

Complexity of Regeneration Dynamic at the Ecocline between Mixedwood and Coniferous Domains of the Southernmost Boreal Zone in Eastern North America

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Abstract

To explain the ecocline between the southern mixedwood and the northern coniferous bioclimatic domains dominated, respectively, by balsam fir (*Abies balsamea* (L.) Mill.) and black spruce (*Picea mariana* (Mill.) B.S.P.), 59 field sites and 7010 sample plots (from the Quebec Ministry of Forests, Wildlife, and Parks), with no major disturbances, were selected throughout the two bioclimatic domains. Regeneration (seedlings and saplings), mortality (difference between seedlings and saplings) of balsam fir, and black spruce (saplings) were examined, accounting for parental trees, main soil type (clay and till), summer growing degree-days above 5° C (GDD_5), and total summer precipitation (May–August; PP_MA). Balsam fir regeneration was more depended on parental trees and soil type than black spruce. Balsam fir mortality was related to seedling competition, species composition of the canopy, and the soil type. GDD_5 and marginally PP_MA were beneficial and detrimental for respectively balsam fir and black spruce regeneration. The ecocline mixedwood/coniferous bioclimatic domains was attributed to a northward gradual decrease of balsam fir regeneration and increase of its mortality, due to cooler temperatures, shorter growing seasons, and decrease of the parental trees. However, balsam fir persists above this ecocline, where parental trees populations and good establishment substrates occur.

Keywords: balsam fir, black spruce, natural regeneration, mortality, ecological conditions, climate change

1. Introduction

In North America, the southern limit of the continuous boreal zone decreases in latitude from Alaska eastward [1, 2] and reaches its southernmost (*circa* 48°N) in

eastern Canada, between eastern Ontario and western Quebec. At this point, this is where the boreal zone reaches its most southerly limit worldwide, except for pockets at high elevations [3]. In Quebec, the area is composed of two bioclimatic domains that are characterized by different late-successional species in mesic sites: the southern balsam fir—paper birch (*Betula papyrifera* Marsh.) bioclimatic domain (hereafter, referred to as mixedwood forest) with some species reaching their northern distribution limit, 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.) [4, 5], and the northern black spruce—feather moss bioclimatic domain (hereafter, referred to as coniferous forest [6]. Trembling aspen (*Populus tremuloides* Michx.), paper birch, and jack pine (*Pinus banksiana* Lamb.) are abundant immediately after fire in both bioclimatic domains.

The ecocline between the mixedwood and coniferous bioclimatic domains occurs at *circa* 49°N, which represents the shift in dominance for the two species instead of their range limit. Indeed, black spruce extends farther south into the temperate forest zone, where it reaches its southern limit at *circa* 40°N [7], while balsam fir reaches its northern limit at 54°N [8].

Balsam fir and black spruce have contrasting ecological traits. In fact, balsam fir is more shade-tolerant but less cold-tolerant than black spruce. Furthermore, balsam fir does not have seed bank, while black spruce cones containing seed remain in the canopy for several years [9]. In addition, balsam fir is less resistant to fire than black spruce given that the former has a thinner bark [10]. Therefore, extreme fire is not conducive to the regeneration of balsam fir, and the availability of seeds depends to a large extent on the living parental trees in protected areas from fire. Moreover, balsam fir is less adapted to saturated soil water conditions compared with black spruce [11].

Regeneration dynamics are closely dependent on seed availability and recruitment potential, which may be limited by many factors [12, 13]. Tree seedlings, the first stage of regeneration, are specially dependent on seed source (parental trees) and soil substrates that are suitable for their establishment [14]. Since their root systems are shallower and less extensively developed, seedlings may be unable to explore and exploit soil resources compared with later regeneration stages, which make them particularly sensitive or susceptible to spatiotemporal variability in microenvironments and the variability of regeneration niches [15].

Climate is well known to directly and indirectly limit regeneration dynamics [16, 17]. As a direct effect, low temperatures and diminished precipitations can reduce seedling survival in northern Holarctic forests [18, 19]. As indirect effects, low temperature reduces the organic matter decomposition (low soil fertility) and soil evaporation (water surplus and paludification), unsuitable substrates for establishment of many species [20]. In addition, forest fires also influence regeneration, depending upon the species' fire tolerance [21].

At the leading woody species range expansion, regeneration becomes more temperature-limited as latitude and elevation increase, thereby decreasing seedling abundance due to lower seed inputs and higher mortality that prevents them from establishing further northward [22]. Yet, fewer studies have been conducted at the transition between abutting, closed-canopy forest ecosystems [23]. In North America, some studies on tree regeneration dynamics [23, 24] have been conducted at the ecocline between the boreal and temperate zones that lies further to the south. The former is dominated by balsam fir, while the latter is dominated by sugar maple. These studies showed that although balsam fir did not reach its tailing range [2], regeneration is better adapted to colder climate, yet it is limited by sugar maple

litter thickness. In contrast, sugar maple is limited at its leading range by soil acidity and cold temperature.

The objective of the study is to determine if the location of the ecocline between the mixedwood and coniferous bioclimatic domains is explained by the contrast regeneration dynamic between the two dominant tree species. We expect a decrease of balsam fir regeneration and increase of its mortality in the coniferous bioclimatic domain compared with mixedwood domain, due to unfavorable climate and substrate conditions. What makes this study unique is that it is conducted not only between two forested areas, but also at the shift between two species dominance. In addition, we verify to what extent the maintenance of balsam fir and black populations is linked with parental trees and regeneration potential driven by climate and site conditions. This chapter was derived from the two projects conducted by Messaoud *et al.* [25, 26].

2. Study design

2.1 Survey area

The area was located in western Quebec (Canada) and is a part of the Quebec and Ontario Clay Belt, formed by lacustrine sediments left by the former proglacial lake Barlow-Ojibway ([27]; **Figure 1**). The altitude ranges from 300 and 400 m asl, with low hills scattered in a flat landscape. The area has a continental climate, with cold winters and warm summers. Yet, climate differs between the two bioclimatic domains (**Table 1**).

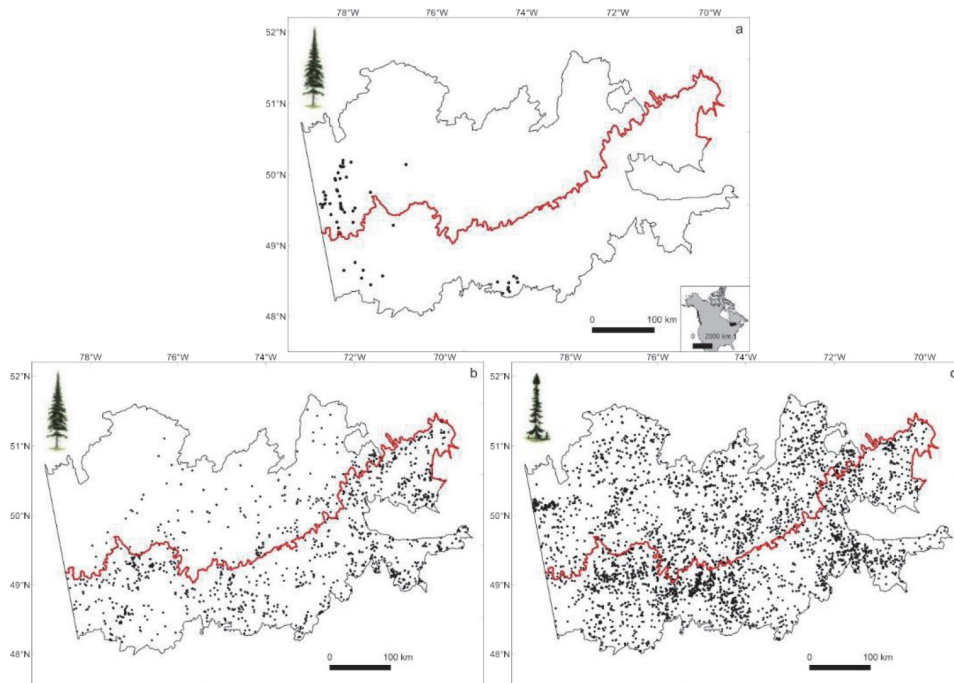


Figure 1.
 Study area showing the field sites (a) and sample plots for balsam fir (b) and black spruce (c) stands that were established for the collection of forest inventory data by Ministry of forest, fauna, and parks of Quebec (MFFPQ). The bold red line that runs from east to west depicts the boundary between the southern mixedwood and northern coniferous bioclimatic domains in western Quebec (after [6, 25, 26]).

	Bioclimatic domains	
	Mixedwood	Coniferous
Mean annual temperature (°C)	0–1	-2.5 to 0
Length of the growing season (days $\geq 5^{\circ}\text{C}$)	150–160	120–155
Total annual precipitation (mm)	800–1200	700–1000
Percentage of precipitation falling as snow	40–45	25–50

Table 1.
Climatic variables for the western bioclimatic domains.

2.2 Sampling design

2.2.1 Field design

Fifty-nine closed-stand sites were selected along a latitudinal gradient throughout the ecocline between the mixedwood and coniferous domains (**Figure 1a**). These sites are located on public land, easily accessible from nearby roads, with no major disturbance, had a moderate moisture regime [28], and the surface deposits consist of either clay or till.

In each site, a transect was established perpendicular to the nearby road, where five circular plots (40 m^2) were randomly selected independently from each other. Within each plot, balsam fir dynamics were surveyed by counting the number of seedlings (diameter at breast height, DBH $< 2\text{ cm}$), saplings (DBH between 2 and 9 cm inclusively), and mature trees ($\geq 10\text{ cm}$ DBH). DBH of the mature trees was measured. The data from all five plots in each site were combined to compute an average number of seedlings, saplings, and mature trees to account for plot variability. These data were subjected to a basic negative exponential model, which may properly reflect the depletion of balsam fir populations over a very short period of time, for example, from seedlings to saplings [29]. This model assumes a consistent balsam fir mortality rate for different age classes at a given site. As a result, we computed the difference between seedling and sapling numbers, which were also reported as percentages, to assess absolute mortality between two age classes in each site.

2.2.2 Inventory design

A total of 7010 sample plots (400 m^2 each) characterized by closed-stand and no major disturbance were provided by the Quebec Ministry of Forest, Wildlife, and Parks (MFFFPQ) and used to test the natural regeneration of balsam fir and black spruce in the mixedwood and coniferous domains (**Figure 1b** and **c**; [30]). Balsam fir was more common in the mixedwood bioclimatic domain than black spruce, which was more common in the coniferous ones. Within each sample plot, balsam fir and black spruce saplings ($2\text{ cm} \leq \text{DBH} < 10\text{ cm}$) were counted and measured including all mature trees, irrespectively for species (DBH $\geq 10\text{ cm}$) and downloaded from the database, as well as with latitude, longitude, elevation, and soil type (clay or till, which are the dominant parent materials in both forests). The basal area (m^2/ha) of mature trees in each plot was estimated and then converted to a percentage of total mature trees. To classify the evolution of the sites toward black spruce or balsam fir, a threshold was used as follows: when the proportion is 60% or more of black spruce, the site is considered to be developing toward black spruce dominance. Whereas when the proportion of balsam fir was $\geq 40\%$ of the coniferous component, the site is considered to be developing toward balsam fir

dominance. This threshold was set based on the competitive ability and shade tolerance of the two species; under similar condition, balsam fir is generally more competitive and more shade-tolerant than black spruce [2, 10]. In addition, disturbed sites and sites with <20% balsam fir or spruce in the canopy and jack pine sites were excluded from the analyses [11].

2.3 Climate

Geographic locations (latitude, longitude, and elevation) of each sample plot or site were used to extract climate variables using the BIOSIM11 modeling software (<https://cfs.nrcan.gc.ca/projects/133>). Climate variables concerned cumulative growing degree-days >5°C (GDD_5) and total summer precipitation (May to August, PP_MA, mm). The GDD_5 threshold is the temperature at which plant growth begins. The influence of climate on regeneration was determined using averages of climatic parameters corresponding to climate normals for the years 1981–2010 [31].

2.4 Statistical analyses

A MIXED procedure of SAS software (V 9.1, SAS Institute Inc., Cary, N.C., USA) was used to estimate the parameters of Eqs. (1) and (2), adjusted to field and inventory data, respectively:

$$Y_{ij} = \beta_0 + \beta_1 BD_{ij} + \beta_2 P_{ij} + \beta_3 S_{ij} + \beta_4 G_{P-ij} + \beta_5 G_{T-ij} + \beta_6 G_{S-ij} + \beta_7 BD_{ij} S_{ij} + \beta_8 BD_{ij} G_{P-ij} + \beta_9 BD_{ij} S_{ij} G_{P-ij} + \varepsilon_{ij} \quad (1)$$

where Y is the dependent variable indicating the germination or mortality rate (in percent) for bioclimatic domain i and site j . BD indicates the bioclimatic domain, P is the sample plot, S is the soil type, G_P is the parental tree basal area ($\text{m}^2 \text{ha}^{-1}$), G_S is the other tree species basal area ($\text{m}^2 \text{ha}^{-1}$), and ε_{ij} ($\varepsilon_{ij} \sim N(0, \sigma^2)$) is a normally distributed error term. The influence of soil on regeneration or mortality between bioclimatic domains was represented by the interaction between bioclimatic domain and soil type. The influence of parental tree basal area on regeneration or mortality was represented by the interaction between BD and G_P . For deduction purposes, the bioclimatic domain was considered as a random variable. To consider for distinction in total basal area that could differentially influence the regeneration or mortality, G_T was included in the model as a covariate. Climate influences on regeneration were evaluated employing a different model including GDD_5 and PP_MA, together with their interaction with the bioclimatic domain. All comparisons were conducted using t tests with significant difference being declared at $p < 0.05$.

$$Y_{ijk} = \beta_0 + \beta_1 BD_i + \beta_2 P_{ij} + \beta_3 SP_i + \beta_4 S_{ijk} + \beta_5 S_BA_{ijk} + \beta_6 T_BA_{ijk} + \beta_7 BD_{ijk} S_BA_{ijk} + \beta_8 F_i S_{ijk} T_BA_{ijk} + \varepsilon_{ijk} \quad (2)$$

where Y is the response variable indicating the sapling number for the i th bioclimatic domain, j th sample plot and the k th species. The explained fixed effect variables are BD for the bioclimatic domain, P for sample plot, SP for species, S for soil type, and S_BA for parental tree basal area. To consider for total basal area of a given sample plot, affecting somehow regeneration, total sample plot basal area (T_BA) was included as a covariate. To evaluate how regeneration was affected by a combination of numerous site factors, we also included in the model interactions between bioclimatic domain, soil type, and parental trees or total basal area. The model

intercept is β_0 , while β_1 – β_7 are the parameters to be estimated for the explained fixed effects and their interactions. The error term, ε_{ijk} , was expected to be normally distributed ($\varepsilon_{ijk} \sim N(0, \sigma^2)$). Before analyses, and to meet the assumption of homoskedasticity of the residuals, sapling number and basal area were subjected to natural logarithmic transformation. The main categorical influences as bioclimatic domain, species, and soil type were evaluated using the PDIFF option of the LSMEANS statement. The interaction factors including categorical and continuous variables were evaluated by contrast analyses using the ESTIMATE statement. Altogether, an influence was considered significant for $p < 0.05$ based on t-tests of the fixed effects. To test the influence of climate on regeneration, relationships between regeneration and GDD_5 and PP_MA were achieved using correlation analyses.

For a given species, an index that was named “anomaly of sapling abundance” (A_{SA}) was assessed at the sample plot scale, as the difference between plot sapling abundance (SA_P) and mean sapling abundance of the total study area (SA_M). Subsequently, A_{SA} was plotted against the percentage basal area of parental trees (S_{BA}) to calculate a threshold of percent parental tree basal area from which a species maintains itself within the overall mean of the total study area (same value as the mean) or “overflows” (above this mean). A comparative method was carried out at the level of bioclimatic domain and another one controlling for both bioclimatic domains and soil type, using Eq. (3):

$$\begin{cases} A_{SA} = a + bS_{BA} \\ SA_P = SA_M S_{BA} = \text{mean threshold} \\ SA_P SA_M S_{BA} = \text{overflow} \end{cases} \quad (3)$$

In Eq. (3), the coefficients a and b are derived from a regression analysis. Prior to analyses, we tested the possible multicollinearity between the explaining variables. The results showed that for both data sources, the Pearson correlation values between different explaining variables were mostly below 0.600 or not significant ($\alpha < 0.05$; **Table A1**).

3. Results and discussion

3.1 Seedling dynamic

Balsam fir seedlings abundance was positively and strongly linked with parental tree basal area regardless for the soil type (**Figure 2a**), indicating the importance of the seed source of its parental trees, which agrees with a previous study [24]. As well, the proximity of parental trees appears to be crucial for effective regeneration, suggesting that the large size of balsam fir seed decreases their dispersal capacity [10, 32]. Furthermore, for a similar parental tree basal area, balsam fir regeneration was higher in the mixedwood than in the coniferous domain. Controlling for the soil type, balsam fir showed overall significantly higher regeneration on till than on clay soils ($p = 0.022$; **Figure 2a**). In the mixedwood bioclimatic domain, there was no evidence of the soil type effect on the regeneration. In contrast, a significantly higher regeneration was observed on till compared with clay soils in coniferous bioclimatic domain ($p < 0.001$). On till soils, basal area of other tree species had no effect on balsam fir regeneration, while it decreased and increased balsam fir regeneration in the mixedwood and coniferous bioclimatic domains, respectively ($p = 0.016$; **Figure 2b**), indicating a less suitability for balsam fir regeneration. Clay soils exhibit low temperatures and high water-holding capacity, slowing the organic matter decomposition, which leads to lower nutrient availability [33].

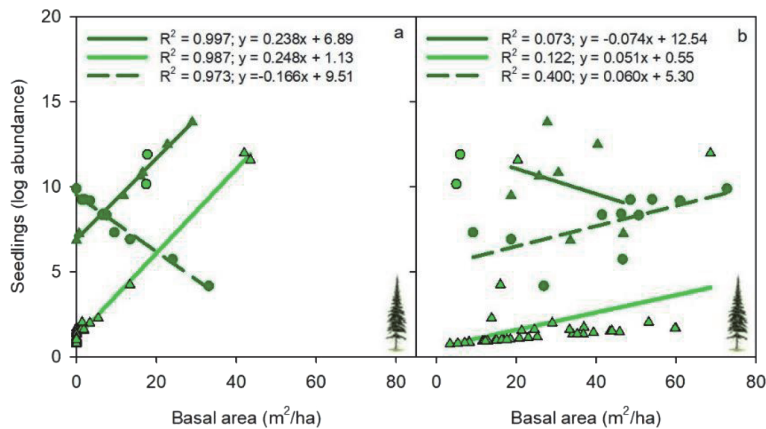


Figure 2.

Abundance of balsam fir seedlings (normal log of the number of seedlings per hectare (log abundance)) with basal area ($\text{m}^2 \text{ha}^{-1}$) of (a) parental trees and (b) other tree species according to bioclimatic domain and soil type. The dark green triangles and solid lines represent clay soils, while the dark green circles and dashed lines indicate till soils in the mixedwood bioclimatic domain. The light green triangles and solid lines indicate clay soils, while the light green circles indicate till soils in the coniferous domain [25].

The anomaly of balsam fir seedling abundance, representing the deviation from the mean of the total seedling abundance of the study area, was significant and positive in both bioclimatic domains except on clay soil in coniferous bioclimatic domain, where it was negative (**Figure 3**). Messaoud *et al.* [9] found in the same region a higher balsam fir reproductive capacity in the mixedwood than in the

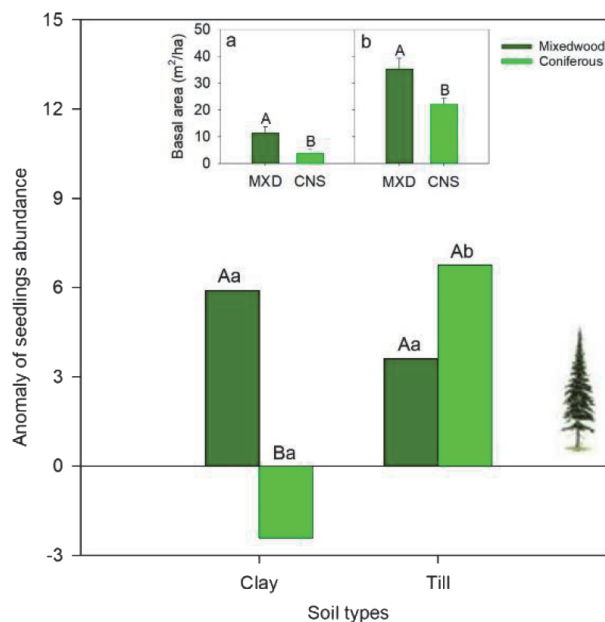


Figure 3.

Anomaly of balsam fir seedling abundance (normal log of the number of seedlings per hectare) according to bioclimatic domain and soil type. An anomaly represents a deviation from the mean of the total seedling abundance of the study area (positive = overflow, and negative = lower seedlings than the average). Inset panels indicate the basal area ($\text{m}^2 \text{ha}^{-1}$) between the two bioclimatic domains (MXD, mixedwood; CNS, coniferous) for (a) parental trees of balsam fir and (b) other tree species. The letters at the top of the histograms indicate nonsignificant (same letters) or significant (different letters) differences between the mixedwood and coniferous bioclimatic domains. The lowercase letters show the comparison between till and clay soils within each bioclimatic domain (modified from [25]).

coniferous domains. For a similar balsam fir basal area, there are more seed trees involved in the regeneration in the mixedwood than in the coniferous domains. However, we found a highest positive value on till soil in coniferous bioclimatic domain and secondly on clay soil in mixedwood bioclimatic domain. Controlling for the bioclimatic domain, anomaly values were higher on clay than on till soil in mixedwood bioclimatic domain, although it was not significant. Yet, the difference was strongly significant in coniferous bioclimatic domain, which corresponded with the lower parental trees basal area (results not shown). However, in mixedwood bioclimatic domain, the importance of the parental trees was higher on till than on clay soil. Thus, our findings confirm the importance of the substrate for the regeneration success, besides the strong importance of parental tree seed source (**Figure 3a** and **b**). Indeed, in coniferous bioclimatic domain, where climate is colder, clay appears to be detrimental for seedlings establishment because of its water surplus and cold temperature [33], whereas till soil became more suitable for seedling success. Note that water surplus (clay) appears to have greater effect than a possible water deficit due to more water evaporated till on the shallow seedling roots. This is obvious since forest canopy shading protects seedlings from a high soil evaporation and prevents from a high water demand of seedlings, whereas it might add the negative effect of low temperature and water surplus.

In addition, there was not only a positive relationship between balsam fir seedling mortality rate and parental tree basal area ($p = 0.045$), but also an unexpected higher mortality in the mixedwood compared with the coniferous domain ($p < 0.004$; **Figure 4a**) regardless for the soil type. Balsam fir seedling mortality declined with increasing basal area of other tree species ($p = 0.020$; **Figure 4b**). Thus, balsam fir mortality appears to be related to its seedling density

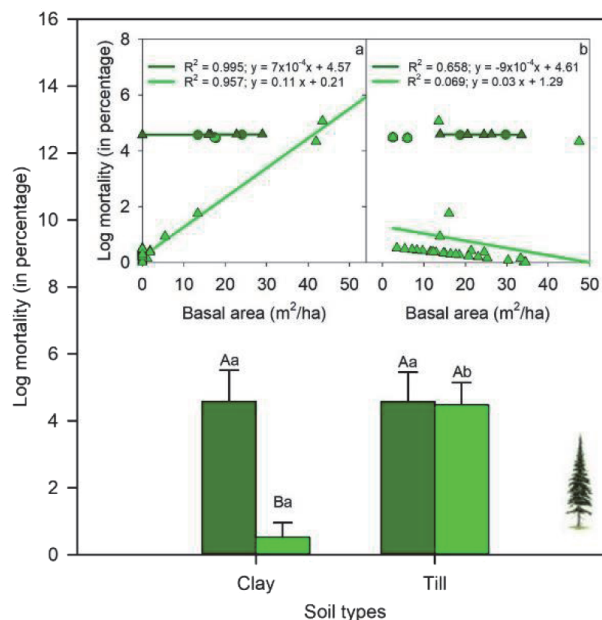


Figure 4.

Mortality rate of balsam fir seedlings according to bioclimatic domain and soil type. The inset panels indicate the basal area ($m^2 ha^{-1}$) between the mixedwood and coniferous bioclimatic domains for (a) parental trees of balsam fir and (b) other tree species. The dark green triangles and solid lines indicate the mixedwood bioclimatic domain, while the light green circles and solid lines indicate the coniferous domain. The letters at the top of the histograms indicate nonsignificant (same letters) or significant (different letters) differences between the mixedwood and coniferous bioclimatic domains. The lowercase letters show the comparison between till and clay soils within each bioclimatic domain (modified from [25]).

(competition) associated with the high seed source (parental trees). Understory shrubs and herbaceous plants are quite nonexistent in our site (personal observation), excluding any competition other than between balsam fir seedlings. In the mixedwood bioclimatic domain, seedlings are in similar shading environments; therefore, the competition between balsam fir seedlings may be for water and nutrients owing to similar quantity of soil resources being shared between a higher number of balsam fir seedlings. However, the other species had no effect or decreased mortality respectively in mixedwood and coniferous bioclimatic domains, probably due to the abundance of deciduous tree species, which may promote balsam fir establishment, notably in coniferous bioclimatic domain [34]. Another unexpected finding is that mortality rate was higher in mixedwood than in coniferous bioclimatic domains, less obvious on till soil, adding the effect of the competition between the seedlings (**Figure 4**). Moreover, higher mortality on till soils may also result from dryer conditions characterizing till soils, which easily release water during drainage or through evaporation as mentioned above [35].

The effect of climate on balsam fir seedling dynamic demonstrated a positive relationship with the growing degree-days above 5°C (GDD_5; $p < 0.001$; **Table 2**) regardless for the soil type, while total summer precipitation (PP_MA) had a negative effect on clay soil. As well, a decline of GDD_5 was observed in the coniferous bioclimatic domain compared with the mixedwood domain (**Figure A1**). Thus, lower balsam fir regeneration found in the coniferous bioclimatic domain could be linked to decrease of GDD_5 and increase of PP_MA, which worsen the water surplus of clay soil, hence showing an additional soil effect on regeneration. To test the effect of drought on regeneration, we used the interaction between GDD_5 and PP_MA [36]. The results demonstrated a positive and significant relationship with balsam fir regeneration irrespectively of the soil type, indicating a positive effect of drought. In the study area, balsam fir seedlings were in the shade of the canopy trees, where soil moisture is pretty much higher than in opened area. Furthermore, the positive effect of drought appears to prevent seedlings from a water surplus occurring on clay soil. In addition, balsam fir seedlings occurred mostly on a particular substrate such as woody mounds and thin moss cover [37], known to have a high water capacity, which may explain the absence of the PP_MA effect and the positive effect of drought on seedling abundance [38, 39].

3.2 Sapling dynamic

Balsam fir sapling abundance was significantly higher in the mixedwood than in the coniferous bioclimatic domain, while it was opposite for black spruce (**Table 3**). Moreover, this tendency was also similar for both species irrespectively of soil type. The abundance of balsam fir sapling was greater on till than on clay soils in mixedwood, whereas it was alike within the coniferous bioclimatic domain. In

Soil type	GDD_5	PP_MA	GDD_5*PP_MA
FS	0.827**	−0.437*	0.857**
MM	0.810**	−0.192	0.897**
Total	0.857**	−0.041	0.912**

*Correlations that significantly different from zero ($p < 0.05$) are shown in boldface type: * $p < 0.01$; ** $p < 0.001$.*

Table 2.

Person correlation (r) between balsam fir seedlings abundance and climate variables summer growing degree-days above 5°C (GDD_5) total summer precipitation (May to August; PP_MA), and the interaction between the two climate variables accounting for soil type (till or clay).

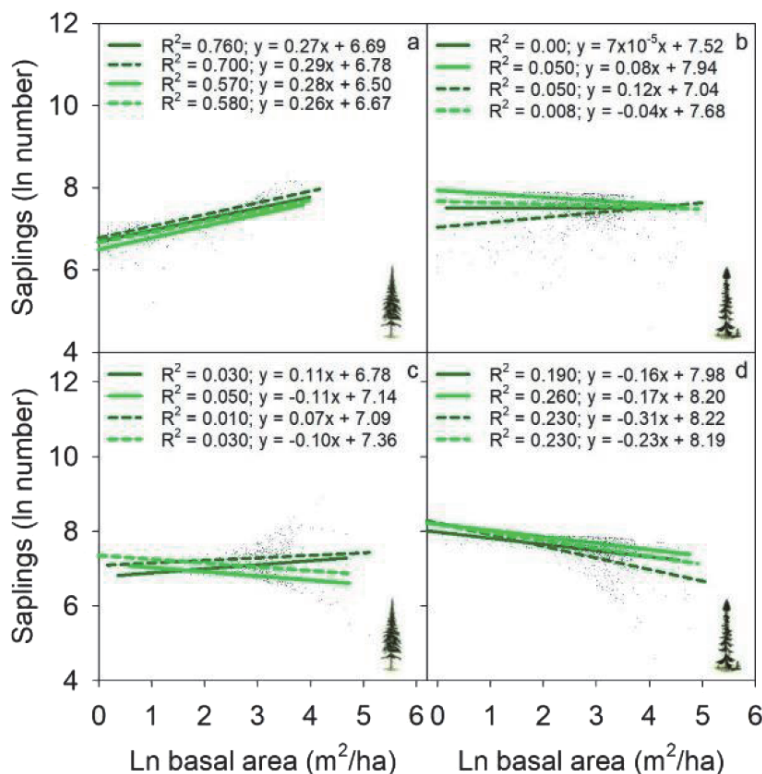
Species	Soil type	Bioclimatic domain	
		Mixedwood	Coniferous
Balsam fir	Clay	1264.86 ^{Aa} (91.06)	625.52 ^{Ba} (80.44)
	Till	1682.75 ^{Ab} (54.75)	620.36 ^{Ba} (45.87)
	Total	1598.73^A (47.48)	621.68^B (39.86)
Black spruce	Clay	2511.30 ^{Aa} (119.82)	3925.72 ^{Ba} (189.76)
	Till	2079.37 ^{Ab} (49.50)	2864.29 ^{Bb} (75.49)
	Total	2166.21^A (46.38)	3137.25^B (74.83)

Superscripts indicate nonsignificant (same letter) or significant (different letters) differences between mixedwood and coniferous domains. Uppercase letters are comparisons between bioclimatic domains, while lowercase letters are comparisons between soil types within bioclimatic domain.

Table 3.

Sapling abundance of balsam fir and black spruce (means, standard errors in parentheses) according to bioclimatic domain and soil type.

contrast, black spruce sapling abundance was higher on clay than on till in both bioclimatic domains. Our results demonstrated a significant positive role of the parental trees as seed sources on regeneration abundance for both species ($p < 0.001$). Balsam fir sapling abundance and parental tree basal area exhibited a positive relationship on both soil type, regardless of bioclimatic domain (Figure 5a). We noticed that although the model demonstrated no significant

**Figure 5.**

Abundance of balsam fir and black spruce saplings ($\ln(\text{stems/ha})$) with basal for parental trees (a and b) and for the stand (c and d), according to bioclimatic domain and soil type. The dark green solid and dashed lines respectively indicate clay and till soils in the mixedwood domain, while the light green solid and dashed lines respectively indicate clay and till soils in the coniferous domain [26].

relationship, sapling abundance was greater on till than on clay soils in the mixedwood bioclimatic domain. As well, the relationship between saplings abundance and parental tree basal area was stronger in the mixedwood than in the coniferous bioclimatic domain on clay soils. With respect to black spruce, the results indicated a decline sapling abundance linked to increasing parental tree basal area, excluding on till and barely on clay soils in the mixedwood bioclimatic domain, where the relationship between sapling abundance and parental tree basal area was positive (**Figure 5b**). The relationship between sapling abundance and parental tree basal area was also stronger on clay soils. Furthermore, greater abundance of black spruce sapling arose in the coniferous domain ($p = 0.027$). For balsam fir and regardless of soil type, total basal area positively impacted sapling abundance in the mixedwood, but negatively influenced it in the coniferous bioclimatic domain, although the general distinction prevailed nonsignificantly (**Figure 5c**). The relationship between black spruce sapling abundance and total basal area was negative, irrespectively of soil type or bioclimatic domain (**Figure 5d**). The negative impact of total basal area on regeneration seemed to be significantly stronger on till soils in the mixedwood ($p < 0.001$) and coniferous ($p = 0.003$) bioclimatic domains. In differentiating both bioclimatic domains, the negative influence of total basal area on abundance of black spruce sapling was more grounded in the coniferous than in the mixedwood bioclimatic domain, regardless of the soil types ($p < 0.001$). This indicates that with the increase of the parent tree base area, the influence of soil type on black spruce regeneration is greatly reduced, which may be due to the convergence of soil temperature and organic layer thickness conditions between the forest domain and the soil type. Therefore, stands dominated by black spruce seem to change its own microclimate and soil conditions by increasing soil moisture and lowering the soil temperature, which is conducive to promoting its seedling abundance. However, on clay soils in the coniferous bioclimatic domain, black spruce regeneration is more likely to be negatively affected, due to soil moisture saturation and soil temperature decrease, which both lead to paludification [31, 40].

Figure 6 shows a different regeneration pattern between balsam fir and black spruce. Balsam fir parental tree basal area was higher in mixedwood bioclimatic domain, while the opposite was true for black spruce in coniferous bioclimatic domain, which overlapped with regeneration abundance. Again, the presence of nearby seed trees has been previously reported as an important factor explaining regeneration abundance [41, 42]. For comparable parental tree basal area between both bioclimatic domains, regeneration for balsam fir was higher in the mixedwood domain, with black spruce demonstrating higher regeneration in the coniferous domain. As well as to parental tree influences on regeneration abundance, their potential seed production appears to play a crucial role in regeneration. As noticed before, balsam fir of comparable basal area has been demonstrated to produce fewer seeds in the coniferous than in the mixedwood bioclimatic domain [9], resulting in lower subsequent regeneration in the coniferous domain. In the same study, Messaoud *et al.* [9] found that black spruce showed similar seed production between the two bioclimatic domains. Thus, the regeneration pattern seems to be related to the reproductive capacity of both species. However, the reproductive capacity is not enough for the regeneration success. Indeed, balsam fir saplings abundance is still below the average of the total saplings in the study area on the clay soil, more pronounced in coniferous than in mixedwood bioclimatic domains, while it was only positive in mixedwood bioclimatic domain on the till soil. For black spruce, regeneration abundance was positive regardless of the bioclimatic domains and soil type, except on till soil in mixedwood bioclimatic domain. The negative effect of clay soils on balsam fir has already been reported in a previous

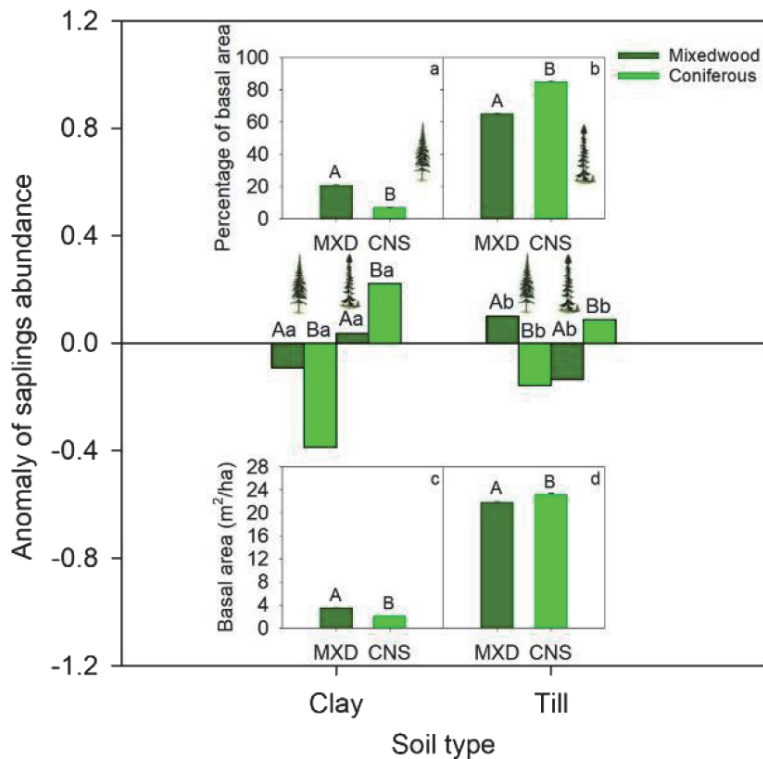


Figure 6.

Anomaly of balsam fir and black spruce sapling abundance $\ln(\text{stems/ha})$, according to bioclimatic domain and soil type. The anomaly represents the deviation from mean abundance of saplings for each species across the entire study area (positive = sapling excess, negative = sapling deficiency). Inset panels indicate percentage of basal area between the two bioclimatic domains (MXD = mixedwood, CNS = coniferous) for parental trees of balsam fir (a), black spruce (b), and the absolute values of the basal area for other tree species (c), and for the stand (d). The dark and light green histograms indicate the mixedwood and coniferous domains, respectively. The letters at the top of the histograms indicate nonsignificant (same letters) or significant (different letters) differences between the mixedwood and coniferous bioclimatic domains. The lowercase letters show the comparison between till and clay soils within each bioclimatic domain (modified from [26]).

research [11]. Negative influences of clay soils on balsam fir appear to be related to higher water content often characterizing clay soils, having lower temperatures and lower rates of evaporation. Saplings of balsam fir growing on clay are bound to encounter oxygen deprivation in the rooting zone due to waterlogging and reduced gas exchange, conditions that are transcendently found in the coniferous domain. It has been additionally mentioned that lower temperatures in clay soils seem to promote increased organic matter accumulation, unfavorable for balsam fir establishment and survival [11, 33]. This suggests that site species composition, local climate, or soil characteristics are also factors, determining regeneration success, especially for balsam fir. In addition, the hard link between parental trees and regeneration for balsam fir on the one hand and the noticed inconsistency noted for black spruce on the other proposes that balsam fir is more dependent on parental tree proximity compared with black spruce. Contrasting large balsam fir seeds falling beneath or close to their parent tree, the small size of black spruce seeds allows them to spread further (effective distances of 20–80 m; [10, 40] from the parent tree. The basal area of other species on sites that are primarily composed of balsam fir or black spruce can be used as a proxy for forest composition, which could influence sapling abundance to some extent. In fact, basal area of other tree species dominated by deciduous species was greater in the mixedwood than in the coniferous bioclimatic domain (Tables A2 and A3). The presence of deciduous species, such as paper birch or

trembling aspen, two dominant deciduous species in our study area, may favor suitable conditions (e.g., higher soil temperatures, increased organic layer decomposition, and impeded paludification), hence increasing sapling survival, especially for the balsam fir [34]. Indeed, our results confirmed the higher sensibility of balsam fir regeneration to the environment condition than black spruce. In addition, large balsam fir seeds can be protected from seed predation and competition with herbaceous plants by a broadleaf litter layer, as long as it arises from the small leave trees such as birch and aspen [24, 43, 44]. In contrast, thicker broadleaf litter layers appear to be detrimental for small seeded tree species, such as black spruce, because their seeds contain fewer nutritional reserves for germination and sufficient root elongation to penetrate the mineral soil through the litter layer [45]. Thus, the lower density of other species in the coniferous domain could trigger a population shift from warmer balsam fir conditions to colder conditions to which black spruce and associated species are better adapted [10]. We would posit that a higher diversity of forest composition exerts two major effects upon the regeneration: facilitation for balsam fir and exclusion for black spruce. Yet, the effects of exclusion were linked more indirectly to the negative effects of broadleaf litterfall on black spruce regeneration, as previously mentioned.

To maintain mean regeneration, balsam fir required on clay soil at least 40% and 44% of parental trees in the mixedwood and coniferous bioclimatic domains, respectively. However, the requirement was only 27% and 37% of parental trees on till soil in the mixedwood and in the coniferous domain, respectively (**Figure 7a**). Conversely,

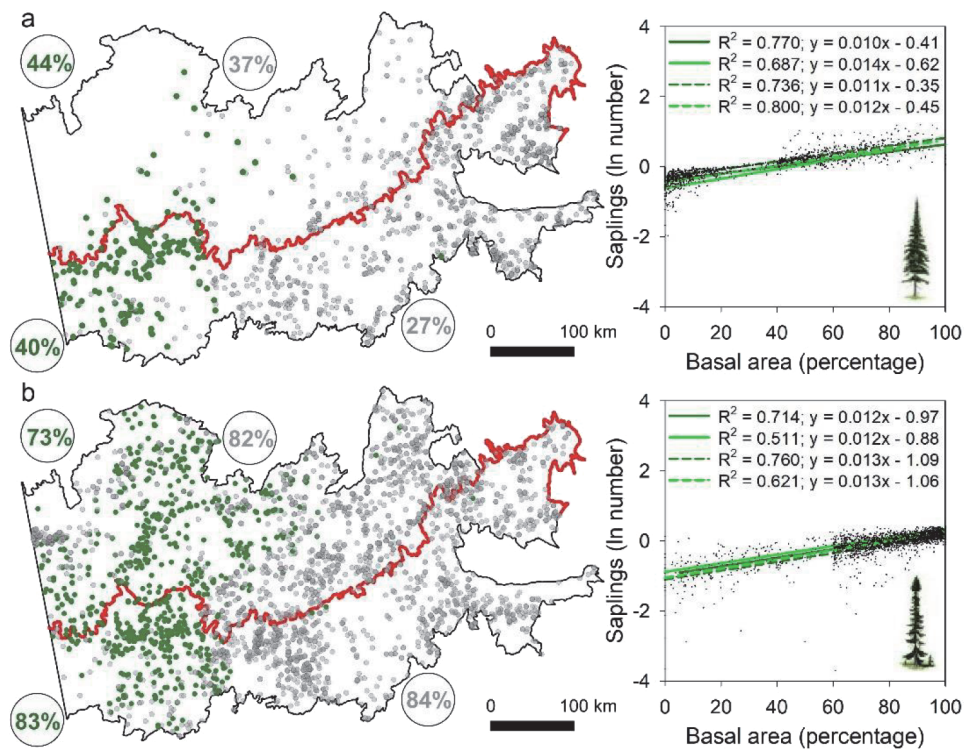


Figure 7. Dark green and gray circled values pertain to the respective clay and till soils inside a given forest domain. Scatter plots and trend lines depict relationships between the anomaly of sapling abundance and percent basal area of parental trees. The dark green solid and dashed lines respectively indicate clay and till soils in the mixedwood domain, while the light green solid and dashed lines respectively indicate clay and till soils in the coniferous domain.

black spruce required 82–84% of parental trees to maintain mean regeneration, except on clay soils in the coniferous bioclimatic domain (73%; **Figure 7b**). This indicates that balsam fir required more parental trees (seed source) to maintain mean regeneration in coniferous than in mixedwood bioclimatic domains. This contrasts with black spruce, which requires higher numbers of parental trees than does balsam fir, although the percentage was slightly lower in coniferous bioclimatic domain, especially in clay soil. This might be explained by lower black spruce seed inputs compared with those of balsam fir, due the smaller semi-serotinous cones constituting an aerial seed bank for former, which can release small quantities of seed continuously but episodically with the occurrence of fire [9, 46]. Another explanation may be related to higher seedling mortality within the low light understory for the less shade-tolerant black spruce. Another interesting finding is that black spruce regeneration required an equivalent percentage of parental trees basal area, except on clay soil in coniferous bioclimatic domain, where the percentage was the lowest. Conversely, balsam fir regeneration required more parental trees basal area on clay than on till soils regardless of the bioclimatic domain, adding the stronger role of the substrate on the balsam fir regeneration success compared with black spruce.

The effect of the climate on regeneration showed a contrasting effect of GDD_5, with a positive and negative relationship on balsam fir and black spruce regeneration, respectively (**Table 4**), illustrating greater adaptation to warmer environments that was shown by balsam fir compared with black spruce [10]. The effect of GDD_5 was stronger and positive because clay is known to be colder, with a greater water-holding capacity than till soils [33, 47], which are not only warmer, but are subject to greater rates of moisture evaporation [48]. Although, saplings have deeper roots than seedlings, saplings are tall individual, making them less shaded by the forest canopy. This may explain the positive and the absence of the PP_MA on balsam fir saplings on till and clay soils, respectively. Another explanation is that the absence of significant effect of PP_MA on balsam fir saplings on clay soil could be due to the contrasting effect of the clay. Indeed, in mixedwood bioclimatic domain, clay soil prevents balsam fir regeneration from the water stress due to warmer temperature, while it has a negative effect in coniferous bioclimatic domain due to its lower temperature and higher amount of water, unfavorable condition for balsam fir establishment. The negative effect of GDD_5 on black spruce regeneration irrespectively of the soil type confirmed its lower tolerance to higher temperatures than balsam fir [10], which are found mostly in southern locations. More, the effect of PP_MA on black spruce regeneration was negative on till and not significant on clay soils. On clay soils, black spruce demonstrated its adaptation to cold soil temperatures and higher water content [49]. The negative relationship between PP_MA and black spruce regeneration found on till soils appears to be due to competition for water with coexisting deciduous species, since till soils are subject to greater water drainage and higher rates of evaporation. The interaction between GDD_5 and PP_MA, indicating the drought effect, showed a significant positive and negative relationship for balsam fir and black spruce

Species	Soil type	GDD_5	PP_MA	GDD_5*PP_MA
Balsam fir	Clay	0.140**	−0.043	0.129*
	Till	0.091**	0.190**	0.189**
Black spruce	Clay	− 0.246**	0.055	− 0.221**
	Till	− 0.052*	− 0.191**	− 0.134**

Correlations that significantly different from zero ($p < 0.05$) are shown in boldface type: * $p < 0.01$; ** $p < 0.001$.

Table 4.

Person correlations (r) between species saplings abundance and climate variables according to the soil type.

regeneration, respectively of the soil type (**Table 4**). This indicates that drought did not influence negatively on balsam fir regeneration, while it did on black spruce regeneration. Therefore, balsam fir seems to be more drought-tolerant compared with black spruce, explaining the adaptation of balsam fir to warmer conditions compared with cooler and moister conditions for black spruce [10]. Unexpectedly, the positive effect of drought on balsam fir regeneration was more obvious on till than on clay soils ($r = 0.189$ vs. 0.129), probably due to the higher occurrence of till soil in central and eastern parts of the study area, where precipitation increases eastward (**Figure A1**). Thus, balsam fir was less adapted to the occurrence greater soil moisture levels. Another explanation is that since black spruce is less shade-tolerant than balsam fir [10], black spruce regeneration occurs under lower forest cover and, thus, is more exposed to drought conditions [44, 50]. Although, levels of PP_MA were comparable between the two bioclimatic domains, drought seemed to arise more frequently in the warmer mixedwood than in the cooler coniferous bioclimatic domain (**Figure A1**).

The ecocline between the two bioclimatic domains of eastern North America constitutes a shift from balsam fir to black spruce dominance rather than the northern limit of balsam fir, which extends further north (54° ; [7]). This clarifies the persistence of scattered balsam fir populations in the matrix of black spruce in coniferous bioclimatic domain, where reduced regeneration did not deal with the stability of such populations, just as long as a minimum parental tree basal area remained to support mean regeneration. The insight provided by the current study agrees with prior findings indicating that these few balsam fir populations can seemingly exist for a long time in the absence of severe disturbance such as fire [8]. Indeed, wildfire is a major disturbance in the boreal forest, and it can have a significant impact on the composition and dynamics of the vegetation at any particular place [21, 51]. Balsam fir is well known to be fire-intolerant species because its thin bark offers weak protection against fires [10]. Unlike black spruce, balsam fir cannot maintain a seedbank in the tree crown. Thus, its low abundance has been linked to large and intense fire regimes [10]. Furthermore, large fires may kill the parental trees of balsam fir, compromising regeneration success [52]. In contrast, black spruce is well adapted to fire because of its thick bark, which offers efficient protection against fire. Also, black spruce benefits more from large fires, owing to its aerial seed bank that persists in serotinous cones remaining in the canopy for many years [9], until a fire opens them to liberate seeds.

4. Conclusion

The ecocline between the mixedwood and coniferous bioclimatic domains of boreal zone in eastern North America represents a shift of the balsam fir and black spruce dominance below and above this ecocline. Thus, a decline of this dominance strongly impacted the regeneration success for both species, especially for balsam fir. Soil type played a different role below and above this ecocline depending on the species, the bioclimatic domain, climate, and at the lesser extend the regeneration stage (seedlings vs. saplings). However, in coniferous bioclimatic domain, clay soil (lower temperature and higher water holding), increase of black spruce, and decrease of deciduous stand tree basal area, lower air temperature affected negatively balsam fir regeneration. Unexpectedly, mortality rate was higher in mixedwood than in coniferous bioclimatic domains regardless for the soil type and higher on till than on clay soils in coniferous bioclimatic domain. This highlights the importance of the competition as the regeneration density increases. In addition, mortality rate declines with increasing the basal area of other tree species in coniferous bioclimatic domain, adding the importance of

deciduous species promoting balsam fir regeneration in more limiting environment. The results also confirmed the contrasting adaptation of balsam fir and black spruce to the temperature and drought conditions through their regeneration dynamic. To maintain regeneration equivalent to the mean for the entire study area, balsam fir and black spruce required, according to the soil type, respectively 4–10% more and 2–10% less parental trees in the coniferous than in the mixedwood bioclimatic domain. This is related to the lower adaptation of balsam fir to lower temperatures and shorter growing seasons in coniferous bioclimatic domain. Moreover, the parental trees basal area requirement for the black spruce regeneration success was pretty much less affected by the bioclimatic domain and soil type, except on clay soil in coniferous bioclimatic domain, where it was the most successful. Conversely, this requirement for the balsam fir success was associated to the bioclimatic domain and to the soil type, but higher on clay soil regardless of the bioclimatic domain, confirming the lower adaptation of balsam fir to the more water-holding soil compared with black spruce. Nonetheless, the threshold of parental tree basal area required for species regeneration to be equal to the mean study area is lower for balsam fir compared with black spruce, irrespectively of the bioclimatic domains, explaining the occurrence of mixedwood balsam fir populations well above the ecocline between the two bioclimatic domains. Consequently, our research confirms that this ecocline does not reflect the northern limit of balsam fir species, as shown by scattered but viable balsam fir populations found in the matrix of the coniferous forest domain, even further north of the ecocline. Another new insight given by this study is the both spatial scales (local and landscape) that were tended to, which significantly builds our comprehension of vegetation dynamics in the boreal biome inside the setting of future global change.

Acknowledgements

This work received no funding.

Conflict of interest

There is no conflict of Interest.

Notes/thanks/other declarations

No declaration.

A. Appendix

Data	Stand	Variables	BF_BA	BS_BA	Others_BA	Total_BA
Field		BF_BA				
		BS_BA	−0.164			
		Others_BA	0.085	0.918**		
		Total_BA	0.508**	0.732**	0.875**	
Inventory	Balsam fir	BF_BA				
		BS_BA	0.126**			
		Others_BA	0.331**	−0.278**		
		Total_BA	0.873**	0.307**	0.620**	

Data	Stand	Variables	BF_BA	BS_BA	Others_BA	Total_BA
	Black spruce	BF_BA				
		BS_BA	0.124**			
		Others_BA	0.035	0.213**		
		Total_BA	0.228**	0.975**	0.397**	

BF_BA and BS_BA indicate the basal area for balsam fir and black spruce respectively, while Other_BA and Total_BA indicate the basal area for other tree species and the basal area of the stand respectively. In bold significant level ($0.01 < \alpha < 0.05$, $*0.001 > \alpha < 0.01$, $**\alpha < 0.001$).

Table A1.
Pearson correlation coefficient between the different basal areas.

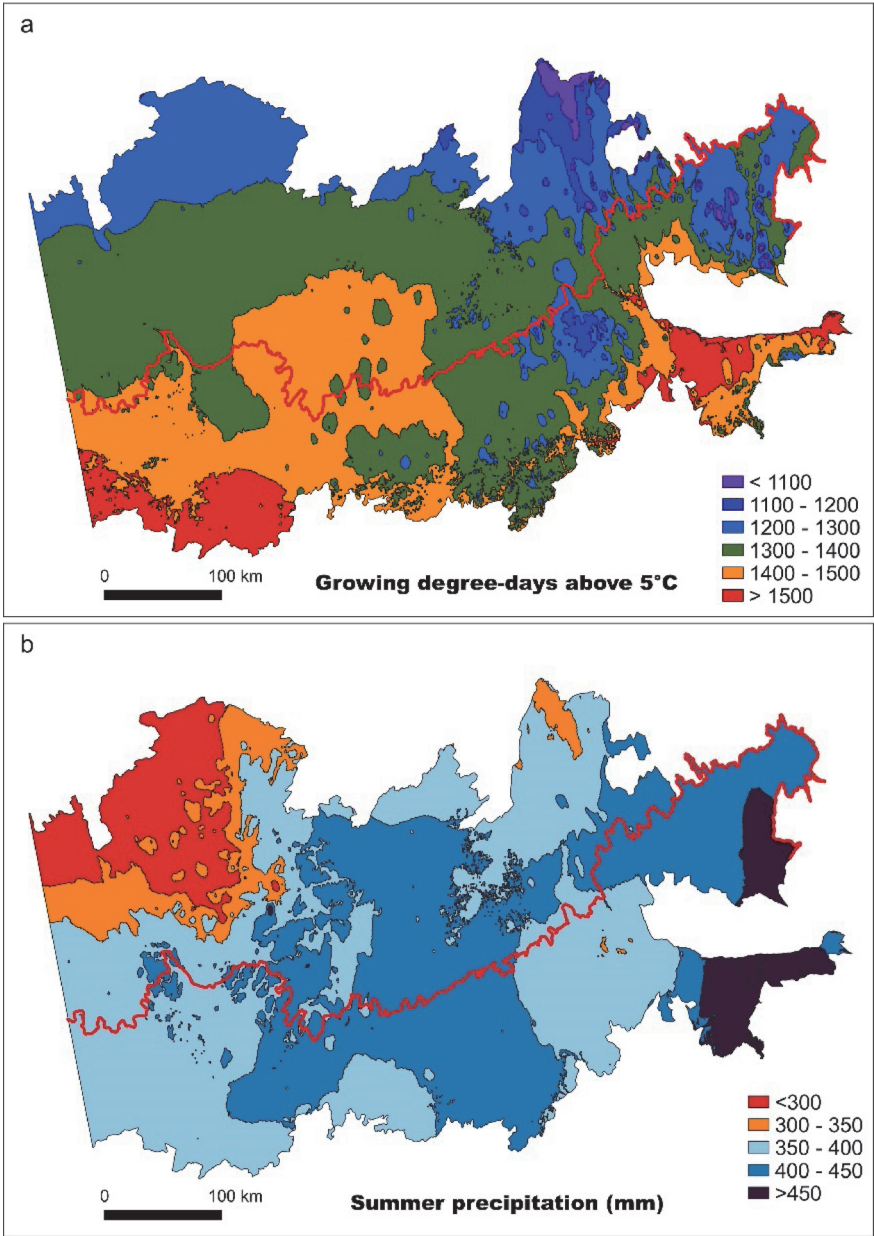


Figure A1.
Distribution of the climate variables in the study area: (a) growing degree-days; and (b) total summer precipitation (May–August). Red line indicates the boundary between the mixedwood and coniferous bioclimatic domains.

Species	Scientific name	Balsam fir stand		Black spruce stand	
		Mixedwood	Coniferous	Mixedwood	Coniferous
Deciduous	<i>Sorbus americana</i> Marsh.	0.051 (0.010)	0.006 (0.003)	0.000 (0.000)	0.000 (0.000)
	<i>Populus balsamifera</i> L.	0.029 (0.016)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	<i>Prunus serotina</i> Ehrh.	0.004 (0.004)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	<i>Alnus viridis</i> (Vill.) Lam. & DC.	0.021 (0.007)	0.024 (0.008)	0.000 (0.000)	0.000 (0.000)
	<i>Alnus incana</i> (L.) Moench	0.213 (0.042)	0.023 (0.013)	0.000 (0.000)	0.000 (0.000)
	<i>Betula populifolia</i> Marsh.	0.000 (0.000)	0.003 (0.003)	0.000 (0.000)	0.000 (0.000)
	<i>Acer spicatum</i> Lam.	0.020 (0.007)	0.002 (0.002)	0.000 (0.000)	0.000 (0.000)
	<i>Sorbus decora</i> (Sarg.) Schneid.	0.000 (0.000)	0.006 (0.003)	0.000 (0.000)	0.000 (0.000)
	<i>Betula papyrifera</i> Marsh.	3.932 (0.277)	2.137 (0.200)	1.178 (0.095)	0.604 (0.065)
	<i>Prunus pensylvanica</i> L. f.	0.089 (0.018)	0.004 (0.004)	0.000 (0.000)	0.000 (0.000)
	<i>Acer rubrum</i> L.	0.078 (0.024)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
	<i>Amelanchier canadensis</i> (L.) Medik.	0.006 (0.003)	0.002 (0.001)	0.000 (0.000)	0.000 (0.000)
	<i>Populus tremuloides</i> Michx.	1.025 (0.158)	0.573 (0.119)	0.505 (0.061)	0.294 (0.043)
	<i>Salix</i> sp.	0.166 (0.028)	0.051 (0.013)	0.085 (0.012)	0.052 (0.007)
	<i>Betula alleghaniensis</i> Britt.	0.092 (0.045)	0.000 (0.000)	0.000 (0.000)	0.000 (0.000)
Coniferous	<i>Pinus banksiana</i> Lamb.	0.398 (0.067)	0.652 (0.171)	1.026 (0.084)	1.386 (0.094)
	<i>Thuja occidentalis</i> L.	0.000 (0.000)	0.010 (0.010)	0.000 (0.000)	0.000 (0.000)
	<i>Picea rubens</i> Sarg.	0.033 (0.020)	0.026 (0.026)	0.000 (0.000)	0.000 (0.000)
	<i>Larix laricina</i> (Du Roi) K. Koch	0.149 (0.037)	0.223 (0.087)	0.278 (0.040)	0.189 (0.034)
	<i>Pinus strobus</i> L.	0.004 (0.004)	0.000 (0.000)	0.005 (0.005)	0.000 (0.000)
	<i>Picea glauca</i> (Moench) Voss.	1.136 (0.145)	0.696 (0.144)	0.232 (0.039)	0.081 (0.022)

Standard errors are included in parentheses.

Table A2.

Composition of canopy species other than black spruce and balsam fir in the study area and their mean basal area ($\text{m}^2 \text{ha}^{-1}$) in each bioclimatic domain.

Deciduous tree cover	Soil type	Bioclimatic domain	
		Mixedwood	Coniferous
Regeneration			
Balsam fir	Clay	74.81 ^A (3.02)	61.63 ^B (5.69)
	Till	73.14 ^A (1.48)	73.07 ^A (2.74)
	Total	73.56^A (1.43)	70.48^A (2.49)
Black spruce	Clay	55.11 ^A (3.24)	42.37 ^B (3.38)
	Till	55.99 ^A (1.97)	44.26 ^B (2.06)
	Total	55.75^A (1.68)	43.78^B (1.76)

The uppercase superscript on each mean value indicates a nonsignificant (same letter) or significant (different letters) difference between mixedwood and coniferous bioclimatic domains. Standard errors are in parentheses.

Table A3.
Average proportion of deciduous species on sites that were dominated by balsam fir or black spruce regeneration in the mixedwood and coniferous bioclimatic domains.

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