

The Relative Importance of Natural Disturbances and Local Site Factors on Woody Vegetation Regeneration Diversity across a Large, Contiguous Forest Region

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Stand-level diversity after natural disturbance can potentially differ across a large, contiguous forest region despite being dominated by the same canopy species throughout as differences in disturbance types and local site conditions can regulate species distribution. Our main objective was to examine the relative importance of natural disturbances (spruce budworm (*Choristoneura fumiferana*) outbreak, windthrow, and their interaction) and local site factors (climate, physiography, and stand structure and composition variables) on woody vegetation diversity among three, physiographically distinct locations across a large, contiguous forest region. Seventy-six *Abies balsamea*-*Betula* spp. stands affected by natural disturbance were compared and analysed using canonical ordination methods, diversity indices, and ANOVA. Different combinations of factors were important for vegetation re-establishment at each location. Differences in alpha (α), beta (β), gamma (γ), Shannon's H' , and evenness (J) diversity indices were observed among locations across the study region. Our findings indicate that while certain processes are important for maintaining canopy dominance by *Abies balsamea* and *Betula* spp. throughout the region, different combinations of factors were important for creating variation in woody species diversity among locations that resulted in greater woody species diversity at the regional scale.

Keywords: Regeneration; Natural Disturbance; Environmental Factors; Species Diversity; Eastern Boreal Mixedwood Region

Introduction

Climate determines the regional species pool (Dansereau, 1954; Neilson et al., 1992; Messaoud et al., 2007). However, woody species distribution and abundance across the landscape is largely determined by the disturbance regime (Gromtsev, 2002; Belote et al., 2009). Consequently, a distinct spatio-temporal arrangement of woody species is often observed at local scales due to variation in disturbance type, severity, and frequency across the landscape (Chen & Popadiouk, 2002; Reyes et al., 2010). Apart from natural disturbances, local site factors also play key roles in forest development, as they are capable of influencing the disturbance regime itself, and can directly affect species diversity after disturbance (Peterson, 2000; McGuire et al., 2002; Wang et al., 2006).

Different types of disturbance influence regeneration patterns in distinctive ways depending on the severity of effects on forest vegetation and stand structure, and the variation in the temporal release of newly available resources. Windthrow and spruce budworm (*Choristoneura fumiferana*) outbreak, for example, have been shown to result in alternative successional

trajectories in boreal ecosystems due to differences in the degree of soil disturbance and in the timing of tree mortality (Krasny & Whitmore, 1992; Nagel & Diaci, 2006). In the case of windthrow, this disturbance type can substantially alter canopy species dominance whereas budworm damage can simply delay or promote development towards late-succession conditions (Bergeron, 2000; Chen & Popadiouk, 2002). However, variation in forest regeneration among stands experiencing the same disturbance type can also occur because of differences in local site conditions (Turner et al., 1997; Reyes & Kneeshaw, 2008). For example, where advance regeneration is abundant, windthrow may cause only structural *versus* compositional changes in the tree canopy (Peterson, 2000; Reyes et al., 2010). Moreover, the sub-canopy tree and shrub community can display variation in responses to natural disturbances depending on light availability and level of soil disturbance; and depending on the relative speed of development and growth after disturbance, can ultimately impact the composition of the regenerating tree canopy (Gray et al., 2005; Hart & Chen, 2006). Other local site factors such as pre-disturbance stand composition, physiography, and stand structural characteristics have been shown to affect woody vegetation diversity after natural disturbance at the stand scale (Dupont et al., 1991; Osumi et al., 2003;

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Rodriguez-Garcia et al., 2011). However, it is unclear if the same factors play key roles in determining re-vegetation patterns throughout an entire forest region. Factors can differ in importance among locations across a region, operate at local or regional scales, and can work synergistically to affect species diversity (Wimberly & Spies, 2001; Hillebrand & Blenckner, 2002; Huebner & Vankat, 2003). Examining woody vegetation distribution after natural disturbances at various locations across a large, contiguous forest region dominated by the same canopy species can thus help to resolve potential contrasts by determining the different factors responsible for any observed variation across the region, for differences in responses to the same factors, or conversely, potentially link fine and broad-scale vegetation recovery patterns to a few important factors that have consistent effects on woody species diversity across the region as a whole.

The purpose of our study is to document the relative importance of natural disturbances and local site factors on woody vegetation regeneration diversity among three, physiographically distinct locations across a large, contiguous forest ecosystem dominated by the same canopy species throughout. We specifically addressed the following questions: is the canopy composition maintained after disturbance or are different successional trajectories occurring? Does the type of natural disturbance determine woody species diversity or do local site factors more strongly influence regeneration distribution? Alternatively, do natural disturbances work synergistically with local site factors in determining woody species diversity? Lastly, do different combinations of disturbances and local site factors influence woody species diversity for specific locations or can a few common factors explain species distribution across the region? We hypothesized that given the physiographical differences among locations across the region, that different combinations of factors would be responsible for woody species diversity after natural disturbance at the local level; and consequently, that if different factors influence regeneration dynamics at local scales, it is likely that species diversity will differ across the region. Thus, although woody species diversity should be the highest at the regional scale, diversity should also reflect the intra-regional differences in disturbance history and the unique local site characteristics of these forests.

Study Area

The *Abies balsamea*-*Betula* spp. boreal mixedwood zone spans east to west across southern Quebec, Canada from 46° to 50°N and 64° to 80°W (Figure 1). It encompasses 23.8 million ha and represents 18.6% of the forested land of the province (MRNQ, 2003). The physiography of the region is highly variable. The western portion is continental, and is relatively flat to rolling. Topography becomes increasingly hilly to montane towards the east, as the eastern portion of the region includes the northeastern limit of the Appalachian mountain chain that runs southwest into the United States. The eastern portion also borders the Gulf of St. Lawrence, and thus contrasts with the western portion of the region by having a maritime influence. Elevations of forested areas range from 80 to 400 m in the west, and from sea level to 900 m in the east. Surface deposits are mostly glacial till or of lacustrine origin (Robitaille & Saucier, 1998). The soil moisture regime is classified as xeric-mesic to mesic, while soil drainage ranges from imperfect to rapid.

Numerous disturbances such as fire, insect pests, and windthrow occur at varying frequency and severity in eastern boreal mixedwoods. The current return interval length for catastrophic

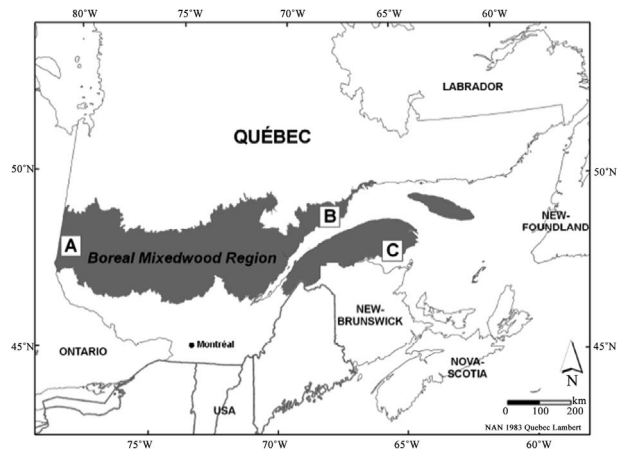


Figure 1.

Study locations within the boreal mixedwood region of Quebec, Canada. (A) continental—Abitibi-Temiskaming; (B) northern coastal—the North Shore; (C) southern coastal—the Gaspé Peninsula.

fires across the region ranges from 170 to 645 years (Bergeron et al., 2006), suggesting that less severe, but more frequent disturbances now assert greater influence on post-disturbance boreal mixedwood dynamics than in the recent past. Thus, we focused our attention on three types of non-fire disturbances that are common to boreal mixedwood forests: spruce budworm (*Choristoneura fumiferana*) outbreak, windthrow, and their interaction (nb., where a stand affected by spruce budworm outbreak is then subjected to windthrow prior to canopy recovery).

We sampled within three physiographically distinct, widely dispersed locations (between 200 and 500 km) across the boreal mixedwood region of Quebec, Canada (Figure 1). The western sites are located in the Abitibi and Temiskaming municipalities (77°30' to 79°10'W and 47°30' to 48°20'N). These sites have a flat to rolling topography and are influenced by continental climate conditions. The two eastern coastal locations both have hilly to rolling topography but differ mainly by latitude and elevation. The northern coastal sites are situated along the north shore of the St. Lawrence River, within the Haute Côte Nord and Manicouagan municipalities, and between 48°30' N and 68°00' to 69°50'W. Stands in this location are near the northern limit of the boreal mixedwood region. The southern coastal sites are situated within the southern part of the Gaspé Peninsula, along the Chaleur Bay area of the Atlantic Ocean (between 48°10' to 48°35'N and 65°45' to 66°15'W). Other climate, physiographic, and forest structure and composition characteristics are compared among geographic locations in Table 1.

Relative species composition of the forest canopy can be quite variable within this forest type. We limited sampling to stands having two of the more common relative species compositions: stands were either conifer-dominated ($\geq 75\%$ density of conifers in canopy) or mixed coniferous-deciduous (50% - 74% density of conifers in canopy) prior to disturbance. In all cases, *Abies balsamea*, *Betula papyrifera*, and *Betula alleghaniensis* dominated the forest canopy prior to disturbance, and represented at least 60% of the coniferous and deciduous components within each stand, respectively. *Picea glauca*, *Picea mariana*, and *Acer rubrum* were also abundant in some sites while *Thuja occidentalis*, *Pinus resinosa*, *Pinus strobus*, *Pinus*

Table 1.

Comparison of climate, physiographic, and forest structure and composition variables at each location using factorial ANOVA. Values in parentheses indicate ± 1 Standard Error of the mean. Unlike letters along a row indicate values are significantly different among locations ($p < 0.05$).

Variable	Location		
	Continental	Northern coastal	Southern coastal
Annual rain (mm)	691.3 (5.2) a	691.0 (7.5) a	724.3 (2.0) b
Annual snow (mm)	274.3 (6.2) a	303.4 (4.5) b	238.6 (0.6) c
Annual precipitation (mm)	965.6 (11.4) ab	988.9 (10.3) b	963.1 (1.4) a
Annual temperature (°C)	2.1 (0.1) a	2.2 (0.1) a	3.6 (0.1) b
Mean monthly temperature-summer (°C)	16.3 (0.1) a	15.3 (0.1) a	16.6 (0.1) a
Mean monthly temperature-winter (°C)	-10.4 (0.1) a	-8.8 (0.1) b	-7.3 (0.1) c
Mean windspeed (km·h ⁻¹)	12.9 (0.1) a	15.6 (0.0) b	18.7 (0.1) c
Maximum windspeed (km·h ⁻¹)	52.8 (0.7) a	75.6 (0.1) b	76.0 (0.2) b
Maximum gust speed (km·h ⁻¹) [†]	98.4	105.2	no data
Physiography			
Elevation (m)	311.2 (11.8) a	274.2 (25.4) a	421.4 (9.7) b
Slope* (%)	1.0 (0.0) a	1.2 (0.2) a	2.1 (0.1) b
Latitude (degrees)	47.3 (0.1) a	49.0 (0.1) b	48.5 (2.3) b
Longitude (degrees)	78.4 (0.1) a	68.8 (0.1) b	66.1 (2.8) c
Soil drainage [‡]	3.5 (0.2) a	3.1 (0.2) a	2.3 (0.1) b
Forest structure and composition			
Mean disturbance area (ha)	11.6 (1.6) ab	8.9 (1.7) a	13.2 (1.0) b
Snag density (ha ⁻¹)	138.2 (17.8) a	294.1 (33.3) b	499.3 (29.4) c
Course woody debris density (ha ⁻¹)	1176.4 (10.9) a	1729.1 (82.2) b	2159.9 (105.2) c
Percentage of trees uprooted	28.0 (3.5) a	31.9 (3.4) a	37.2 (1.9) a
Decay class average [‡]	11.2 (0.1) a	11.2 (0.1) a	10.4 (0.1) b
Tree regeneration density (ha ⁻¹)	126 + 907.9 (1936.6) a	36825.6 (2593.6) b	15284.5 (1525.3) a
Shrub regeneration density (ha ⁻¹)	11982.9 (2288.1) a	33,969.6 (3407.6) b	7 454.0 (732.1) a
Total regeneration density (ha ⁻¹)	24890.7 (2043.0) a	70,895.2 (3279.9) b	22 738.6 (1463.2) a
Coniferous legacy tree density (ha ⁻¹)	1.3 (.3) a	8.9 (1.2) b	0.1 (0.2) c
Deciduous legacy tree density (ha ⁻¹)	0.1 (0.03) a	2.7 (0.6) b	0.2 (0.2) a
Crown cover of coniferous legacy trees (%)	3.5 (0.8) a	3.5 (0.9) a	4.2 (1.0) a
Crown cover of deciduous legacy trees (%)	1.6 (0.7) a	1.7 (0.6) a	6.8 (1.2) b
Stand density prior to disturbance (ha ⁻¹)	926.6 (89.3) a	1474.0 (83.8) b	1718.7 (80.7) b

Note: [†]Insufficient data to include in analyses. *1: 0° to 10°, 2: >10° to 20°, 3: >20° to 30°, 4: >30° to 40°, 5: >40°; [‡]2: good, 3: moderate; 4: imperfect; [‡]See Imbeau & Desrochers (2002).

banksiana, *Larix laricina*, *Acer saccharum*, *Fraxinus americana*, *Fraxinus nigra*, *Populus balsamifera*, and *Populus tremuloides* were occasionally present.

Sampling Methods

Disturbance type, climate, and physiological data were derived from digitised aerial photos, eco-forestry maps, or

sourced from various provincial and federal government agencies (MNRQ, 2003; Environment Canada, 2004), with the exception of slope and elevation, which were determined on site using a clinometer and GPS unit, respectively. A total of 76 sites affected by spruce budworm outbreak, windthrow, or their interaction were examined: 24, 22, and 30 sites for the continental (Abitibi-Temiskaming), northern coastal (North Shore), and southern coastal (Gaspé Peninsula) locations, respectively.

Up to six 20 × 20 m quadrats were sampled within each disturbed site. We limited our sampling to mature stands (≥80 years old-verified within each site by counting annual rings of remnant trees or old stumps) having at least 0.2 ha of contiguous canopy mortality to reduce variation resulting from differences in stand age, disturbance severity, and the spatial extent of disturbance. Further, all quadrats were at least 40 m from the nearest intact forest and 30 m from the nearest logging road to avoid edge effects.

Density of tree and shrub regeneration was quantified within each quadrat for three size classes: (1) 1 to 2 m tall, (2) >2 m tall and <4 cm dbh (1.37 cm), and (3) between 4 and 8 cm dbh using a nested plot design. Different height classes were used to determine which individuals were more or less likely to be recruited into the canopy. Some species in the region such as *Abies balsamea* can produce 1000 s of regenerating seedlings per hectare, many of which remain suppressed even after canopy disturbance (Reyes & Kneeshaw, 2008). Class 1 regeneration was sampled in a 2 × 10 m area, class 2 in a 5 × 10 m area, and class 3 within the entire quadrat. Density of snags (standing dead trees >10 cm dbh) and coarse woody debris (downed trees >10 cm dbh) were determined and classified using a modified decay classification scale developed by Imbeau & Desrochers (2002). Coarse woody debris was also categorised as uprooted or snapped when possible; n.b., past research has shown that certain boreal species establish better in exposed mineral soils *versus* other substrates (Kuuluvainen & Juntunen, 1998). Thus, if more coarse woody debris is uprooted *versus* snapped, then one could expect a greater proportion of these types of species as well. Crown cover (m²) of legacy trees (mature overstory trees that survived the natural disturbance) within each quadrat, and density of deciduous and coniferous legacy trees within a 35 m radius of the quadrat centre were also determined. This was done to provide some indication of the amount of shade available to the regeneration, which can thus potentially influence what species regenerate in close proximity, and provide information on potential sources of seed rain, respectively.

Analyses

Various analyses were used to compare and contrast woody vegetation diversity after natural disturbance between the continental, northern coastal, and southern coastal locations. Comparisons of the climate, physiographic, and forest structure and composition characteristics that were quantified for each location were made using analysis of variance (ANOVA) (SPSS 10.0, 1999) followed by the Student-Newman-Keuls multiple range test when significant differences were observed (at $p < 0.05$) (Table 1).

Direct Gradient Analyses

We used a series of redundancy analyses (RDA) (van den Wollenberg, 1977) to examine the relationships between local site factors (i.e., the various disturbance types, climate, physiographic, and stand structure and composition variables) and woody vegetation species distribution for each of the three study locations. For each analysis, the forward selection option was implemented to both rank the importance of each site factor variable and to exclude redundant and non-significant variables from the model. The significance of the explanatory effect of a site factor variable was determined using a Monte Carlo permutation test (200 permutations, $p < 0.05$) prior to the addi-

tion of the next best fitting variable. CANOCO 4.0 software (ter Braak & Smilauer, 1998) was used to run the analyses. Variables were centred and standardized as the site factor variables were measured using different units.

Species Diversity Estimates

Five measures of species diversity were calculated at two spatial scales: for both the entire study region and for each of the three study locations (continental, northern coastal, southern coastal). Thus, comparisons between regional and local diversity levels, as well as among the three study locations could be made. Calculations were also made for the entire woody vegetation community and for each of the woody vegetation layers separately; i.e., canopy tree regeneration *versus* sub-canopy tree & shrub regeneration. This was done as different disturbance types can affect the understory community differently (Veblen & Ashton, 1978; Hart & Chen, 2006). Thus, diversity of the canopy tree regeneration may be influenced by the sub-canopy tree and shrub community that survived the disturbance or by sub-canopy species that can quickly establish soon after (Gray et al., 2005).

Regional level species diversity estimates were the following: alpha diversity (α) represented mean site level richness, beta diversity (β) represented differences in richness among sites across the study region; i.e., the differences in species composition among spatial units, while gamma diversity (γ) represented the total richness across the study region (Whittaker, 1960; Novotny & Weiblen, 2005). Beta diversity (Whittaker, 1960) was computed as:

$$\beta = (\gamma/\alpha) - 1 \quad (1)$$

Shannon's diversity index (Shannon & Weaver, 1949):

$$H' = -\sum p_i \ln p_i \quad (2)$$

where p_i = proportion of the total sample belonging to species i (in our case, the relative density of a species), and evenness (J):

$$J = H' / \ln \alpha \quad (3)$$

where J is an index of how relative abundances of species are distributed (Pielou, 1966), were determined for each regeneration layer for each site. Analysis of variance followed by the Student-Newman-Keuls multiple range tests were used to compare the various diversity estimates among study locations and vegetation layers ($p < 0.05$).

Species richness is partly a function of spatial scale (Palmer & White 1994). We acknowledge that differences in richness could be an artifact of sampling effort among locations. The total disturbed area examined for the continental, northern coastal, and southern coastal sites were 405.2, 505.6, and 1238.3 ha, respectively. We sampled the three locations using 35, 57, and 95 quadrats, respectively, to make sampling effort more equitable among locations. However, bias in species richness may also occur due to the unequal number of quadrats. Sample rarefaction (Krebs, 1989) was used to compute a species accumulation curve as a function of the number of quadrats examined for each location. PAST version 1.94b (Hammer et al., 2001) was used to run analysis. Results show that differences in species richness due to differences in the number of quadrats examined in each location was negligible (Figure 2). Thus, we felt that making comparisons of diversity estimates among the three locations using our sampling protocol was a valid undertaking.

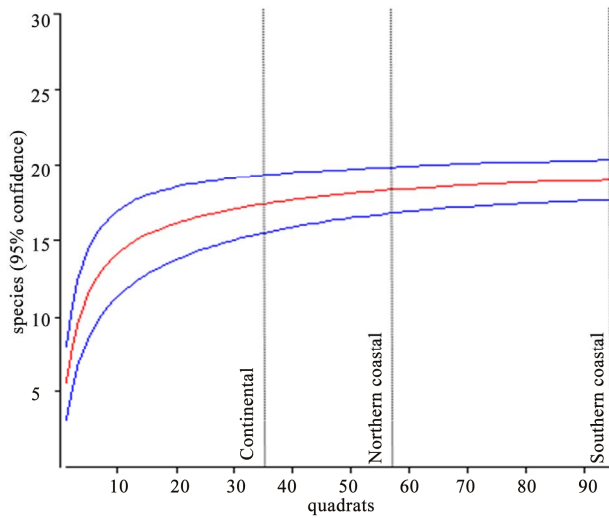


Figure 2. Sample rarefaction analysis to determine if differences in species richness estimates were associated with variation in sampling effort. A total of 35, 57, and 95 quadrats (20×20 m) were used in the continental, northern coastal, and southern coastal locations, respectively. Curves (in blue) above and below mean species values represent 95% confidence intervals.

Table 2. Canonical correlation coefficients between significant environmental variables and the first four ordination axes for redundancy analysis examining species-environment relationships for each study location ($p < 0.05$; ns indicates non-significance).

Location & Environmental Variable	Axis			
	1	2	3	4
Continental				
Windthrow	-0.70	-0.33	ns	ns
Annual rainfall (mm)	0.75	-0.39	ns	ns
Coarse woody debris density (ha^{-1})	0.27	ns	-0.66	ns
Northern coastal				
Latitude	0.57	ns	ns	ns
Elevation (m)	-0.18	ns	0.24	0.39
Annual rainfall (mm)	-0.19	0.35	ns	ns
Coarse woody debris density (ha^{-1})	ns	0.24	-0.25	0.39
Windthrow	-0.10	-0.01	-0.43	ns
Southern coastal				
Conifer-dominated stand prior to disturbance	0.54	ns	ns	ns
Coarse woody debris density (ha^{-1})	0.51	ns	-0.30	ns
Decay class	-0.29	-0.34	-0.31	ns
Spruce budworm outbreak	0.28	ns	ns	0.30
Elevation (m)	ns	-0.44	ns	ns

Results

Factors Influencing Vegetation Distribution across the Forest Region

Disturbance type was not the primary driver of species distribution patterns in all locations across the boreal mixedwood region. The different disturbance types had only a minor influence on regeneration distribution in the coastal sites, whereas windthrow produced distinctive woody vegetation distribution patterns in the continental sites (**Table 2**). There was no common group of variables that influenced regeneration distribution at all locations. Different combinations of factors strongly influenced woody vegetation regeneration at each location (**Table 2**). In decreasing order of importance, woody vegetation distribution in the continental sites was primarily driven by windthrow, annual rainfall, and coarse woody debris density. Species distribution for the northern coastal sites were most strongly associated with latitude, elevation, annual rainfall, coarse woody debris density, and windthrow, while species distribution in the southern coastal sites were associated mostly by stand composition prior to disturbance, coarse woody debris density, decay class, spruce budworm outbreak, and elevation (**Table 2, Figure 3**). Coarse woody debris density was the sole factor affecting distribution patterns in all locations, accounting for a large proportion of the variation throughout the boreal

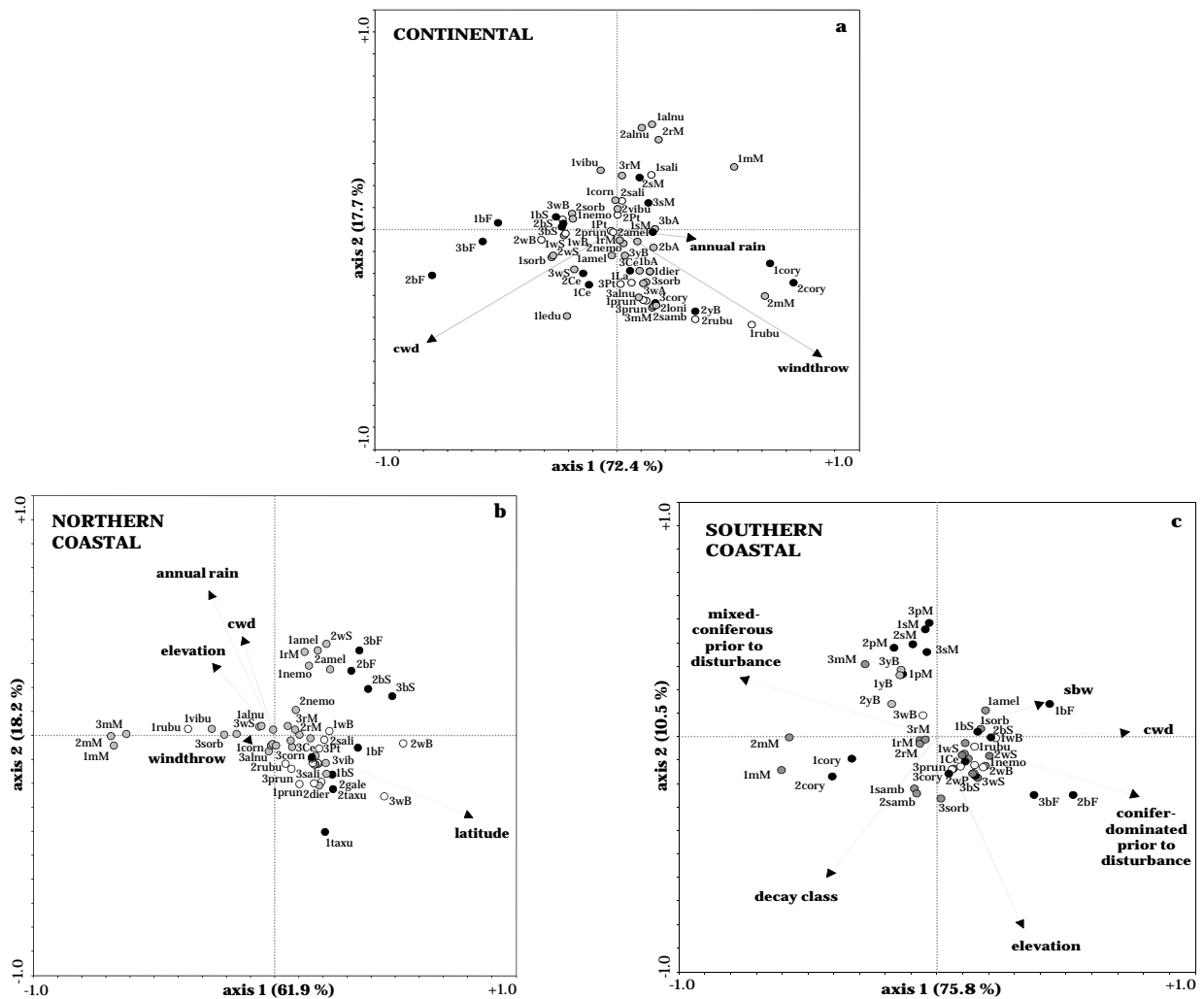


Figure 3.

Examination of woody vegetation distribution patterns for three locations within the boreal mixedwood region of Quebec, Canada in relation to disturbance type, climate, physiography, and stand structure and composition variables using Redundancy analysis (RDA). The first two canonical axes in RDA explained 27.2% and 6.6%, 15.3% and 4.5%, and 18.2% and 2.6% of the cumulative variance in the species data for the continental, northern coastal, and southern coastal sites, respectively. Length and position of vectors and points from the origin in relation to axes 1 and 2 indicate strength of relationships among variables in ordination space, where greater distances from the origin in conjunction with closer positions to either axis 1 or 2 indicate stronger associations. Only the environmental variables having significant relationships with axes 1 or 2 are shown. Some species names were removed to reduce clutter. Numbers preceding species codes indicate the following regeneration size classes: (1) 1 to 2 m tall, (2) >2 m tall and <4 cm dbh (1.37 m), (3) 4 to 8 cm dbh. Species and environmental variable codes are as follows: wA = *Fraxinus americanus*, bA = *Fraxinus nigra*, wB = *Betula papyrifera*, yB = *Betula alleghaniensis*, Ce = *Thuja occidentalis*, bF = *Abies balsamea*, La = *Larix laricina*, mM = *Acer spicatum*, pM = *Acer pensylvanicum*, rM = *Acer rubrum*, sM = *Acer saccharum*, Pt = *Populus tremuloides*, wP = *Pinus strobus*, bS = *Picea mariana*, wS = *Picea glauca*, alnu = *Alnus* spp., amel = *Amelanchier* spp., corn = *Cornus stolonifera*, cory = *Corylus cornuta*, dier = *Diervilla lonicera*, gale = *Myrica gale*, kalm = *Kalmia angustifolia*, ledu = *Ledum groenlandicum*, loni = *Lonicera* spp., nemo = *Nemopanthus mucronata*, prun = *Prunus* spp., rubu = *Rubus* spp., sali = *Salix* spp., samb = *Sambucus* spp., sorb = *Sorbus* spp., vibe = *Viburnum edule*, vibu = *Viburnum cassinoides*, taxu = *Taxus canadensis*, BF-WB = *Abies balsamea*-*Betula papyrifera* Ecozone, BF-YB = *A. balsamea*-*B. alleghaniensis* Ecozone, and cwdb = coarse woody debris. Shade tolerance: ● high, ● mid, ○ low.

mixedwood region. Further, all height classes of each species generally responded in the same manner, indicated by the clustering of intra-specific species points in the biplots (Figure 3).

Species Diversity across the Region

A total of 33 woody species were observed in the system (12 canopy trees, 21 sub-canopy tree and shrubs) (Table 3). No species were considered rare or endangered. Relative abundances of *Abies balsamea*, *Betula papyrifera*, and *Betula al-*

leghaniensis, the dominant coniferous and deciduous species in the system, were generally maintained, although the northern coastal sites had increases in the coniferous component relative to pre-disturbance conditions in mixed-coniferous stands (Figure 4). Cyclical regeneration patterns occurred in stands that were conifer-dominated prior to disturbance as *Abies balsamea*, a shade-tolerant conifer species, dominated the regeneration layer (Figure 4, Table 3). Stands that were mixed-coniferous prior to disturbance maintained their deciduous canopy tree components, while deciduous sub-canopy tree and shrub com-

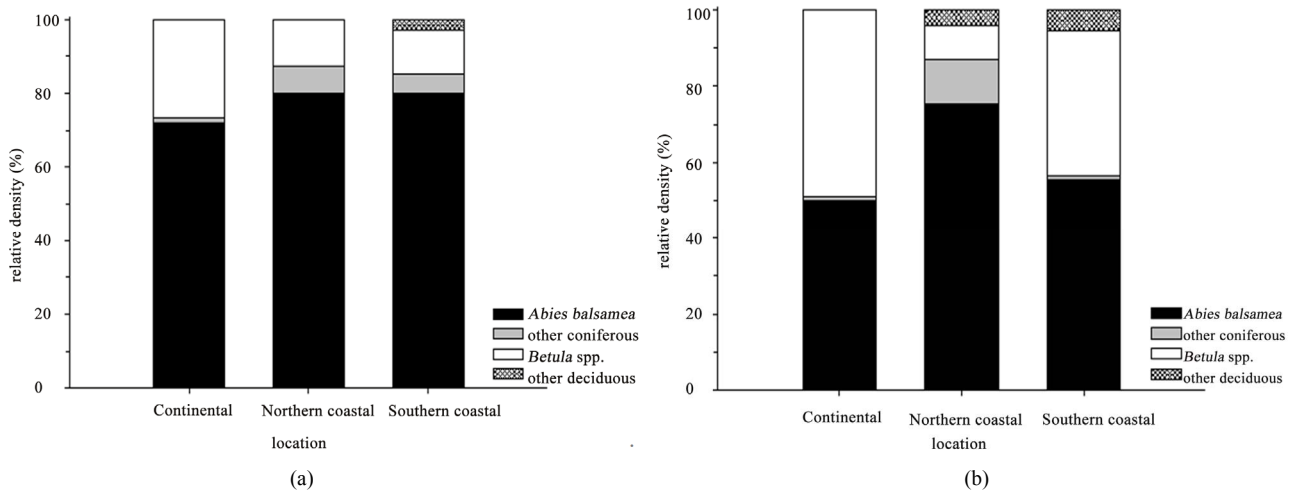


Figure 4. Relative densities of principal canopy tree species regeneration for each location within the boreal mixedwood study region for (a) conifer-dominated stands ($\geq 75\%$ conifer canopy prior to disturbance) and (b) mixed-coniferous stands (50% - 74% conifer canopy) prior to disturbance.

petitors such as *Acer spicatum* and *Corylus cornuta* were more abundant there. Shade-tolerant conifer tree species were strongly associated with high densities of coarse woody debris. However, *Betula papyrifera*, a shade-intolerant deciduous species, was able to maintain its relative abundance in stands that were conifer-dominated prior to disturbance, and was able to establish in areas with high coarse woody debris densities. Closer examination showed that most of the *Betula papyrifera* regeneration was restricted to microsites with exposed mineral soils resulting from tree uprooting (G. Reyes, personal observation).

Comparing Species Diversity among Locations

Alpha (α) diversity for canopy tree species was similar at all locations throughout the region ($p > 0.05$) (Table 4). Alpha diversity for total woody vegetation regeneration and for sub-canopy tree and shrub regeneration was higher in the northern coastal versus the southern coastal sites ($p < 0.05$) while α diversity in the continental sites was intermediate between the other two locations and did not significantly differ from either coastal location ($p > 0.05$). Beta (β) diversity for all vegetation layers was generally higher in the continental sites, indicating greater variation in species diversity among sites there. This coincided with the continental sites having the largest species pool among the three locations (n.b., 28 woody species observed Table 4), as gamma (γ) diversity was the highest there for all vegetation layers. Shannon's diversity index (H') was similar among locations for total woody vegetation and for the canopy tree layer ($p > 0.05$). Sub-canopy tree and shrub H' was greater in the northern coastal versus the southern coastal locations ($p < 0.05$). Dominance by certain canopy tree species was more prevalent in the northern versus southern coastal locations, as indicated by the lower evenness (J) estimates ($p < 0.05$). Indeed, the majority of the canopy tree regeneration in the northern coastal sites consisted of either *Abies balsamea*, *Picea mariana*, or *Betula papyrifera* (Table 3). The continental sites had intermediate J values and did not differ from either coastal location. Alpha, β , γ , and H' values were greater for the sub-canopy tree and shrub layer relative to the canopy tree regeneration within and among all geographical locations and for

across the region as a whole.

Discussion

Factors Influencing Vegetation Distribution across the Forest Region

While different factors influenced post-disturbance community composition among locations across the region, relative species compositions of the tree canopy were either maintained or were developing towards dominance by the shade-tolerant conifer, *Abies balsamea*. The likely mechanisms by which this is occurring are via the competitive advantage provided by an abundant advance regeneration layer and the protection provided by coarse woody debris.

Because the disturbances examined here did not cause extensive damage to the understory vegetation present prior to disturbance, stand composition after natural disturbance was dominated by *Abies balsamea*, a species that develops an abundant advance regeneration layer over time (Morin, 1994). The presence of advance regeneration reduced the ability of shade-intolerant deciduous species to establish after natural disturbance by limiting available growing space, light, and other resources (Morin et al., 2008).

Density of coarse woody debris was the only environmental factor significantly affecting regeneration patterns across the entire region. Its irregular spatial distribution and variation in level of decay throughout the landscape was important for the creation of stand heterogeneity, to which the various species responded. For example, shade-tolerant conifer tree species such as *Abies balsamea* and *Picea mariana* dominated areas where the density of coarse woody debris was high. Coarse woody debris was beneficial for the survival of the advance regeneration perhaps by mitigating the adverse changes in microsite conditions after disturbance by providing cover and shade (Gray & Spies, 1997; Elliott et al., 2002). Consequently, cyclical regeneration patterns (Baskerville, 1975) were observed in conifer-dominated stands. Conversely, areas where coarse woody debris densities were low or where it was absent altogether allowed for the establishment of more shade-intolerant deciduous species such as *Populus tremuloides*, *Betula*

Table 3.

Mean regeneration density (ha^{-1}) for woody species establishing within the boreal mixedwood region of Quebec, Canada. Shade tolerance: high, ● mid, ○ low.

Species	Location		
	Continental	Northern coastal	Southern coastal
Canopy trees			
<i>Abies balsamea</i> ●	2576.1	7427.8	2714.7
<i>Picea mariana</i> ●	194.3	459.8	22.5
<i>Thuja occidentalis</i> ●	22.9	1.0	0.8
<i>Acer saccharum</i> ●	21.4	-	-
<i>Picea glauca</i> ●	73.7	211.7	25.1
<i>Betula alleghaniensis</i> ●	7.3	-	183.1
<i>Pinus strobes</i> ●	-	-	2.1
<i>Fraxinus americanus</i> ●	1.4	-	-
<i>Fraxinus nigra</i> ●	8.6	-	-
<i>Larix laricina</i> ○	1.4	-	-
<i>Betula papyrifera</i> ○	268.9	1103.4	856.7
<i>Populus tremuloides</i> ○	50.3	2.8	16.2
Sub-canopy trees & shrubs			
<i>Acer pensylvanicum</i> ●	-	-	38.0
<i>Corylus cornuta</i> ●	1004.5	-	169.0
<i>Taxus canadensis</i> ●	-	1170.6	-
<i>Acer rubrum</i> ●	44.3	90.4	98.3
<i>Acer spicatum</i> ●	491.8	3011.0	884.0
<i>Alnus</i> spp. ●	437.9	525.1	-
<i>Amelanchier</i> spp. ●	21.4	686.5	204.2
<i>Cornus stolonifera</i> ●	15.7	104.4	2.1
<i>Diervilla lonicera</i> ●	1.4	58.3	-
<i>Kalmia angustifolium</i> ●	-	318.9	-
<i>Ledum groenlandicum</i> ●	5.7	26.3	-
<i>Lonicera</i> spp. ●	1.4	-	-
<i>Myrica gale</i> ●	-	31.6	-
<i>Nemopanthus mucronata</i> ●	90	30.3	3.7
<i>Sambucus</i> spp. ●	1.4	-	18.9
<i>Sorbus</i> spp. ●	197.1	641.7	348.3
<i>Viburnum cassinoides</i> ●	40.0	-	-
<i>Viburnum edule</i> ●	236.4	486.8	-
<i>Prunus</i> spp. ○	66.6	72.5	83.3
<i>Rubus</i> spp. ○	302.8	1236.8	13.7
<i>Salix</i> spp. ○	37.1	1.3	-

Table 4.

Estimates of alpha (α), beta (β), gamma (γ), Shannon's (H') and evenness (J) diversity indices according to location and regeneration layer. Testing for differences in α , H' , and J among locations for each vegetation layer was made using ANOVA. Within a column, values with post-script indicate significant differences were observed for the particular vegetation layer-where unlike letters among locations for the vegetation layer in question indicate significant differences at $p < 0.05$. Values in parentheses indicate ± 1 Standard Error of the mean.

Location & vegetation layer	Indices				
	α	β	γ	H'	J
Continental					
All woody vegetation	8.5 (0.5) ab	2.3	28	1.3 (0.1)	0.5 (0.1)
Canopy trees	3.7 (0.2)	1.9	11	0.6 (0.1)	0.5 (0.1) ab
Sub-canopy tree & shrubs	4.7 (0.4) ab	2.6	17	1.0 (0.1) ab	0.7 (0.1)
Northern coastal					
All woody vegetation	9.2 (0.5) a	1.4	22	1.4 (0.1)	0.5 (0.1)
Canopy trees	3.7 (0.2)	0.6	6	0.7 (0.1)	0.4 (0.1) a
Sub-canopy tree & shrubs	5.8 (0.4) a	1.8	16	1.1 (0.1) a	0.6 (0.1)
Southern coastal					
All woody vegetation	7.5 (0.4) b	1.5	19	1.2 (0.1)	0.5 (0.1)
Canopy trees	3.4 (0.2)	1.4	8	0.7 (0.1)	0.6 (0.1) b
Sub-canopy tree & shrubs	4.1 (0.4) b	1.7	11	0.8 (0.1) b	0.6 (0.1)
Regional					
All woody vegetation	8.3	3.0	33	1.3	0.5
Canopy trees	3.6	2.3	12	0.6	0.6
Sub-canopy tree & shrubs	4.8	3.4	21	1.0	0.6

spp., and *Acer spicatum*. Retaining a deciduous tree canopy component in areas with a high density of coarse woody debris was also observed, but was mostly restricted to microsites with exposed mineral soils resulting from tree uprooting. Uprooting occurred in approximately 1/3 of all tree mortality throughout the region, and accordingly, may be an important mechanism for maintaining the proportion of *Betula* spp. and other shade-intolerant species across the landscape.

Mixed-coniferous stands either maintained their relative coniferous-deciduous species ratios or increased in the deciduous component. However, much of this increase was related to greater densities of deciduous sub-canopy tree and shrub species. The influx of sub-canopy tree and shrub species can temporarily alter species composition ratios relative to pre-disturbance conditions and/or delay canopy development for a number of years (Hart & Chen, 2006), but will have little effect on canopy species composition once the tree canopy grows beyond a few metres in height. In fact, when considering only the tree canopy regeneration, mixed-coniferous stands generally maintained their pre-disturbance relative coniferous-deciduous species ratios or displayed increases in the conifer component.

Species Diversity across the Region

Differences in species diversity among locations was largely due greater gamma (γ) diversity in the tree canopy layer in continental sites relative to coastal sites, and to variation in the

sub-canopy tree and shrub layer γ diversity among coastal locations. The greater degree of variation in the sub-canopy and shrub component in the coastal locations suggests that these species were more sensitive to differences in local site conditions while canopy tree species had a wider range of habitat tolerances. This is shown via the lower beta (β) diversity values for canopy trees *versus* sub-canopy trees and shrubs in all locations.

Comparing regional γ diversity *versus* γ diversity at each location suggests that the continental sites were more limited by the regional species pool, whereas local processes and conditions were important limiting factors in the coastal sites. Only five of the 33 species observed throughout the region were not observed in continental sites whereas 11 and 14 species were absent in the northern and southern coastal sites, respectively. Thus, it appears that a broader depth of habitat types is available in the continental sites relative to coastal locales. This is corroborated by the highest β diversity being observed in the continental sites, followed by the northern coastal then southern coastal sites.

Previous studies have reported a β diversity-latitude gradient of decreasing values from south to north (Qian & Ricklefs, 2007; Lenoir et al., 2010). Similar patterns were observed here for the canopy tree layer and for total woody vegetation as β diversity was greatest in the continental areas (lowest latitudes) and lowest in the northern coastal locations (the highest latitudes). The sub-canopy tree & shrub layer did not follow this

pattern as β diversity was higher in the northern *versus* southern coastal sites. Further, α and γ diversity for sub-canopy tree & shrubs did not follow this latitudinal pattern along the coast either, as these diversity components were also higher in northern coastal sites. Other site-level factors, such as density of coarse woody debris may have been important in influencing regeneration distribution. Differences in β diversity among locations coincided with coarse woody debris and snag densities being lowest in the continental sites and the highest in the southern coastal sites, which would suggest greater availability of growing space in the continental areas and lowest available space in the southern coastal sites.

Conclusion

The effects of windthrow, spruce budworm, and interaction natural disturbances on local site conditions were not severe enough to alter canopy species dominance. Dominance by the main canopy species, *Abies balsamea* and *Betula* spp. was maintained throughout the region, suggesting that these species had a wider tolerance range and wider niche overlap relative to other woody species, and/or that the severity of these natural disturbances wasn't sufficient to alter succession trajectories. Moreover, differences in the importance of factors influencing responses of the woody vegetation among locations across the boreal mixedwood region reinforces the concept that species distribution is not controlled by natural disturbance alone, but that local environmental characteristics and constraints on plant biology also dictate re-establishment success. Each location across the region had different and unique site characteristics, and accordingly, species composition and abundance varied from one location to the next. Thus, while the specific disturbance types did not considerably alter canopy tree composition, as development towards old-growth, conifer-dominated conditions was maintained, these natural disturbances were important for creating a mosaic of structural legacies that promote stand heterogeneity, which can ultimately help to maintain biodiversity in the region.

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