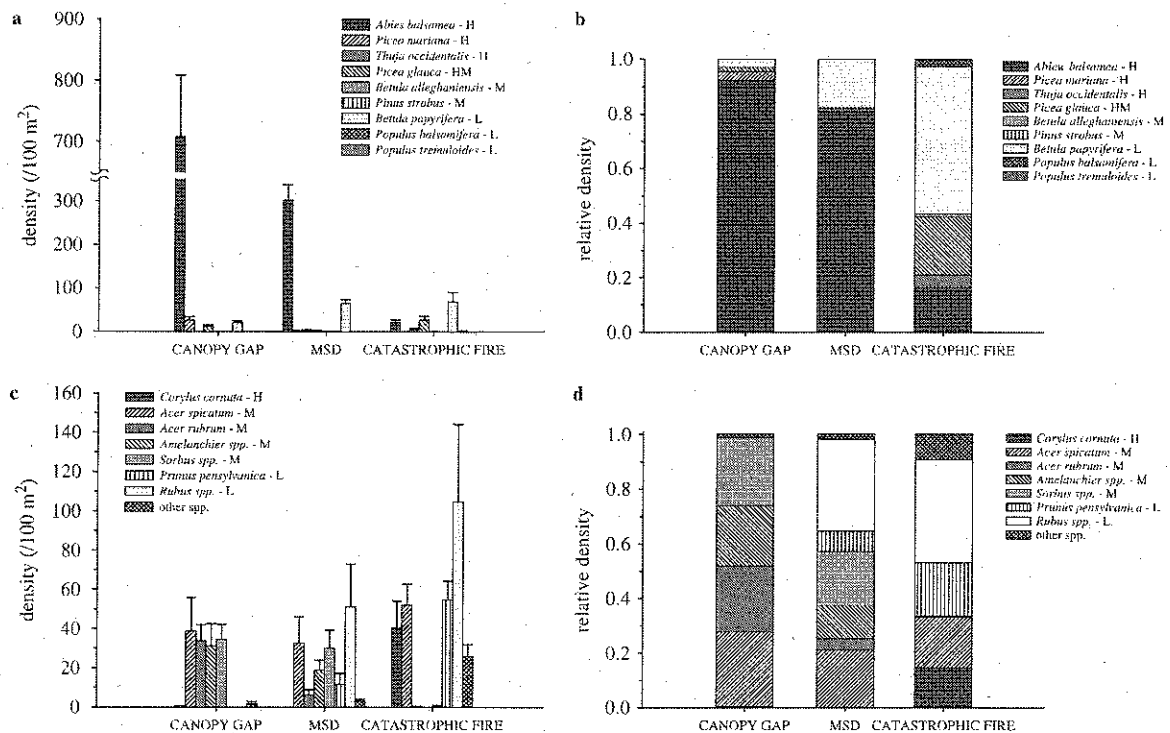
Fig. 1. (a-d) Total and relative tree and sub-canopy tree and shrub regeneration density after canopy gap disturbance, moderate-severity disturbance (MSD), and large catastrophic fire in *A. balsamea–B. papyrifera* boreal mixed-wood forests. Letters after species name indicate shade tolerance: H = high, HM = high to mid, M = mid, and L = low shade tolerance. Shade tolerance levels were derived from Humbert et al. (2007).

conditions, suggesting that its distribution is mediated by other factors more than variation in the amount of disturbance-caused mortality. *Corylus cornuta*, *Rubus* spp., and *A. spicatum* exhibited aggregated distributions, and produced dense thickets that precluded establishment of other species. *Nemopanthus mucronata*, *Sorbus* spp., and *Amelanchier* spp. pooled to the left along axis 1, but more towards moderate-severity disturbances along axis 2.

Species richness and diversity in relation to variation in disturbance-caused mortality

Twenty-two tree and shrub species were observed within the system (Table 1). Tree species richness (*R*) was lowest after moderate-severity disturbances and greatest after catastrophic fire (Table 2). Sub-canopy tree and shrub *R* and total woody plant species *R* was highest after catastrophic fire. Greater *R* after catastrophic fire relative to either canopy gap or moderate-severity disturbance is attributable to the influx of

early-successional, shade-intolerant species. Shannon's diversity index (*H'*) for canopy trees was similar among disturbance-caused mortality classes (Table 2). Sub-canopy tree and shrub *H'* and total woody plant species *H'* were lower after moderate-severity disturbances relative to either canopy gap or catastrophic fire disturbances. Tree species compositions were most similar after canopy gap and moderate-severity disturbances, while sub-canopy tree and shrub regeneration was most similar after moderate-severity disturbances and catastrophic fire disturbances. Thus, moderate-severity disturbances shared commonalities with both extremes of the disturbance-caused mortality gradient, but for different forest regeneration layers. Irrespective of the amount of disturbance-caused mortality, canopy tree regeneration was dominated by one or two species, whereas sub-canopy tree and shrub regeneration was more evenly distributed among component species (Fig. 1). Five species established exclusively after catastrophic fire, one after moderate-severity disturbances, while no tree, sub-canopy tree, or shrub species was exclusive to canopy gap disturbances (Table 1).
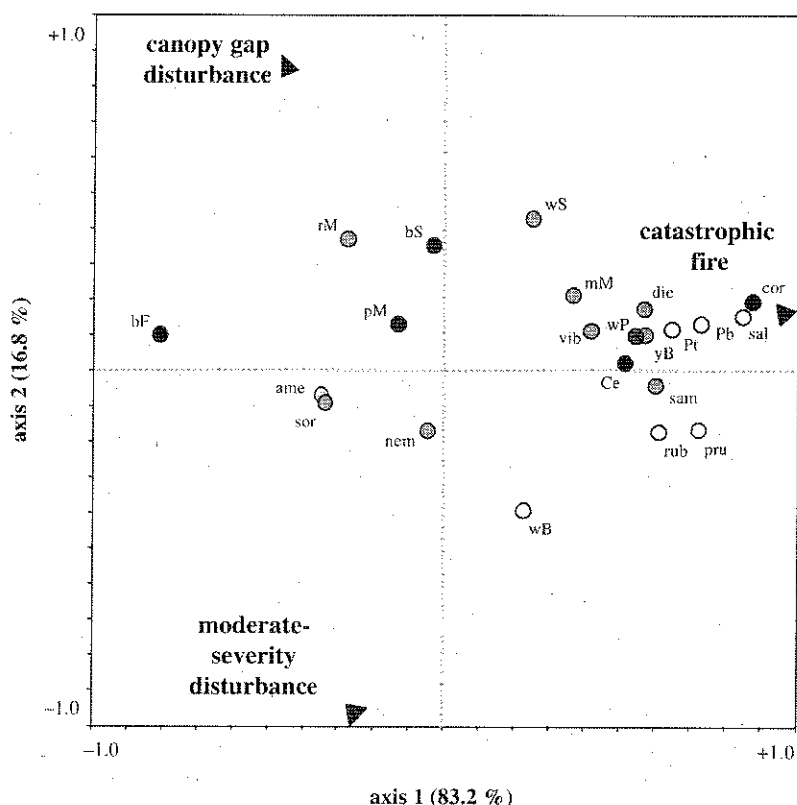
Fig. 2. Redundancy analysis (RDA) of species density in relation to variation in disturbance-caused mortality. The first two canonical axes in RDA explained 26% and 5% of the cumulative variance in the species data, respectively. Species codes are as follows: bF = *Abies balsamea*, bS = *Picea mariana*, Ce = *Thuja occidentalis*, mM = *Acer spicatum*, Pb = *Populus balsamifera*, Pt = *Populus tremuloides*, pM = *Acer pensylvanicum*, rM = *Acer rubrum*, wB = *Betula papyrifera*, wS = *Picea glauca*, wP = *Pinus strobus*, yB = *Betula alleghaniensis*, ame = *Amelanchier* spp., cor = *Corylus cornuta*, die = *Diervella lonicera*, pru = *Prunus* spp., nem = *Nemopanthus mucronata*, rub = *Rubus* spp., sal = *Salix* spp., sam = *Sambucus* spp., sor = *Sorbus* spp., and vib = *Viburnum edule*. Shade tolerance: ● high, ◕ high to mid, ◉ mid, ◎ mid to low, ○ low.

Discussion

Effects of variation in disturbance-caused mortality on regeneration abundance and diversity

Distinct regeneration patterns were observed after canopy gap, moderate-severity, and catastrophic fire disturbances. Marked changes from pre-disturbance conditions, wherein shade-tolerant conifer species dominated the tree community, only occurred after catastrophic fire. The abundance of advance regeneration facilitated cyclical regeneration patterns after canopy gap and moderate-severity disturbances, while destruction of most of the regeneration layer after catastrophic fire allowed for the establishment of more shade-intolerant species. For example, the shade-intolerant *B. papyrifera* dominated the tree community after catastrophic fire, but was only a minor component after canopy gap and moderate-

severity disturbances. *B. papyrifera* densities were similar and low after canopy gap and moderate-severity disturbances, respectively, despite large differences in the spatial extent among many of the canopy gap and moderate-severity disturbances examined here (disturbances ranged from 0.0005 to 95 ha).

Given that the moderate-severity disturbances examined in this study caused more than 75% contiguous canopy mortality, and that the spatial extent of some moderate-severity disturbances was larger than that after catastrophic fire, it would be reasonable to expect greater changes in the tree community after such disturbances (e.g., Miller 1982; Peterson 2000). Yet, despite causing major structural changes, relative tree species composition was not substantially altered from pre-disturbance conditions. This was the case irrespective of the type of moderate-severity disturbance, be it spruce budworm outbreak, windthrow, or their interaction,

Table 1. Species shade tolerance, presence/absence (±), and richness (R) estimates in relation to amount of disturbance-caused mortality for *Abies balsamea–Betula papyrifera* boreal mixed-wood stands. Shade tolerance levels were derived from Sack & Grubb (2002); Humbert et al. (2007).

Species	Shade tolerance	Canopy gap disturbance (n = 23)	Moderate-severity disturbance (n = 33)	Catastrophic fire (n = 10)
Trees				
Abies balsamea	High	+	+	+
Picea mariana	High	+	+	+
Thuja occidentalis	High	−	+	+
Picea glauca	High to mid	+	+	+
Betula alleghaniensis	Mid	−	−	+
Pinus strobus	Mid	−	−	+
Betula papyrifera	Low	+	+	+
Populus balsamifera	Low	−	−	+
Populus tremuloides	Low	−	−	+
Shrubs				
Acer pensylvanicum	High	+	+	−
Corylus cornuta	High	+	−	+
Acer rubrum	Mid	+	+	+
Acer spicatum	Mid	+	+	+
Diervella lonicera	Mid	+	−	+
Nemopanthus mucronatus	Mid	−	+	−
Sambucus spp.	Mid	−	+	+
Sorbus spp.	Mid	+	+	+
Viburnum edule	Mid	+	+	+
Amelanchier spp.	Mid to low	+	+	+
Salix spp.	Low	−	−	+
Prunus pensylvanica	Low	−	+	+
Rubus spp.	Low	−	+	+
Tree richness (R)		4	5	9
Sub-canopy tree and shrub R		8	10	11
Total R		12	15	20
Number of unique species		0	1	5

Table 2. Comparison of plot-level species richness (R) and Shannon's diversity index (H') according to disturbance-caused mortality class (n = 10). Dissimilar letters along each row indicate significant differences among classes at α = 0.05.

Richness (R)	Canopy gap disturbance	Moderate-severity disturbance	Catastrophic fire
R trees	3.9 ± 0.10 a	2.9 ± 0.23 b	4.7 ± 0.21 c
R sub-canopy trees and shrubs	1.6 ± 0.58 a	2.5 ± 0.43 a	5.4 ± 0.40 b
R total	5.5 ± 0.62 a	5.4 ± 0.52 a	10.1 ± 0.55 b
H' trees	0.58 ± 0.00 a	0.58 ± 0.0028 a	0.58 ± 0.0016 a
H' sub-canopy trees and shrubs	1.95 ± 0.001 a	1.8 ± 0.034 b	1.94 ± 0.0023 a
H' total	1.52 ± 0.0010 a	1.47 ± 0.015 b	1.53 ± 0.0015 a

and despite the presence of shade-intolerant tree species in nearby clearcut or fire-originated stands functioning as potential seed sources. So, while the spatial extent and degree of canopy tree mortality of some moderate-severity disturbances can be similar to or greater than that of catastrophic fire, severity between these disturbance types differs considerably. Much of the regeneration layer remains intact, availability of residual material is greater, and proximity to legacy trees that function as seed sources is generally closer after moderate-severity disturbance. Thus, potential for recovery to pre-disturbance conditions is greater, and the time needed for recovery is reduced relative to after catastrophic fire. Our results are consistent with those of Knee-

shaw & Bergeron (1998), Webb & Scanga (2001), and Rich et al. (2007), who found that smaller and/or less severe disturbances can hasten or maintain stand development towards late-succession conditions by favoring shade-tolerant species. Splechtna et al. (2005) observed similar general patterns, although the mechanisms involved were different, as canopy closure was also the result of lateral expansion of deciduous canopy trees.

The presence of a mostly intact regeneration layer likely had the greatest impact in retaining late-successional species dominance after both canopy gap and moderate-severity disturbances. In this forest system, *A. balsamea* and *Picea glauca* seedlings establish and persist in the understory as advance

regeneration for long periods of time until a canopy disturbance occurs (Morin & Laprise 1997). *A. balsamea* advance regeneration, in particular, already occupied much of the available growing space. Many shade-intolerant tree species in our study region that can regenerate from seed require exposed mineral soils or recently burned organic soils to establish; e.g., *Populus tremuloides, Pinus banksiana* (Zasada et al. 1992). Seed dispersal constraints (Le Page et al. 2000) and low-pre-disturbance densities of canopy tree species that can regenerate via root suckering may also have played a role (e.g., *Populus* spp.); moreover, seeds of the canopy tree species in the region do not persist in the soil seed bank for more than a few years (Frank & Safford 1970; Greene et al. 1999), suggesting that the soil seed bank had little role in tree regeneration patterns.

High densities of coarse woody debris can affect seedling establishment (Reyes & Kneeshaw 2008). Downed logs in our sites inhibited germination by physically covering potential establishment sites, and reduced light availability to the surface. Conversely, downed logs can also act as nurse sites when sufficiently decomposed (Stevens 1997; Iijima et al. 2007). However, in our study, advance regeneration had already grown over the majority of these potential regeneration sites, negating any potential benefits (such as reduced competition) that nurse sites can provide. Species regenerating from seed may thus be limited to establishing on exposed mineral soil resulting from tree uprooting after windthrow, and in areas with lower densities of advance regeneration and coarse woody debris (Reyes & Kneeshaw 2008). The importance of advance regeneration on post-disturbance dynamics has also been reported elsewhere (Leemans 1991; Ban et al. 1998; Grassi et al. 2004). Nevertheless, the deciduous component in mixed-wood stands is often maintained after moderate-severity disturbance (Bergeron 2000; Déry et al. 2000). Although *B. papyrifera* did not increase in relative abundance after moderate-severity disturbances in our study, the species maintained its importance in the canopy. Thus, moderate-severity disturbances may also act to slow successional trajectories towards late-succession conditions or to stabilize the current landscape structure over many generations (Bergeron 2000; Woods 2004; Papaik & Canham 2006).

While tree regeneration was similar after canopy gap and moderate-severity disturbances, considerable differences in the sub-canopy tree and shrub community were observed. Differences in establishment success of sub-canopy tree and shrub

species between canopy gap and moderate-severity disturbance are related to different life-history characteristics of the component species and the availability and use of specific resource requirements. Certain species such as *Prunus pensylvanica* and *Rubus* spp. were quick to respond to ephemeral resources, and could take better advantage of subtle microenvironment differences between canopy gap and moderate-severity disturbances. *Rubus* spp., in particular, are disturbance specialists that can remain dormant for many years in the seed bank, and do not require exposed mineral soils for germination (Lautenschlager 1991; Palmer et al. 2000). Further, nitrate (NO_3) pulses generally occur in forest soils 1 to 2 years after more severe disturbances (e.g., fire, soil scarification) (Truax et al. 1994), which can trigger germination of dormant *Rubus* spp. seeds (Jobidon 1993). Greater abundance of intolerant sub-canopy tree and shrub regeneration within larger gaps has been observed elsewhere in the boreal mixed-wood region (Kneeshaw & Bergeron 1998).

Species richness and diversity in relation to variation in disturbance-caused mortality

Our study supports the view that groups of species differing in important life-history characteristics exhibit different responses across a range of disturbance-caused mortality. However, for the range of natural disturbances occurring in eastern boreal mixed-woods, our results for species richness and diversity of the woody plant community did not follow Connell's intermediate disturbance hypothesis (1978). Also, in contrast to Miller (1982), large spatial differences between canopy gap and moderate-severity disturbances did not equate to significant increases in species richness or diversity. Richness and diversity estimates were, in fact, similar or lower after moderate-severity disturbances relative to both disturbance-caused mortality extremes. Our results show that the intermediate-disturbance hypothesis is not always observed when catastrophic fire is the primary disturbance. Schwilk et al. (1997) obtained comparable results after fires in Mediterranean climate shrublands, finding lowest plant diversity estimates at intermediate fire frequencies. Mackey & Currie (2001) and Sasaki et al. (2009) also show that the unimodal pattern of diversity characteristic of the intermediate-disturbance hypothesis is not always realized in other terrestrial systems.

Mean species richness estimates and Shannon's diversity index were unable to account for differences in the actual species present among the

disturbance-caused mortality classes. Distinct changes in the sub-canopy tree and shrub community occurred when transitioning from canopy gap and moderate-severity disturbances, while several species were unique to catastrophic fire. Proliferation of disturbance specialists and shade-intolerant species, along with persistence of shade-tolerant, late-successional species, resulted in higher species richness estimates after catastrophic fire. The absence of several mid-tolerant and shade-intolerant species after canopy gap disturbances suggests that some of these species would be extirpated from the system without periodic, moderate-severity or catastrophic fire disturbances. Thus, variation in disturbance-caused mortality is crucial to creating habitat diversity, allowing different species functional groups to persist across the landscape. Further, change in the vegetation community from canopy gap to the catastrophic fire range of disturbances is not a linear, continuous species replacement process. Moderate-severity disturbances have distinct attributes, and subsequently effects, on regeneration abundance and diversity. The difficulty in characterizing disturbances within the moderate-severity range is that vegetation responses have important similarities (and differences) to both disturbance-caused mortality extremes, depending on the vegetation layer examined.

Conclusions

Natural disturbances can have lasting and distinct effects on the landscape. Expected changes in global climate will have considerable effects on mortality, recruitment patterns, and disturbance regimes. While fire cycles are expected to shorten and the incidence and severity of insect disturbances is predicted to increase in much of the boreal region (Stewart et al. 1998; Volney & Fleming 2000), eastern North American boreal mixed-wood fire cycles have been lengthening (Bergeron et al. 2001; Lauzon et al. 2007). Current return interval lengths for the various disturbances in *A. balsamea–B. papyrifera* boreal mixed-wood forests is consistent with a disturbance regime characterized by relatively frequent partial events and rare catastrophic events. Given that canopy gap and moderate-severity disturbances do not appreciably change relative species composition of the canopy tree layer from pre-disturbance conditions, convergence towards late-successional forest conditions is promoted throughout the landscape. The projected increase in time intervals

between catastrophic fires may lead to reduced diversity within the system.

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