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RESEARCH PAPER

Ecological factors explaining the location of the boundary between the mixedwood and coniferous bioclimatic zones in the boreal biome of eastern North America

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ABSTRACT

Aim Climate is often regarded as the primary control determining the location of an ecotone between two vegetation zones. However, other ecological factors may also be important, especially when the northern limit of the dominant species of a vegetation zone extends further than the limit of the zone itself. This study aimed to identify the ecological variables explaining the transition between two zones within the boreal biome in Quebec (eastern Canada): the southern mixedwood forests dominated by balsam fir (*Abies balsamea*) and white birch (*Betula papyrifera*), and the northern coniferous forests dominated by black spruce (*Picea mariana*).

Location Quebec (eastern Canada).

Methods Data from 5023 sampling plots from the ecological inventory of the Québec Ministry of Natural Resources distributed throughout the two bioclimatic zones were used in logistic regressions to determine the relationships between the presence or absence of balsam fir stands and different abiotic and biotic variables, at both stand and landscape scales.

Results The presence of balsam fir stands was negatively related to the thick organic horizons, coarse xeric deposits and low positions on the slope, whereas stands were favoured by high elevations, steep slopes and moderate drainage. These results defined the suitable conditions for the development of balsam fir stands. In the coniferous zone these suitable conditions were less abundant. Furthermore, the saturation level of suitable sites was lower, as well as the incidence of balsam fir stands in unsuitable sites (overflow). Balsam fir stands were mostly located near lakes and rivers. All significant variables at both the stand and landscape scales explained between 34 and 42% of the location of the potential northern distribution limit of the mixedwood zone.

Main conclusions Our results suggest the important role of historical factors related to post-glacial vegetation and past disturbances in determining the relative abundance of balsam fir in both zones of the boreal biome.

Keywords

Boreal biome, coniferous forest, eastern North America, ecological factors, logistic regression, mixedwood forest, northern distribution limit, scale.

INTRODUCTION

In North America, the southern limit of the continuous boreal biome, dominated by coniferous species such as black spruce (*Picea mariana* (Mill.) B.S.P.), white spruce (*Picea glauca* (Moench) Voss) and balsam fir (*Abies balsamea* (L.) Mill.), decreases in latitude from Alaska eastwards (Fowells, 1965; Burns & Honkala, 1990) and reaches its lowest latitude (*c.* 48° N) in eastern Canada, between eastern Ontario and western Quebec. Except for pockets at high elevations, this is where the boreal biome reaches its most southerly limit world-wide (Pouliot, 1998). In eastern Canada, this boreal biome is subdivided into two zones; to the south, between *c.* 48° and *c.* 49° N, lies the mixedwood, a forest dominated by balsam fir and white birch (*Betula papyrifera* Marsh.), with white spruce also abundant (Bérard, 1996). Some species reach their northern distribution

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Table 1 Ecological classification of the studied territory (according to the Québec Ministry of Natural Resources)

Domains	Zones	Ecological regions	Description	Area (km^2)
Balsam fir–white birch	Western balsam fir–white birch	5a	Abitibi lowlands	≅ 27,000
		5b	Gouin reservoir hills	≅ 16,000
		5c	Saint-Maurice highlands hills	≅ 22,100
		5d	Lake Saint-Jean hills	≅ 20,100
Black spruce–moss	Western black spruce–moss	6a	Lake Matagami lowlands	≅ 49,100
		6c	Lake Opémisca lowlands	≅ 21,600
		6e	Nestaocano lake hills	≅ 22,400

limit in the mixedwood zone, such as sugar maple (*Acer saccharum* Marsh.), yellow birch (*Betula alleghaniensis* Britton), red pine (*Pinus resinosa* Ait.), white pine (*Pinus strobus* L.) and red maple (*Acer rubrum* L.) (Bergeron *et al*., 1985; Bergeron & Gagnon, 1987; Engelmark *et al*., 2000; Tremblay *et al*., 2002). To the north lies the coniferous zone, where black spruce dominates.

Ecotones separating vegetation zones are highly sensitive to climatic conditions (Brubaker, 1986; Houle & Filion, 1993; Hogg & Schwarz, 1997; Loehle, 2000). Because these conditions vary in time and space, they can induce changes in the location of ecotones. It is generally supposed that the effects of the ongoing climate change may be more readily detected or predicted in boundary areas. While numerous studies have examined the transition between the boreal and tundra zones (Payette & Filion, 1985; Earle, 1993; Lavoie & Payette, 1994; Sirois, 1997; Luckman & Kavanagh, 2000; Pellatt *et al*., 2000; Rupp *et al*., 2000, 2001), few studies have focused on ecotones between two forested zones (Loehle, 2000).

Balsam fir and white spruce reach their northern distribution limit in the James Bay region, well above the 49th parallel, near the 54th and 56th parallels, respectively (Tremblay & Simon, 1989; Payette, 1993; Sirois *et al*., 1999). According to Richard (1993), balsam fir stands are more scattered in western than in eastern Quebec. This suggests that climate may not be the only factor determining the location of the boundary between the mixedwood and coniferous zones of the boreal biome (Bergeron *et al*., 1985; Hofgaard *et al*., 1991).

Several hypotheses could be put forward to explain the location of the boundary between the mixedwood and coniferous zones. For instance, a northwards reduction in the abundance of suitable sites for balsam fir could explain the transition (Bakusis & Hansen, 1965; Bergeron & Dubuc, 1989). If so, the location of the boundary may be a result of changes in edaphic conditions such as soil fertility or pH. Since the decomposition of organic matter is often reduced at low soil temperatures during the growing season, increased accumulation of organic matter and possibly soil acidification could prevent the establishment of balsam fir in the coniferous zone, as this species is intolerant of low pH levels (Fowells, 1965; Béland & Bergeron, 1993; Paré & Bergeron, 1996). A colder climate and the accumulation of organic matter may favour bryophytes, particularly *Sphagnum* species, and further limit the establishment of balsam fir in humid sites. Black spruce promotes conditions unsuitable to balsam fir by influencing soil microclimatic conditions, i.e. decrease of soil temperature and, at the landscape scale, competitively hampers the expansion of balsam fir in otherwise suitable sites (McCune & Allen, 1985).

Major disturbances such as fires or outbreaks of phytophagous insects may also be responsible for the increasing rarity of balsam fir stands towards the north. Indeed, in the coniferous zone, high-severity disturbances are common and greatly influence vegetation structure and species abundance, and this varies with the severity, frequency and extent of the disturbance (Bergeron *et al*., 1985; Bergeron & Gagnon, 1987). For example, large, severe fires can promote the abundance of species with aerial seed banks such as jack pine (*Pinus banksiana* Lamb.) and black spruce, which are adapted to this type of disturbance, but can be detrimental to species such as balsam fir, white spruce and eastern white cedar (*Thuja occidentalis* L.). Moreover, mature and over-mature balsam fir stands are strongly affected by the spruce budworm (*Choristoneura fumiferana* Clemens); in some cases, this insect can cause nearly complete mortality (MacLean, 1980, 1984; Bergeron *et al*., 1995). Higher balsam fir mortality in northern, almost pure stands, as compared to more southerly stands with a higher percentage of deciduous trees, may also partially explain the northwards disappearance of balsam fir in the black spruce-dominated coniferous zone (Bergeron *et al*., 1995; Cappuccino *et al*., 1998).

The abundance of likely alternative but not mutually exclusive hypotheses illustrates the difficulty in identifying which ecological factors determine the location of the boundary between the mixedwood and coniferous zones. In this context, we ask the following questions: why does the mixedwood zone reach its northern limit around the 49th parallel and why is it replaced by the black spruce-dominated coniferous zone to the north? Our objective is to analyse the ecological factors that could explain the distribution of balsam fir-dominated stands at the stand and landscape scales and examine two hypotheses regarding the northern limit of the mixedwood zone. Our first hypothesis (H1) is that a lack of suitable sites in the coniferous zone is responsible for the northwards decrease in the abundance of balsam fir stands and their replacement by black spruce stands (Gu *et al*., 2002). Our second hypothesis (H2) is that, at the landscape scale, balsam fir cannot spread easily to all suitable sites in the coniferous zone because post-disturbance recolonization problems are increasingly frequent northwards and because of the increasing presence of the dominant black spruce, which is more competitive.

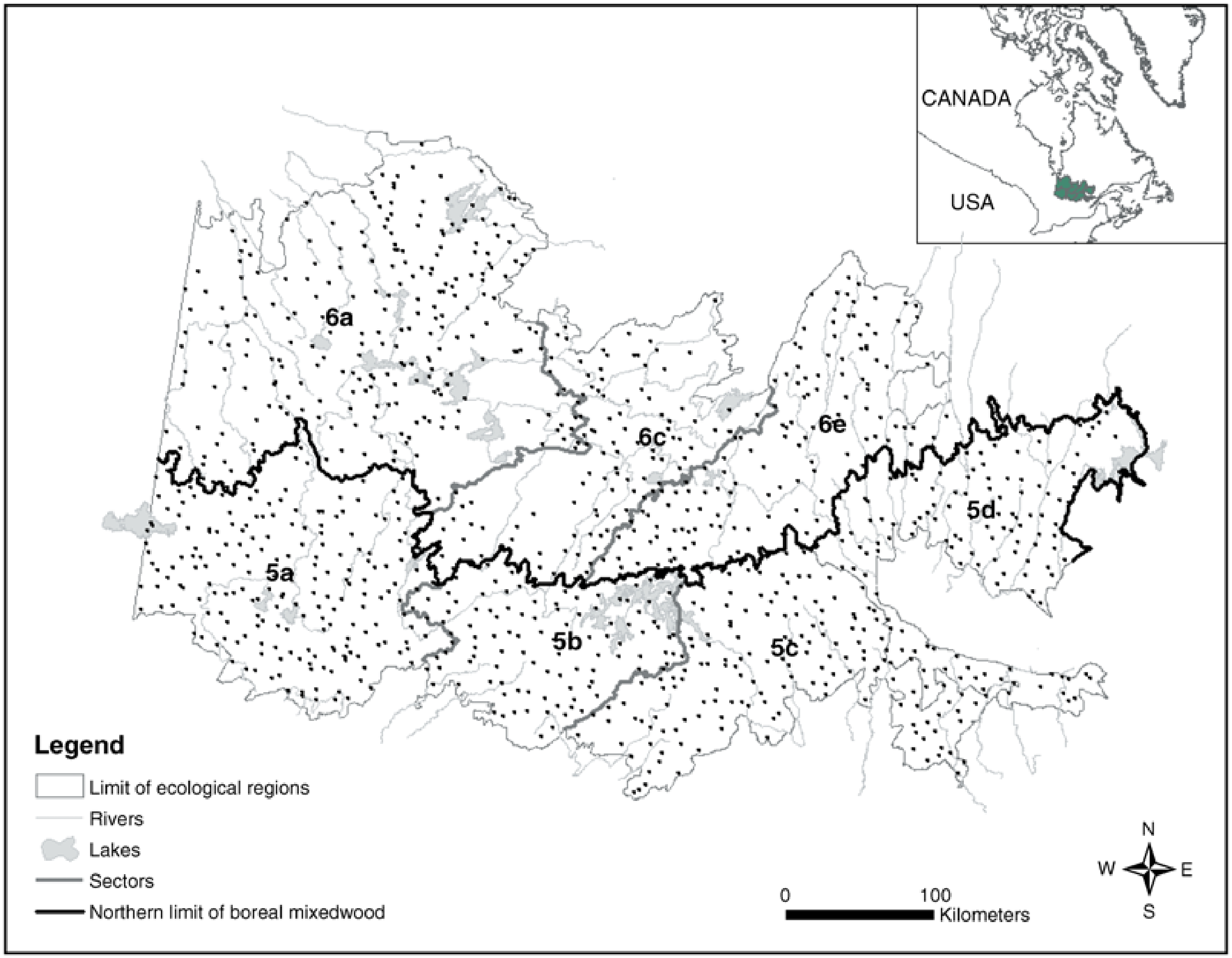

Figure 1 Distribution of the Québec Ministry of Natural Resources temporary sampling plots in the study area (the bold black line indicates the limit between the mixedwood and coniferous subdomains).

METHODS

Study area

The study area is located in Quebec (eastern Canada), between 48° and 51° N and between 70°30′ and 79° W (Fig. 1). The mixedwood zone is represented by the western balsam fir–white birch bioclimatic subdomain, whereas the coniferous zone corresponds to the western black spruce–feathermoss bioclimatic subdomain (Robitaille & Saucier, 1998; Table 1). In the ecological classification system of forested zones of Quebec, bioclimatic subdomains are characterized by their late successional tree species, resulting from the equilibrium between climate and vegetation on mesic sites (Robitaille & Saucier, 1998). The mixedwood and coniferous zones differ in important climatic variables (Table 2).

We focused on several ecological regions on both sides of the boundary between the mixedwood (regions 5a–d) and coniferous (regions 6a, c, e) zones (Fig. 1). The western sector (5a and 6a) is generally flat and rich in clayey surficial deposits (Abitibi lowlands), has many lakes and bogs, and is interspersed with knolls, eskers and a few isolated hills. These hills are often rocky or covered with till. The ecological regions in the central sector (5b and 6c) have a more broken topography than in the western sector, as well as many large lakes and till-rich plateaus. To the east, regions 5c, 5d and 6e have an even more accentuated topography, fewer lakes, rocky or till-covered hilltops and organic deposits in depressions.

Table 2 Selected climatic variables for the western bioclimatic zones

	Balsam fir–white birch	Black spruce–moss
Average annual temperature (°C)	0–1	−2.5–0
Length of the growing season (days ≥ 5 °C)	150–160	120–155
Average annual precipitation (mm)	800–1200	700–1000
Percentage of precipitation falling as snow	40–45	25–50

Sampling design

We used raw sampling plot data from the ecological inventory of the Québec Ministry of Natural Resources (MRNQ). Each sampling plot contained detailed information on topography, soils, surficial deposits and canopy and understorey composition. These plots were distributed along 1–1.5-km transects that each contained five to six sampling plots. Plot density was one plot every 25 km^2 in the mixedwood zone, and one plot every 30–50 km^2 in the coniferous zone. A total of 5023 plots were used to characterize the study area. Plots were located in forests that had not been disturbed by large-scale logging activities.

Ecological factors

We examined several ecological factors grouped according to whether they were permanent, i.e. they described abiotic or edaphic conditions at the stand or landscape scale, or dynamic, i.e. they described forest composition at the landscape scale. Because different ecological factors are relevant at different scales, we used a hierarchical approach and proceeded from the stand up to the landscape scale. This approach allowed us to control for local effects and for their interactions with other factors at the landscape scale. We characterized the landscape scale by using the relative abundance of stand types and surficial deposits of ecological districts, a finer unit of ecological classification than the ecological region, with a mean area of 259 km^2 (Robitaille & Saucier, 1998). Ecological regions 5a, 5b, 5c and 5d contained, respectively, 72, 71, 85 and 60 ecological districts. Regions 6a, 6c and 6e contained, respectively, 97, 57 and 54 districts. To control for topographic and elevation gradients that increased from the west (Abitibi lowlands) to the east (where the Canadian Shield emerges), we subdivided each bioclimatic zone into three sectors: West (regions 5a and 6a), Centre (regions 5b and 6c) and East (regions 5c, 5d and 6e) (Fig. 1).

Stand classification according to succession

In the MRNQ plots, the abundance of tree species is recorded as percentage cover in three vertical layers (canopy, shrub and regeneration). We used these percentages for balsam fir, white spruce and black spruce to estimate succession towards either a balsam fir-dominated or black spruce-dominated stand. Percentage cover of white spruce, a species often associated with balsam fir, was added to that of balsam fir to characterize balsam fir stands. The cover classes were: ≥ 81% A; 61–80% B; 41–60% C; 26–40% D; 6–25% E; 1–5% F; sporadic species ≤ 1% + (Saucier *et al.*, 1994). We used the median values of these classes to calculate the respective proportions of balsam fir (balsam fir + white spruce) and black spruce in the coniferous component of the stands. A threshold of 60% black spruce was used to classify sites evolving towards black spruce dominance. This threshold was established according to the competitive ability and shade tolerance of the two species; balsam fir is generally more competitive and shade tolerant than black spruce under similar growing conditions (Bakusis & Hansen, 1965; Burns & Honkala, 1990). Therefore, when the proportion of balsam fir was greater than or equal to 40% of the coniferous component, the site was considered to be evolving towards balsam fir dominance. We excluded from the analyses any disturbed sites, sites with less than 20% balsam fir or spruce in canopy or regeneration layers, and jack pine sites.

Statistical analyses

Logistic regressions were carried out by first including the stand-scale variables, then the landscape-scale variables, allowing for the control of the influence of stand factors before including the landscape factors. Statistical analysis was done by using Wald chi-square tests in a hierarchical framework.

To address H1, 'the lack of suitable sites in the coniferous zone is responsible for the replacement of balsam fir stands by black spruce stands', we used stepwise logistic regressions to identify the factors associated with the development of balsam fir (coded 1) vs. black spruce (coded 0) stands. Stand-scale factors (Table 3) were included first. Each factor entered in the model took into account the intercorrelation among independent factors by working with the residuals of the previously entered factors. We retained the model residuals to later analyse their relationships with landscape factors. Qualitative variables at the stand scale, such as surficial deposit or slope, were coded into dummy variables.

The inclusion of surficial deposit (relative abundance at the landscape level) in the model was interpreted as indicative of the importance of the availability of suitable sites for the probability of occurrence of balsam fir stands where suitable conditions are present (H2: 'increasing post-disturbance recolonization problems northwards'; Table 4). Moreover, the addition of factors describing the relative abundance of stand types within the forest mosaic was interpreted as a landscape effect contributing to lowered risk of recolonization failure because of the occurrence of seed trees near the disturbed sites (H2).

We produced a table with the analysis results to describe the suitable sites per bioclimatic zone, at the stand and landscape scales. This table allowed quantification of the abundance of suitable sites in the mixedwood vs. coniferous zones. In this way, we were also able to quantify the abundance of suitable sites at the scale of the ecological region (Fig. 2). Using the model's predictive ability, we delineated the suitable sites for balsam fir stands by taking into account all of the explanatory parameters that were significant at the stand scale. By doing this, it was

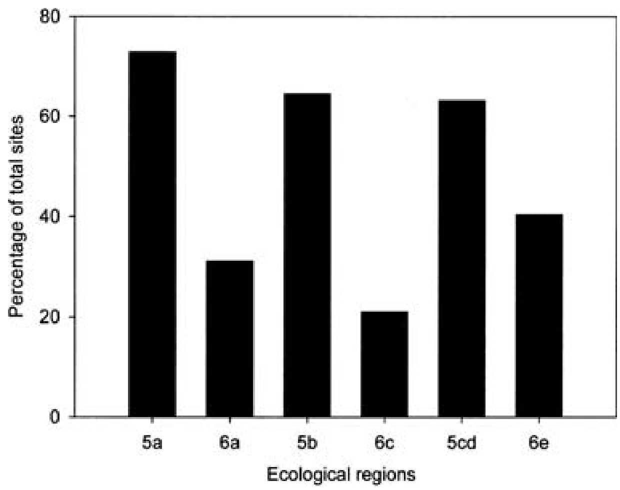

Figure 2 Percentage of the sampling plots suitable for balsam fir stands in each ecological region.

Table 3 Stand scale factors considered in this study

Factor	Value
Aspect	North, north-east, east, south-east, south, south-west, west, north-west, null
Position on the slope	Low, middle, high
Slope	Percentage
Altitude	Metres above sea level
Type of organic horizon*	Mull (MU), moder (MD), mor (MR), organic soil (OS), peat (TO)
Organic horizon thickness	Centimetres
Texture of the B horizon	Fine (FB), medium (MB), coarse (GB)
Deposit type	Fine subhydric (FS), mesic middle (MM), mesic (GM), organic soil (OH), bedrock (R)
Gravel	Percentage
Drainage (classes)	00–19 (well); 20–39 (moderate); ≥ 40 (imperfect and poor)

*These types are accorded to the level of organic matter decomposition: mull, well decomposed; moder, moderate; mor, low; organic soil, thickness of organic matter is ≥ 40 cm; peat, presence of stagnant water permanently near the surface of soil.

Table 4 Landscape scale factors significant in this study

		Value
Physical parameters	Relief	Dominance of Lowland (LL), hillside (HS), hills (H), high hills (HH) in each ecological district
	Elevation range	The length of the slope in metres
	A_FS	Area of fine subhydric deposit (%)
	A_MM	Area of middle mesic deposit (%)
	A_GM	Area of coarse mesic deposit (%)
	A_OH	Area of organic deposit (%)
	A_WATER	Area of water (%)
	Nb lakes/100km^2	Number of lakes per 100 km^2
Forest cover parameters (%)	WBF	White birch stands with fir
	WBR	White birch stands with conifers
	SF	Black spruce stands with fir
	F	Pure fir stands
	SS	Pure black spruce stands
	JP	Pure jack pine stands

possible to classify suitable and unsuitable sites for balsam fir stands and determine the occupation rate of suitable sites at the scale of ecological regions. The relative availability of suitable sites was calculated for each zone, as well as the real occupation rate. The occupation rate provided information on the saturation of potential habitats by balsam fir stands according to ecological regions.

Ecological profiles were built to illustrate the relationship between the presence or absence of balsam fir stands and the variables identified by the logistic regression. Any deviations exceeding 20% of the expected value were statistically significant at the $\alpha = 0.05$ level (Fig. 3; Legendre & Legendre, 1998).

RESULTS

Many factors were significantly associated with the presence of balsam fir stands (Table 5). The chi-square values indicate the relative importance of each variable in explaining balsam fir presence. At each step of the regression, the cumulative R^2 increased with each additional explanatory variable being entered. For all sectors, most of the variation is explained by stand-scale factors. However, the addition of landscape-scale factors was significant in all cases, with the saturated models explaining 34% (West sector), 42% (Centre sector) and 41% (East sector) of the variation.

Stand scale

Irrespective of the sector, there was a significant relationship between the presence of balsam fir stands and the thickness of the organic horizon, the drainage and the slope (Table 5). Balsam fir stands were frequently encountered on sites with a thin layer of organic matter, moderate to strong slopes (11–20%; > 20%), and moderate drainage (20–39; Fig. 3). This preference for mesic sites was more accentuated in the coniferous than in the mixedwood zone.

Table 5 Results of logistic regressions between the presence/absence of balsam fir stands and the environmental variables at the stand and landscape scales, for each sector. The number of plots is 1986, 1142 and 1894 for the West, Centre and East sectors, respectively, in both zones

Sector	Scale		Variable	Relationship	Chi-square	*P*	R^2
West	Stand		Organic horizon thickness	–	179.82	< 0.001	0.2386
			Altitude	+	61.08	< 0.001	
			Drainage	–/+*	45.79	< 0.001	
			Slope	+	31.54	< 0.001	
			MD	+	14.65	0.001	
			MB	+	10.10	0.002	
	Landscape	Permanent	A_OH	–	49.02	< 0.001	0.2922
			Nb lakes/100 km^2	+	37.21	< 0.001	
			A_FS	–	22.80	< 0.001	
		Dynamic	WBR	+	64.43	< 0.001	0.3352
			SF	+	18.42	< 0.001	
Centre	Stand		Altitude	+	167.80	< 0.001	0.3574
			Drainage	–/+	56.19	< 0.001	
			Slope	+	52.92	< 0.001	
			Organic horizon thickness	–	31.89	< 0.001	
			GM	–	10.91	0.01	
	Landscape	Permanent	A_OH	–	38.32	< 0.001	0.4025
			A_MM	+	11.49	0.001	
		Dynamic	WBF	+	33.97	< 0.001	0.4210
East	Stand		Slope	+	146.05	< 0.001	0.2817
			OH	–	53.69	< 0.001	
			Low	–	40.64	< 0.001	
			Organic horizon thickness	–	37.68	< 0.001	
			Drainage	–/+	25.57	0.001	
			MD	+	12.69	0.004	
			GM	–	12.33	0.004	
	Landscape	Permanent	Elevation range	+	84.99	< 0.001	0.3544
			HH	–	38.17	< 0.001	
			Al_min	–	19.11	< 0.001	
		Dynamic	JP	–	51.30	< 0.001	0.4065
			SS	–	50.83	< 0.001	
			F	+	14.41	0.001	
			WBR	+	10.30	0.001	

*The relationship was positive with moderate and negative with good and imperfect drainage.

The presence of balsam fir stands showed a significant positive relationship with altitude in the West and Centre sectors, with moder humus in the West and East sectors, and with slope position in the East sector. Significant negative relationships were found with coarse mesic deposits in the West sector, and with organic deposits in the East sector.

Landscape scale

The occurrence of balsam fir stands showed a significantly negative relationship with the relative area covered by organic deposits (A_OH) in the West and Centre sectors, and with accentuated topography in the East sector (Table 5). Significant positive relationships were found between the occurrence of balsam fir stands and the number of lakes per 100 km^2 and the relative area of fine subhydric deposits (A_FSH) (West sector), the relative area of medium mesic deposits (A_MM) (Centre sector), and elevation (East sector).

Ecological districts with a high abundance of mixed stands dominated by white birch, a mixture of balsam fir and black spruce, or pure balsam fir stands showed significant positive relationships with the presence of balsam fir stands. Conversely, districts characterized by a high abundance of jack pine stands and pure black spruce stands had significant negative relationships with balsam fir stands. Balsam fir depends on its residual seed trees to recolonize the post-disturbed sites, therefore it will have a greater chance of colonizing a site in a landscape dominated by balsam fir stands than a site in a landscape dominated by black spruce and jack pine stands.

Regional variation in occupation of sites suitable for balsam fir stands

In general, sites potentially suitable for balsam fir stands proved rarer in the coniferous than in the mixedwood zone (Fig. 2).

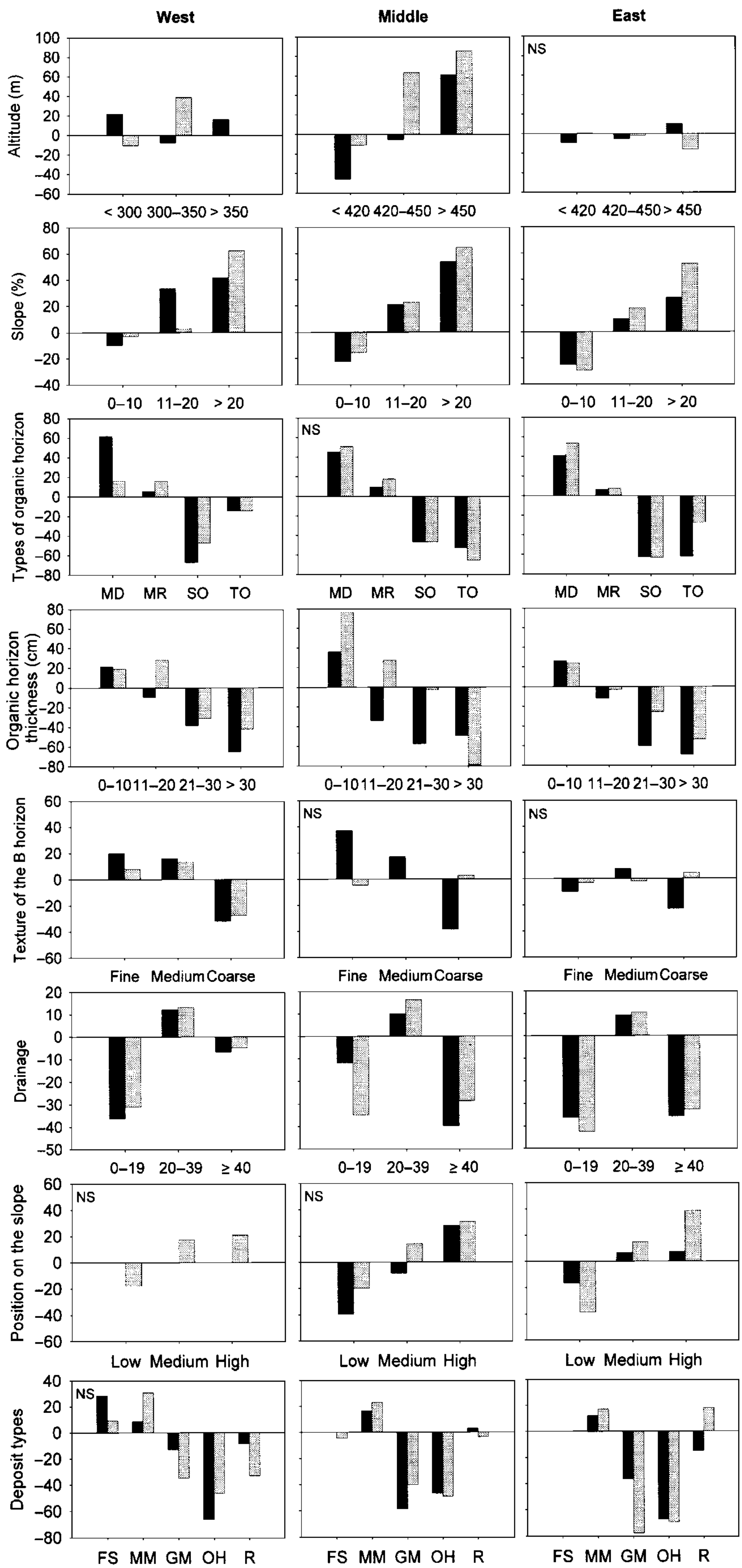

Figure 3 Ecological profiles of balsam fir stands in the mixedwood (black bars) and coniferous (grey bars) zones. The *y*-axis of these profiles represents the ratio of the difference between the observed (Obs) and expected (Exp) values divided by the observed values [(Obs – Exp)/Obs; Legendre and Legendre, 1998]. Positive and negative ratios indicate that balsam fir stands are found more or less often than expected in sites presenting a particular value of a variable (N.S., not significant for the sector). The units of measurement are given in Table 3.

Region 6c had the lowest number of potentially suitable sites (21.03%) of all the ecological regions studied. The difference between the two bioclimatic zones was lower in the East sector than in the other two sectors.

Balsam fir stands occupied fewer of the suitable sites in the coniferous than in the mixedwood zone (Fig. 4a,b), irrespective of sector or spatial scale. At the landscape scale, there is an increasing gradient of saturation of suitable sites from west to east for both bioclimatic zones.

Our ability to predict the occupation of suitable sites increased from the local to landscape scale. This increase suggests an important role for landscape factors, particularly the contribution of forest cover, in explaining the occurrence of balsam fir stands.

In several cases, balsam fir stands occupied unsuitable sites (Fig. 4). In the mixedwood zone, this 'overflow' of balsam fir stands was more common in the East than in the West sector. Balsam fir stands were more common, and thus had a more random distribution, in the mixedwood zone. In the coniferous zone these stands appear more closely associated with the presence of lakes and rivers (Fig. 4a). This phenomenon was readily apparent in the West and Centre sectors, whereas balsam fir stands were more randomly distributed in the East sector.

Unoccupied but suitable sites were more abundant in the coniferous than in the mixedwood zone. These unoccupied suitable sites were more abundant in the West sector and were associated with lakes and rivers (Fig. 4b). This was also the case in region 6c, but suitable sites were less frequent in region 6e. Balsam fir stands on unsuitable sites were more abundant and randomly distributed in the mixedwood zone (Fig. 4c).

DISCUSSION

Effects of stand-scale factors

Overall, the factors that were significantly associated with stands evolving towards dominance of balsam fir illustrate the ecological niche of balsam fir, the dominant species, and white spruce, its companion species. Balsam fir stands were usually restricted to mesic and mesotrophic sites, because balsam fir and white spruce are typically uncompetitive with species that are more tolerant of extreme conditions, such as black spruce, in sites that are too dry or too wet (Carleton & Maycock, 1978; Bergeron & Bouchard, 1984; Gauthier *et al*., 2000).

On mesic sites, early successional stands dominated by trembling aspen and white birch generally evolve into balsam fir stands. On the other hand, dry or humid sites are generally recolonized by jack pine or black spruce after disturbance, evolving into black spruce stands (Bergeron & Dubuc, 1989; Gauthier *et al*., 2000; Lesieur *et al*., 2002; Harper *et al*., 2003). Balsam fir stands therefore tend to be replaced by black spruce stands at the extremes of the environmental gradient, on dry and coarse deposits as well as on humid organic deposits.

Whereas the clay deposits found in the south-western part of the study area constitute mesic habitats that are likely to support balsam fir dominance (Bergeron & Bouchard, 1984), the same deposits are often covered with organic matter in the north (Brumelis & Carleton, 1988; Boudreault *et al*., 2002), therefore favouring black spruce over balsam fir (Gauthier *et al*., 2000; Harper *et al*., 2003). In fact, Brumelis and Carleton (1988) showed that where forest harvesting disturbs the organic layer, black spruce stands can evolve towards trembling aspen and white birch stands that may in turn eventually develop into balsam fir stands.

The northwards decrease of available mesic sites in the West sector (Fig. 3) — due to weak slopes, low elevations and imperfect drainage (see Appendix S1 in Supplementary Material) — partially explains the increasing lack of mixedwood forests, whose successional endpoint is the balsam fir stand (Bergeron *et al*., 2004). However, our logistic regression models explain only part of the variation. Many local habitats suitable for balsam fir stands are occupied by black spruce stands, or the reverse. Both stand types can also be found growing on the same local site conditions.

Climate can partly explain the absence of mesic sites in the coniferous zone by its effect on the limiting factors mentioned above. We found a positive correlation between elevation and balsam fir stands; conditions will be more humid and colder in depressions than on hilltops. Such differences can segregate plant communities according to their tolerance to these habitat types. For example, in the ecotone between the boreal and deciduous forests, sugar maple stands tend to occur on hilltops whereas balsam fir stands are located in depressions (Bergeron *et al*., 1985; Brumelis & Carleton, 1988; Cogbill & White, 1991; Barras & Kellman, 1998; Bigras & Colombo, 2001; Goldblum & Rigg, 2002). Another example comes from the tree line in Alaska, where white spruce is invading upland sites following improving climatic conditions, but not bottomland sites (Hobbie & Chapin, 1998). Lowland soils in the same region are more susceptible to frost than the uplands, and permafrost is more extensive and permanent in the lowlands (Viereck *et al*., 1993).

We therefore expect an inversion of vegetation levels, with balsam fir stands on hilltops and black spruce stands in depressions (Robitaille & Saucier, 1998). Low temperatures slow the decomposition of organic matter and promote its accumulation and acidification, thus limiting the establishment of balsam fir stands (Harper *et al*., 2003). Our first hypothesis, that the lack of ecological sites suitable for balsam fir stands in the north is responsible for the transition between the mixedwood and coniferous zones, is verified, as is the inability of balsam fir stands to saturate these sites. However, this hypothesis cannot by itself explain the entirety of the observed pattern.

Effects of landscape factors

When considered at the landscape scale, the factors significantly associated with balsam fir stands are a reflection of the spatial dynamics of tree populations and their presence as seed sources. These factors can therefore promote the expansion (positive relationship) or regression (negative relationship) of balsam fir stands (see Appendix S2 in Supplementary Material). In other words, the ecological districts with a high abundance of a factor that promotes balsam fir stands have greater saturation of their

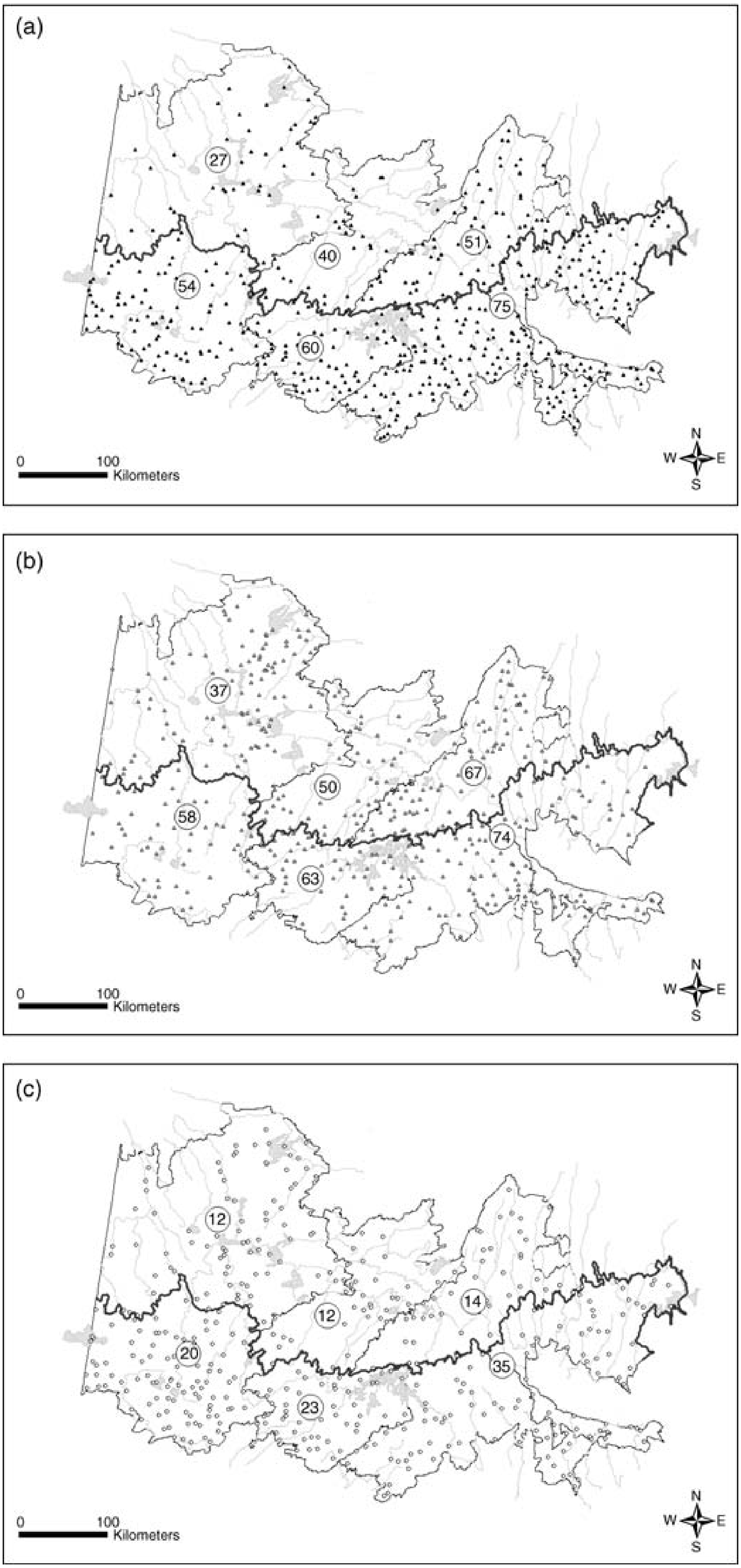

Figure 4 Distribution of suitable sites with (a) presence and (b) absence of balsam fir stands. (c) Overflow of balsam fir stands. Numbers indicate the saturation rate of balsam fir stands (in percentage of total suitable sites) at the (a) stand and (b) landscape scales, and in cases of overflow in unsuitable sites at (c) the landscape scale for each ecological region.

suitable sites. This saturation depends on a sufficient number of balsam fir trees across the landscape, i.e. large source populations that are sufficiently well distributed to maximize the potential invasion of suitable sites (Fig. 4). Indeed, balsam fir is limited in its capacity to recolonize sites after forest fires for two main reasons: (1) recolonization occurs exclusively from seed trees that escaped fire (refuge populations) and (2) its seeds are relatively heavy for a conifer and cannot disperse over long distances (Galipeau *et al.*, 1997; Bergeron *et al.*, 2004). It is only during mast years that seed dispersal is assured outside of balsam fir populations (Zarnovican & Laberge, 1997). This phenomenon seems more crucial in the coniferous zone where mast years occur more rarely than in the mixedwood zone (Y.M. *et al.,* unpublished data). It is therefore not surprising to observe clustering of balsam fir stands, especially where mesic sites are more abundant.

Rugged topography can play an important role in the extent and severity of forest fires. A more pronounced topography and the presence of lakes can limit fire expansion and thus provide a greater number of areas protected from fire (Hély *et al.*, 2000; Kafka *et al.*, 2001; Bergeron *et al.*, 2004; Lefort *et al.*, 2004) from which balsam fir can reinvade disturbed sites. The distribution of balsam fir stands in the coniferous zone (Fig. 4) clearly illustrates their association with water courses that act as firebreaks. The abundance of deciduous species can also decrease fire severity (Hély *et al.*, 2000) and thus may contribute to the presence of balsam fir. Bergeron *et al.* (2004) showed that fires are larger and possibly more severe in the coniferous zone, where the topography is flatter, than in the mixedwood zone. Large fires and the absence of deciduous trees may contribute to the decrease in balsam fir stands to the north.

Historical factors

Our logistic regression models indicate that all the significant factors only explain 34–42% of the variation in the distribution of balsam fir stands. The remaining variation is unexplained and may be related to historical factors (see McCune & Allen, 1985). Site history, whether at the local or the landscape scale, can partially explain the spatial and temporal dynamics of balsam fir stands and their inability to saturate some mesic sites — an inability that is more frequent in the coniferous than in the mixedwood zone.

Two historical phenomena can potentially account for the lack of habitat saturation: (1) initial site colonization and (2) accidental elimination and replacement over the years. According to Richard (1993), black spruce was the first tree species to invade after the retreat of glaciers and pro-glacial lake Barlow-Ojibway in Abitibi-Témiscamingue between 7200 and 8900 years ago (Richard, 1980). Balsam fir migrated afterwards, followed by other species adapted to warmer climate that benefited from an improvement in climate (higher temperature and precipitation) that caused longer fire cycles. According to palynological studies of past vegetation, black spruce has always been dominant in the coniferous zone whereas balsam fir always dominated the mixedwood zone (Richard, 1980, 1993; Liu, 1990; Carcaillet *et al.*, 2001). Since black spruce arrived first and rapidly became dominant in the north, it may have had a competitive advantage over balsam fir.

If balsam fir had a higher saturation rate in the past, its regression, and thus decline in habitat saturation, may have occurred in a gradual manner as fire eliminated populations. Indeed, conditions favourable to balsam fir started to deteriorate around 2600 year BP as climate became colder and drier, conditions leading to increased fire frequencies (Carcaillet *et al.*, 2001). This deterioration caused the southward retreat of several species, such as white pine, eastern white cedar and red pine, and their replacement by jack pine (Richard, 1980; Liu, 1990); it also constrained these species to specific ecological conditions, such as lake shores (Bergeron & Gagnon, 1987; Bergeron *et al.*, 1997).

At the landscape level, it seems that this deterioration in environmental conditions produced a decline in species diversity (i.e. reduced deciduous trees in both bioclimatic zones) that may have been more important in the coniferous zone (Carcaillet *et al.*, 2006). Balsam fir stands, lacking the protection against large fires provided by deciduous trees, gradually became rarer in the coniferous zone. Black spruce, better adapted to these new environmental conditions and freed from competition, was able to invade sites that could have been suitable for balsam fir.

It is therefore probable that balsam fir stands located in mesic sites, although rarer in the coniferous zone, were gradually replaced by black spruce at local and landscape scales (Larocque *et al.*, 2003; Carcaillet *et al.,* 2006). Sites suitable for balsam fir stands, but where balsam fir is now absent, probably contained balsam fir stands during the interglacial maximum around 6000 year BP. The balsam fir stands currently present in the coniferous zone may be the remnants of a formerly more abundant population (Fig. 4c; Liu, 1990). Therefore all these outcomes showed that these population refugia are unable to saturate suitable sites, which agrees with our second hypothesis.

CONCLUSION

This study aimed to explain the ecological factors responsible for the ecotone location between mixedwood and coniferous bioclimatic zones. At the local scale, suitable sites were less abundant in the coniferous zone, which partly explained the rarity of balsam fir stands. At the landscape scale, the abundance of suitable sites and forest composition promoted the occupation level of balsam fir on suitable sites. These landscape conditions were also less abundant in the coniferous zone, which therefore explained the failure of balsam fir stands to reinvade suitable sites.

In the coniferous zone, especially in the western sector, balsam fir stands tend to be more common both on suitable and unsuitable sites, in the vicinity of fire breaks such as rivers and lakes. This suggests that in the past, balsam fir stands were probably more abundant in the coniferous zone, but were gradually extracted and replaced by black spruce following the deterioration of climatic conditions and an increase in fire activity observed since the last 2500 years (Carcaillet *et al.*, 2006).

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SUPPLEMENTARY MATERIAL

The following Supplementary Material is available for this article.

Appendix S1 Stand-scale factors significantly associated with the presence of balsam fir stands in the mixedwood and coniferous zones.

Appendix S2 Landscape-scale factors significantly associated with the presence of balsam fir stands in the mixedwood and coniferous zones.

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