

Climate and disturbance regime effects on aspen (*Populus tremuloides* Michx.) stand structure and composition along an east–west transect in Canada’s boreal forest

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Stand structure and composition play a key role in maintaining the ecological integrity of the boreal forest. However, future changes in climate and disturbance regime could affect these forest attributes. Using provincial forest inventory datasets, we analysed stands dominated by aspen ($\geq 75\%$ of the plot total basal area) distributed along a wide longitudinal gradient of environmental conditions across Canada. Stands were classified into three diameter structure types (inverted J, intermediate and advanced). There was no major difference in the distribution pattern of structural types of aspen-dominated stands between the western and eastern Canadian boreal mixedwood forests, despite a marked contrast in climatic conditions and fire regime. These results suggest that the predominance of juvenile structures in the western aspen forests is mainly related to the frequent recurrence of fires, while within eastern aspen forests, the longer fire cycle was not the controlling factor of stand structure. Anthropogenic activities would have strongly shaped the structure of aspen forests in eastern Canada. White spruce in the west and balsam fir in the east are among the main shade-tolerant conifer companion species associated with these stands. Although stand structure and composition were highly related to stand age and site productivity, regional climate and human activities, through their influence on disturbance regime, might have impacted these forest attributes.

Introduction

Stand structure and composition are important characteristics for maintaining the ecological integrity of forest ecosystems (Kuuluvainen, 2002). In the boreal forest, complex interactions involving biotic and abiotic components of the ecosystem drive these characteristics as well as their evolution over time (Bergeron *et al.*, 2014). Within forested areas, different types of stand structure are found in various proportions from one area to another, depending on the dominant tree species in the canopy, environmental conditions and associated disturbance regimes (Chen and Popadiouk, 2002; Shorohova *et al.*, 2009). For example, regions subjected to short fire cycles tend to develop a majority of young forest stands, which generally exhibit a regular and even-sized structure. Conversely, in regions subjected to longer fire cycles (~200 years and over), old, irregular and uneven-sized stands predominate (Boucher *et al.*, 2003). In the prolonged absence of severe fires, secondary disturbances (e.g. insect outbreaks and other stand-level processes such as

windthrow of low severity) promote the development of irregular structures (Kneeshaw and Bergeron, 1998; McCarthy, 2001). In recent decades, anthropogenic activities such as forest harvesting and silviculture were additionally considered as major disturbances likely to affect forest structure and composition at both the stand and landscape scales (Boucher *et al.*, 2006a, 2009).

Future climate projections predict changes in temperature and precipitation regime, which could lead to substantial changes in the structure and functioning of ecosystems including species composition and distribution (IPCC, 2007). Temperature increases are expected to be particularly pronounced at northern latitudes (Field *et al.*, 2007; IPCC, 2007), which could induce regional-specific alterations in the fire regime, leading to uncertain but potentially significant impacts on ecosystem components in the boreal zone of Canada (Gauthier *et al.*, 2014). Changes in climate, and by extension the natural disturbance regime, will affect not only the composition and structure of forest stands but also the rate at which the changes of these occur. Chen *et al.* (2009) argue that if there is an increase in

fire occurrence due to climate change, the boreal landscape will become dominated by early successional stands mostly composed of hardwoods and mixtures of hardwoods and conifers. The mixed species stands are arguably more structurally diverse than their single species counterparts, due notably to inherent differences in growth rates among tree species (Varga *et al.*, 2005). A better understanding of factors affecting forest characteristics and the relative importance of different spatial patterns of these characteristics across boreal regions offer promising perspectives for implementing a sustainable management approach to preserve the ecological integrity of forest ecosystems.

This study focuses on stands dominated by aspen (*Populus tremuloides* Michx.) and aims to (1) characterize the structure and composition of these stands and to estimate how their abundance changes along an East–West transect across the Canadian boreal forest and (2) analyse the variability observed in these stands along this transect, based on eco-environmental factors. Aspen is the most abundant deciduous tree species in North America (Perala, 1990) and has a transcontinental distribution in Canada, where its ecological and economic contribution has increased in recent decades (Peterson and Peterson, 1992). This pioneer species is relatively short-lived, reaching the age of senescence ~100 years (Cumming *et al.*, 2000). During the process of senescence of the first cohort, a second cohort of aspen as well as coniferous species can grow and emerge in the canopy to form a mixed stand (Chen and Popadiouk, 2002), depending upon the rate at which the aspen stand is invaded by coniferous species (Bergeron, 2000).

The analysis of vegetation dominated by the same canopy species across a wide and continuous forest ecosystem would help to better understand the response of this vegetation in a changing environment. So, the pan-Canadian scope of this study on aspen is quite exceptional in North America. There are large regional variations in climatic factors and fire regime among and within the Canadian regions (Stocks *et al.*, 2002; Bergeron *et al.*, 2004; Boulanger *et al.*, 2012). In most boreal regions of eastern Canada, the fire interval often exceeds the longevity of tree species (Kneeshaw and Gauthier, 2003). In contrast, the shorter fire cycles in the western boreal forest result in a forest matrix dominated by young post-fire stands with patches of older forests dispersed throughout (Johnson, 1996). Based on the regional differences outlined above, we hypothesize that (1) young, even-sized aspen-dominated stands will be more frequent in western Canada, whereas old, uneven-sized aspen-dominated stands will be more frequent in eastern Canada and (2) pure aspen stands will be more abundant in western Canada due to shorter fire cycles that would limit changes in canopy composition. Conversely, longer fire cycles in eastern Canada would tend to increase the proportion of aspen stands with an understorey of shade-tolerant tree species.

Methods

Study area and data selection

The study was located in the boreal mixedwood ecological zone of Canada (Figure 1), using the forest inventory databases available in the different provinces. This forest zone is influenced by a wide range (from east to west) of factors including climate, edaphic conditions, disturbance regimes and management histories (Bergeron *et al.*, 2014). It is

characterized by a complex mosaic of forest types that vary both structurally and in the relative proportion of broadleaf and conifer tree species (Bergeron *et al.*, 2014). Although this forest zone is dominated by mixed species stands, many pure deciduous stands were found in the early successional stages (Bergeron *et al.*, 2014). Studied stands are spread throughout an uninterrupted transcontinental band that extends from British Columbia in the west to Quebec in the east (Figure 1), and whose stand and environmental characteristics are summarized in Table 1.

Data selection was carried out in several steps, as detailed in Nlungu-Kweta *et al.* (2014). We first selected forest stands from the provincial forest inventory datasets that were dominated by aspen, i.e. at least 75 per cent of the basal area ($\text{m}^2 \text{ha}^{-1}$) of live and merchantable trees (diameter at breast height (DBH) ≥ 9 cm) located in all temporary sample plots (TSPs), and in only one set of inventory measures (the most recent available) of permanent sample plots (PSPs) comprised of aspen. The threshold of at least 75 per cent of plot total basal area in aspen was chosen to ensure that stands originated from a stand-replacing disturbance. Then of the preselected stands, we retained only those that were located within the study area by using ArcGIS 9. Overall, 2582 stands dominated by aspen were selected for this study (Table 1).

Characterization of aspen-dominated stands along the study transect

Stands were characterized based on a range of different structural and compositional typologies. All living trees with a DBH ≥ 9 cm in the plot were used to describe stand structure and composition. As the survey areas of trees included in the study differed in size among the Canadian provinces, data from the selected sample plots had to be harmonized before stand characterization. This was accomplished by taking the stem density observed in each plot and extrapolating the said density at the scale of a larger forest (one hectare).

Typological classification of stand structure and composition

The classification of the studied stands into structural types was carried out by combining the relative distributions of density (trees ha^{-1}) and basal area ($\text{m}^2 \text{ha}^{-1}$) per DBH class (in the stand) – an approach developed in British Columbia by Moss (2012), who used stand structure classes to predict ecological succession pathways. DBH data were compiled into 14 classes, as follows: 2-cm-diameter classes between DBHs of 9–28 cm, 4-cm-diameter classes between DBHs of 29–40 cm and DBH >40 cm class. Class limits were determined arbitrarily and refer to the dimensions generally used in silviculture for merchantable stems. In order to adjust the data to a minimum resolution of 400 m^2 (the size of the smallest sampling unit of trees that was common among all studied provinces), we excluded stems of diameter classes where the density was less than 25 trees ha^{-1} ($1 \text{ tree}/400 \text{ m}^2 = 25 \text{ trees ha}^{-1}$) during the stand structural classification process. Following exploratory tests on the optimal number of clusters, stands were automatically classified into one of three main structural types, using the K-means clustering method (Borcard *et al.*, 2011) under R 3.1.2 (R Development Core Team, 2013). This clustering method considered the cumulative distributions of tree diameter classes.

However, to determine if the spatial tree distribution per DBH class in the stand was regular or irregular (even- and uneven-sized stand structures, respectively), the autocorrelation function (Legendre and Legendre, 2012) was used as a supplementary ‘structural index’. For this purpose, the autocorrelation in the diameter class distributions was estimated by computing the Pearson correlation coefficient (r) between observed densities per diameter class and their lags at a distance of 1 shift (lag of order 1). Even- and uneven-sized stand structures were identified by using the critical value for the first-order autocorrelation

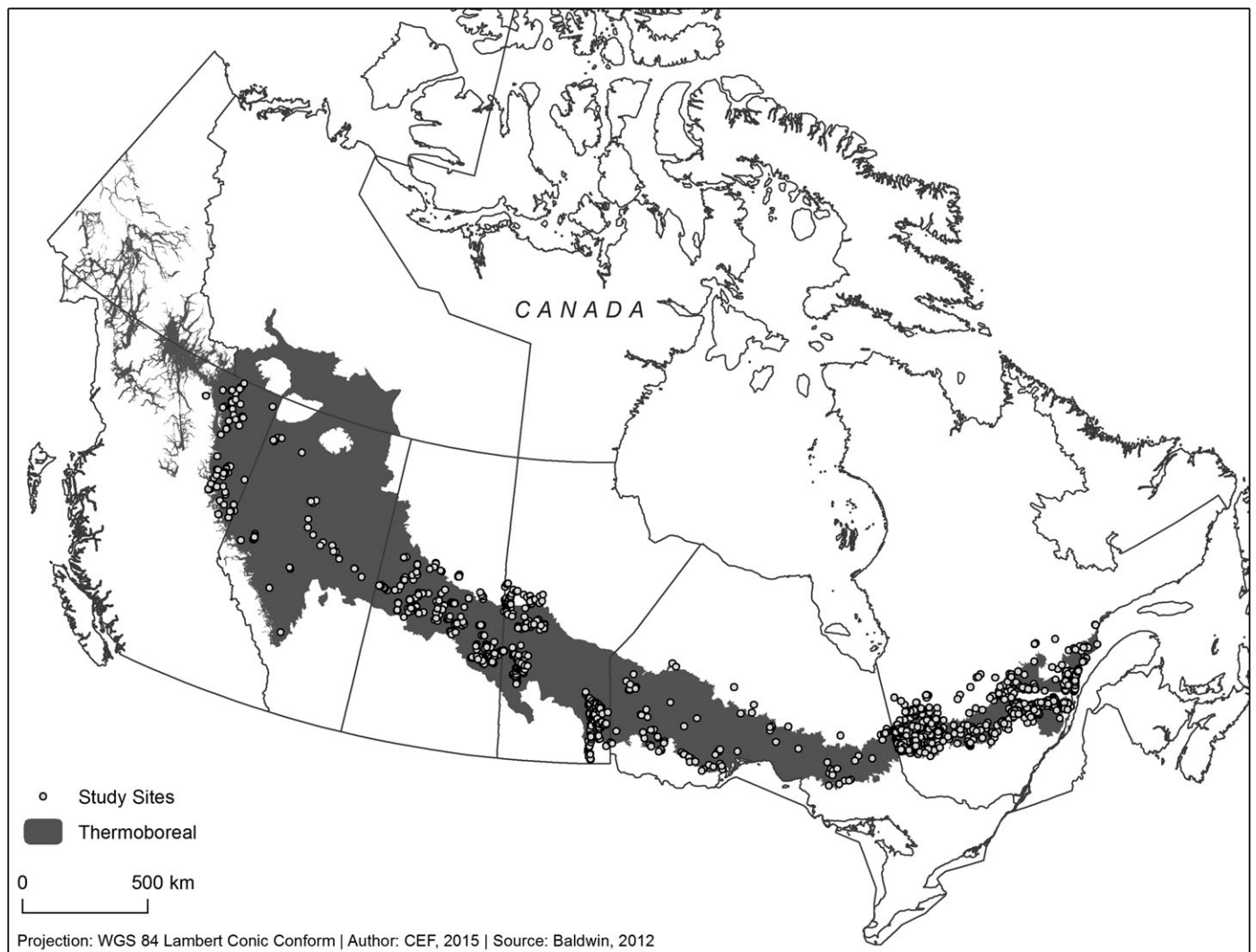


Figure 1 Map of the study area along an east–west transect in Canada. The ‘boreal mixedwood’ (dark grey area) corresponds to the thermoboreal bioclimatic subdivision of the Canadian boreal biome (Baldwin *et al.*, 2012).

(ρ_1) at $P < 0.05$ derived from standard tables. When $r > \rho_1$, the tree distribution was monotonic or unimodal Gaussian, and when $r < \rho_1$, the distribution was random and irregular, in which trees belonged to several diameter classes. We then analysed the relationship between the observed structural types, stand age and site productivity.

Compositional classification was used to categorize the studied stands among three compositional types, depending on the percentage of basal area ($\text{m}^2 \text{ha}^{-1}$) of aspen. A detection threshold for the ‘presence’ of a tree species was set at 25 individuals (trees) per hectare, corresponding to the minimum density of trees for a given species in 400m^2 (the aforementioned minimum resolution). Thus, to standardize information acquired under different sampling protocols, a tree species was excluded from the compositional stand analysis when its density fell below 25trees ha^{-1} . Depending on the dominance of aspen in a stand, we distinguished: (1) ‘pure’ aspen stands to designate those with 100 per cent basal area made up of aspen; (2) ‘almost pure’ aspen stands where aspen represents 90–99.9 per cent of basal area and (3) ‘least pure’ aspen stands where aspen represents 75–89.9 per cent of basal area. In the ‘least pure’ aspen stands category, we then identified the main companion tree species in the stand, i.e. tree

species with commercial value that had the next highest basal area following aspen.

To illustrate the relative distribution of various structural and compositional types at the landscape level along the longitudinal gradient, we quantified their respective frequencies (expressed as %) within the studied provinces. This was done by calculating the ratio between the number of aspen stands with a given structural or compositional type and the total number of aspen stands examined in a province. Pearson’s Chi-squared test was performed to test for significant differences in the structural and compositional frequencies among provinces.

Predictive variables for modelling structural types

The modelling effort was focused solely on stand structure; here, the study challenge was not about the compositional types mentioned above but rather whether species composition had an effect on stand structure. To identify factors influencing stand structure and predict structural types of aspen-dominated stands across the Canadian boreal mixedwood forest, 16 potential predictor variables ($k = 16$) were tested.

Table 1 Stand and environmental characteristics (mean and range) of examined stands by Canadian province

Provinces ¹	No. of stands ²	DBH (cm)	Age (years)	Site index (m) ³	Degree-Day (°C day) ⁴	Fire cycle (years)	DistRoad (km) ⁵	DensRoad15Km (km) ⁶	DensRoad25Km (km) ⁶
BC	100	16.8 (9–60.1)	69.2 (21–146)	17.9 (11.2–25.0)	2117.2 (1771.7–2296.8)	387.4 (326.8–397.9)	5.3 (0–45.1)	81.0 (5.7–513.9)	209.4 (13.6–1151.6)
AB	44	18.9 (9–56.2)	35.3 (25–124)	23.2 (11.4–32.8)	2237.3 (2041.9–2375.9)	332.7 (93–672.9)	1.7 (0–13.9)	158.3 (6.6–410.3)	448.3 (68.5–1114.3)
SK	446	17.3 (9–81.2)	59.9 (19–102.1)	16 (7.5–25.3)	2290.8 (2140.9–2425.8)	301.9 (50.9–1225.6)	1.1 (0–9.6)	127.6 (1–427.8)	336.1 (7.5–1402.4)
MB	574	16.6 (9–63.9)	56.1 (19.7–123.3)	16.7 (7.1–26.7)	2477.5 (2057.8–2801.1)	325.7 (56.2–1225.6)	3.8 (0–29.6)	119.2 (2.4–479.1)	334.6 (9.7–928.7)
ON	155	16.5 (9–56.7)	50.9 (32.4–133)	19.2 (17.2–22.6)	2401.8 (2133.6–2663.2)	748.3 (83.9–1440.2)	3.1 (0–29.1)	169.4 (19.9–447.5)	467.2 (38.1–1100.8)
QC	1263	18.1 (9–84.1)	43.5 (16.6–162)	22 (12.5–32.8)	2296 (1884.5–2562.9)	1360.5 (625.7–3706.6)	1.8 (0–74.7)	289.3 (0.5–1199.3)	762.5 (6–2654.5)
Total or ranges	2582	9–84.1	16.6–162	7.5–32.8	1771.7–2801.1	50.9–3706.6	0–74.7	0.5–1199.3	6–2654.5

¹BC = British Columbia, AB = Alberta, SK = Saskatchewan, MB = Manitoba, ON = Ontario, QC = Quebec.

²Number of study aspen stands (observations) per province. In these observations, only 91 in BC, 40 in AB, 214 in SK, 452 in MB, 91 in ON and 800 in QC for which the stand age (age) was available (i.e. only 1688 over 2582 stands in total).

³A measure indicating the site productivity; defined as mean height of trees at reference age of 50 years.

⁴The cumulative degree-days above 5°C.

⁵The distance from the stand relative to the nearest main road.

⁶Road density in a radius of 15 and 25 km around the stand, respectively. For the inventory data used in the study, the range of the survey years varies from one province to another, i.e. between 1980–2009 in QC, 1992–2006 in ON, 2002–2011 in MB, 1978–2000 in SK, 2001–2008 in AB, and 1970–2008 in BC.

Their sources and descriptions are summarized in Table 2. These are: Tree species richness (RichSp), as the diversity of tree species would imply a variability in tree size (Löhde *et al.*, 1999); Stand age (Age), as the stand structure changes over time; Site productivity, expressed by site index (SI) – which may affect the maturation rate of trees within a stand; Interaction between stand age and site productivity (Age*SI) – since the age effect may be altered by site productivity; Climatic conditions of sites, expressed both by the aridity index (AI) which is the accumulated monthly water deficit and the cumulative degree days above 5°C (DD); Fire cycle (FC), to characterize the fire regime of sites; Nearest distances to various landscape features were estimated in ArcGIS and included major watercourses (DistWater; rivers, lakes and bays), main road (DistRoad) and agricultural area (DistAgri); Percentage of hydrography (PctHydro); road density (DensRoad) and spatial variables (longitude, latitude and elevation).

Several applicable site index models exist across the provinces covered by this study, however, we have chosen to use the model of Nigh *et al.* (2002) to estimate site index because it produced the best fit for the transect data (Anyomi *et al.*, 2015). Since climate is a complex process that affects tree growth, a 30-year average of DI and DD was generated in BioSIM 9 (Régnière and Saint-Amant, 2008) using Environment Canada data (Environment Canada, 2013).

Fire is the most important stand-replacing disturbance agent in the boreal forest (Johnson, 1996), and stand structure is largely a reflection of the time elapsed since the last stand-replacing disturbance event. FC data was obtained using a map that defines areas with a homogeneous

fire regime. Secondary disturbances, mainly forest tent caterpillar (*Malacosoma disstria* Hübner) outbreak, were not included in the modelling effort due to a lack of data at the pan-Canadian scale.

DistRoad and DistAgri, as well as DensRoad15km and DensRoad25km, were estimated and considered as proxies to investigate potential anthropogenic influences on the natural environment. Anthropogenic disturbances can alter landscape dynamics, by acting at similar scales to natural disturbances (Laquerre *et al.*, 2009), particularly through fire occurrence (increased ignition sources). Changes in fire regime due to forest management practices such as harvesting have a direct impact on the composition and structure of forests (Bergeron *et al.*, 2001, 2004). DistWater and PctHydro were added as variables describing the physical environment of sites. An abundance of water (PctHydro) can create micro-climatic conditions that affect surrounding areas, while major rivers can act as natural barriers against forest fires.

Within the North American boreal forest, climatic factors vary according to changes in spatial gradients (Hart and Chen, 2006); hence we also included longitude, latitude and elevation as climatic surrogates in the analysis.

Model selection and logistic regression

A model selection approach based on Akaike's Information Criterion (AIC) (Mazerolle, 2006) was used to identify which among all of the eco-environmental variables cited in Table 2 was the most appropriate to

Table 2 Types and description of predictor variables used in modelling structural types

Variable (abbreviation)	Description	Data source
Climatic		
Aridity index (AI)	Annual mean aridity (1981–2010) (mm)	Environment Canada (2013)
Degree-days (DD)	Annual mean degree-day over 5°C (1981–2010) (°C day)	Environment Canada (2013)
Fire regime		
Fire cycle (FC)	Year interval from cyclic return fire (years)	Boulanger <i>et al.</i> (2012)
Physical environment		
Distance to the nearest great river, lake or bay (DistWater) ¹	Distance to the nearest significant watercourse (km)	Natural resources of Canada – Geobase
Hydrography (PctHydro)	Percentage of area occupied by water in a radius of 15 km around the stand (%)	Natural resources of Canada – Geobase
Anthropogenic		
Distance to the nearest main road (DistRoad)	Distance to the nearest carriage road (km)	Natural resources of Canada – Geobase
Distance to agricultural area (DistAgri)	Distance to the nearest farmland (km)	Natural resources of Canada – Geobase
Road density (DensRoad)	Total length of roads (km)/km ² area, in a radius of 15 and 25 km around the stand	Natural resources of Canada – Geobase
Spatial		
Longitude (Long)	Geographic coordinates	Forest inventory datasets
Latitude (Lat)	Geographic coordinates	Forest inventory datasets
Elevation (Elev)	Geographic coordinates	Forest inventory datasets
Others		
Tree species richness (RichSp)	Number of trees species found within the stand	Tree species number counted in the stand
Stand age (Age)	Time since the last major disturbance (years)	Forest inventory datasets
Site index (SI)	Mean height of aspen stem at 50 years (m)	Estimated as in Nigh <i>et al.</i> (2002)
(Age*SI)	Interaction between stand age and site productivity	Age multiplied by SI

¹The size of the watercourse considered in the analysis ranged from 5 to 35 000 km² (an average of ~340 km²). Data on anthropogenic variables and those describing the physical environment were mainly sourced from the GeoBase of Natural Resources Canada. <http://www.geogratis.ca/geogratis/DownloadDirectory?lang=fr>.

predict the structural types. A cumulative logit model was fitted to determine the relationship between structural types (an ordinal variable) of aspen stands and predictors along the study transect. The model was implemented using the *vglm* function of the *VGAM* (Vector Generalized Additive Model) package in R version 3.1.2 (R Development Core Team, 2013). In modelling, we used a data subset of 1688 stands (observations) for which data of stand age were available in forest inventory datasets and for which we estimated the SI. These two local factors (Age and SI) appear to be determinants for stand structural development, but they are unrelated to the group of factors (climate, fire regime and human impacts) considered at the very large geographical scale of the study area.

Model selection was conducted from a stepwise procedure. We started by identifying the predictor variable that was most significantly (lowest AIC value) related to the response variable, using univariate regression models. From the most significant variable identified, we then added other variables one by one to test if, combined or not, the constructed models could explain the distribution of structural types of aspen-dominated stands across the study transect. To avoid over-fitting, a covariate was retained only if it contributed significantly in improving the model (Burnham and Anderson, 2002). Stepwise procedure terminated when no further variable could be added. A total of 10 candidate models was retained for the final selection process, according to the order of their construction. Finally, we performed a multi-model inference in order to compare the candidate models (Mazerolle, 2006). Differences in AIC values, delta AIC (ΔAIC) and Akaike weights (W_i) among models were used to identify the model that was best supported by our dataset, using the *AICcmodavg* package of R (Mazerolle, 2011). Models with large ΔAIC values (e.g. >2) are less plausible given the data, and W_i provides an additional measure of strength of evidence for a model (Mazerolle, 2006).

Thereafter, the proportion of variance explained by each variable of interest of the best predictive model was extracted from the calculation of log-likelihoods (Burnham and Anderson, 2002), as in Equations (1) and (2):

$$\text{Variance of a variable} = 1 - R^2 \quad (1)$$

$$R^2 = (\log \text{Lik}_3 - \log \text{Lik}_1) / (\log \text{Lik}_2 - \log \text{Lik}_1) \quad (2)$$

where R^2 is the (pseudo) coefficient of determination; $\log \text{Lik}_1$ is the log-likelihood of the null model; $\log \text{Lik}_2$ is the log-likelihood of the best model and $\log \text{Lik}_3$ is the log-likelihood of the best model that is fitted without the variable of interest.

Results

Structural and compositional description of the pan-Canadian gradient

Of our 2582 studied stands, K-means has classified 899 as having an 'inverted J' structure characterizing stands dominated by stems of small DBH classes; 985 as having an 'intermediate' structure characterizing stands dominated by stems of intermediate DBH classes and 698 as having an 'advanced' structure characterizing stands dominated by a wide range of diameters, often including the largest DBH (Figure 2). Analysis of the distribution of structural types based on the site productivity and stand age (Figure 3) revealed that 'inverted J' structure types were most frequent in younger stands (20–50 years old), whereas 'advanced' structure types appeared more in older stands (≥ 50 years old). This interpretation led us to classify the 'inverted J' types as juvenile stands and 'advanced' types as

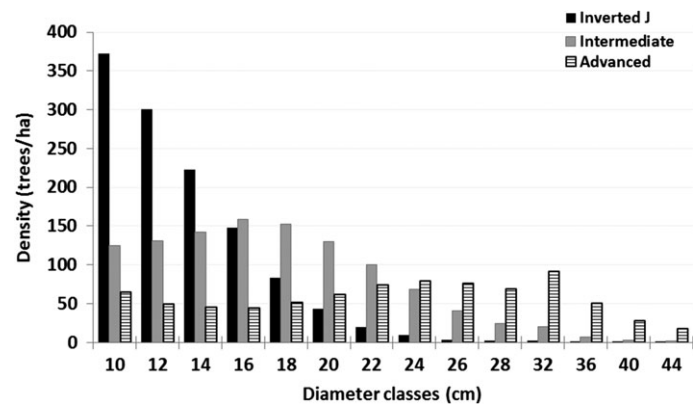


Figure 2 Mean diameter distributions corresponding to the three types of stand structure. Black bars represent the 'inverted J' structure, gray bars represent the 'intermediate' structure and striped bars indicate the 'advanced' structure.

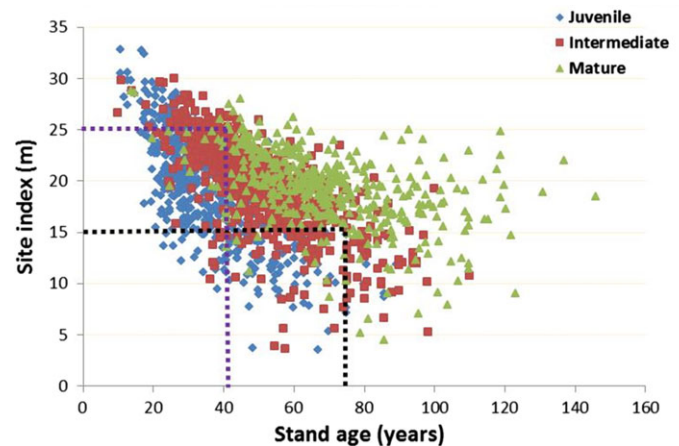


Figure 3 Distribution of structural types based on the site productivity and stand age. 1688 aspen stands were used in analysis including 603 'inverted J' (diamond), 650 'intermediate' (square) and 435 'advanced' (triangle) structures.

mature stands. Moreover, Figure 3 also shows the site productivity effect, which can shorten the forest maturation time on rich sites. It revealed that stands with a high site index (e.g. $SI > 15$ m) tended to reach the mature stage earlier (~ 40 years), whereas those with a low site index (e.g. $SI < 15$ m) tended to reach the mature stage much later (~ 70 years). These results suggest that on poor sites (low SI), aspen-dominated stands tend to remain within a structural stage longer before moving on to another more advanced stage, whereas the succession in the structural stages is more rapid on richer sites (high site productivity).

Figure 4 shows that, contrary to our assumptions, the proportion of 'inverted J' and 'intermediate' structures was higher than that of 'advanced' structures in the eastern portion of the study area including QC and ON. We observed a similar distribution pattern of structural typologies in the western (in BC) and central (in MB) portions of our study area. Conversely, regions of the Canadian boreal mixedwood that were dominated by 'advanced' compared with 'inverted J' aspen stands were found

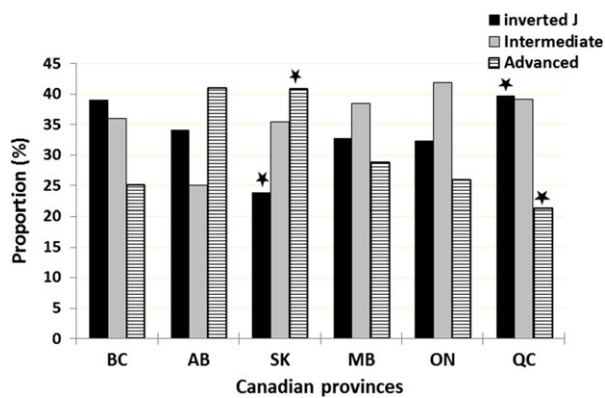


Figure 4 Relative frequencies of structural types by province throughout the longitudinal gradient. Black bars represent aspen stands with ‘inverted J’ structure, gray bars represent aspen stands with ‘intermediate’ structure and striped bars indicate aspen stands with ‘advanced’ structure. The stars above bars refer to statistic Z (Freeman-Tukey deviates). They identify structural types of provinces (QC and SK) in which the number of observations significantly ($P < 0.05$) differs (higher or lower) from the corresponding expected frequency.

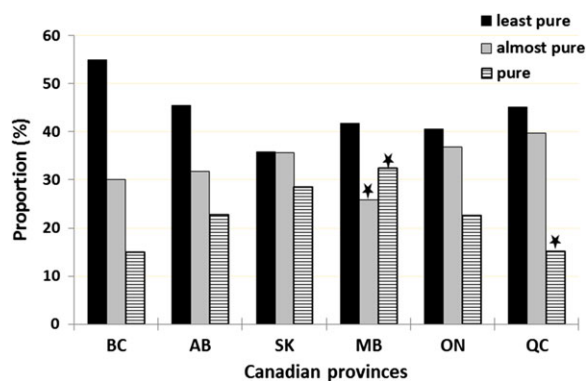


Figure 5 Relative frequencies of compositional types by province throughout the longitudinal gradient. Black bars represent ‘least pure’ aspen stands, gray bars represent ‘almost pure’ aspen stands and striped bars indicate ‘pure’ aspen stands. The stars above bars refer to statistic Z (Freeman-Tukey deviates). They identify compositional types of provinces (QC and MB) in which the number of observations significantly ($P < 0.05$) differs (higher or lower) from the corresponding expected frequency.

in AB and SK. Chi-squared tests showed that the ‘inverted J’ structures are higher and ‘advanced’ structures lower than expected in QC; and conversely, the ‘inverted J’ structures are lower and ‘advanced’ structures higher than expected in SK. The distribution pattern of structural types of aspen-dominated stands did not statistically differ in the remaining provinces relative to the expected average profile.

In terms of aspen stand composition (Figure 5), no differences were observed in the proportion of ‘pure’ aspen stands between the western (BC and AB) and eastern (QC and ON) ends of the study area. The proportion of ‘pure’ aspen stands reached its maximum values towards the middle of the longitudinal gradient (SK and MB), whereas the proportion of ‘least pure’ aspen stands attained its maximum values at opposing ends of this gradient (BC and QC). Further, the distribution

Table 3 Frequency (%) of aspen stands ($n = 2582$) composition according to structure types

		Structure		
		Inverted J	Intermediate	Advanced
Composition	Pure	29.6	19.4	15.4
	Almost pure	37.8	37	29.4
	Least pure	32.6	43.6	55.2

Values in boldface indicate compositional class in which there is the highest proportion of aspen stands for ‘Inverted J’ and ‘Advanced’ structural types, respectively.

pattern of compositional types was observed to be very similar in all studied provinces, in which ‘pure’ aspen stands were relatively less abundant than the ‘least pure’ aspen stands. Chi-squared test showed that the ‘pure’ composition was lower than expected in QC, while the ‘pure’ composition was higher and ‘almost pure’ composition was lower than expected in MB. The distribution pattern of compositional types was not statistically different in the remaining provinces. The aspen stands with ‘inverted J’ structures had mostly ‘pure’ compositions (Table 3) and an ‘even-sized’ distribution (Table 4), while those with ‘advanced’ structures had mostly ‘least pure’ compositions (Table 3) and an ‘uneven-sized’ distribution regardless of the compositional type (Table 4). Particularly in SK, the ‘even-sized’ distribution was more abundant than ‘uneven-sized’ ones in the ‘advanced’ structure stands of ‘almost pure’ and ‘pure’ compositions (Table 4). Only a small proportion of ‘advanced’ stands have maintained a ‘pure’ aspen composition, which is higher in the middle of the transect (SK, MB) and decreases towards the eastern (ON, QC) and western (BC, AB) extremes (Table 4). In addition, uneven-sized pure aspen stands of advanced structure were present in all provinces.

The main companion tree species (Figure 6) found in ‘least pure’ aspen stands were paper birch (*Betula papyrifera* Marshall) and balsam fir (*Abies balsamea* [Miller] L.) in the eastern portion, and white spruce (*Picea glauca* [Moench] Voss) and balsam poplar (*Populus balsamifera* L.) in the western and middle portions of the study transect. Overall, average species richness per stand (Figure 7) was roughly similar across all provinces ranging from 2.0 to 2.6 species.

Prediction of stand structure and individual effect of variables

Among the candidate models considered in Table 5, Mod1, which combines the stand age and site productivity interaction (Age*SI), climate (DD), tree species richness (RichSp), anthropogenic disturbances (DensRoad15Km, DistRoad) and fire regime (FC), was the most significant for describing distribution of structural types in the study area. Mod1 has the highest support ($W_i = 0.53$, $\Delta AIC = 0.0$) to be the best predictive model among all candidate models. With a ΔAIC of 0.26, Mod2 is a competitor of Mod1 but has a slightly lower probability ($W_i = 0.42$) of being the best model. In fact, these two models are similar but differ in that the ‘FC’ variable in Mod1 is

Table 4 Numbers and frequencies (%) of even- and uneven-sized stands by structure type

Prov.	'Inverted J' structure		'Advanced' structure								
	No. of stands	Even-sized (%)	Uneven-sized (%)	By compositional type (%)			Within compositional type (%)				
				Least pure	Almost pure	Pure	Least pure	Almost pure	Pure		
BC	39	89.7	10.3	72.0	24.0	4.0	4.0	4.0	16.0	0.0	4.0
AB	15	93.3	6.7	61.1	27.8	11.1	22.2	38.9	22.2	5.6	5.5
SK	106	99.1	0.9	42.3	34.6	23.1	9.9	32.4	14.8	18.2	4.9
MB	188	90.4	9.6	47.9	28.5	23.6	5.5	42.4	26.7	1.2	22.4
ON	50	96.0	4.0	52.5	35.0	12.5	20.0	32.5	27.5	2.5	10.0
QC	501	80.4	19.6	66.0	27.6	6.3	6.7	59.3	25.4	0.7	5.6
Total	899										

Note: Frequency is the ratio of the number of even- or uneven-sized stands over the total number of stands in each structural type by province. Critical value of the Pearson product-moment correlation coefficient at $df = n-2$ was 0.553 (at $P < 0.05$ and $n = 13$, i.e. 14 DBH classes minus 1).

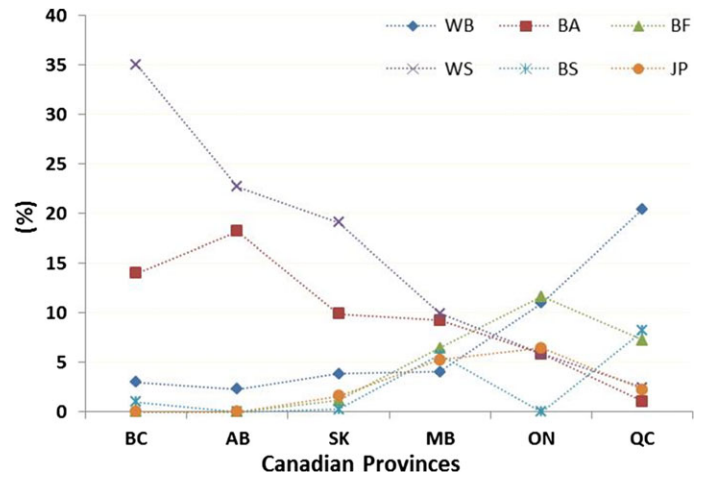


Figure 6 Proportion (%) of 'least pure' aspen stands with the main companion tree species. 'WB' refers to aspen-dominated stands where paper birch (*Betula papyrifera*) is main companion tree species, and 'BA' as balsam poplar (*Populus balsamifera*), 'BF' as balsam fir (*Abies balsamea*), 'WS' as white spruce (*Picea glauca*), 'BS' as black spruce (*Picea mariana*), and 'JP' as jack pine (*Pinus banksiana*).

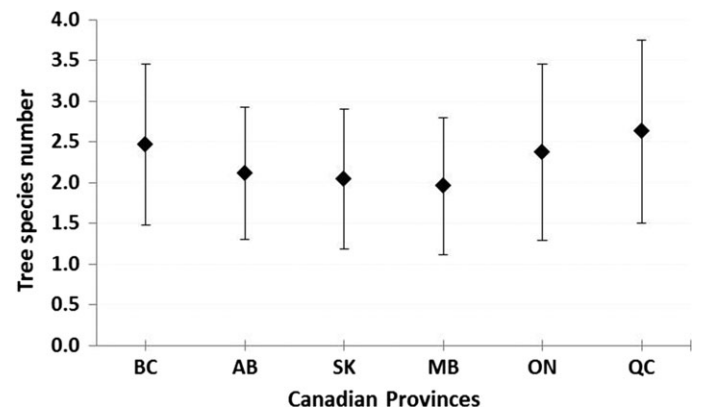


Figure 7 Variability in average species richness per stand in a province. The black diamonds designate the number of tree species while the black line on each diamond represents two standard deviations to indicate the degree of variability existing in stands within a province.

replaced by the 'Lat' variable in Mod2. The other candidate models had a $\Delta AIC > 2$ and a lower W_i , and they are unlikely to be the best fit for our data.

Table 6 displays the statistics and the effect for each variable included in the top-ranked model (Mod1, Table 5). All confidence intervals of these variables exclude 0, and associated P -values indicate that each retained predictor variable significantly improved the model ($P < 0.05$). The model-averaged estimate indicated that the stand age-site productivity interaction had a significantly positive effect on structural type. The 'advanced' structure type was favoured by an increase in degree-days and a decrease in road density and is also positively associated with an increase in species richness. Conversely, the lengthening of the fire cycle and the distance of a stand to a road negatively influenced the 'advanced' structure type.

Table 5 List of models and results of model selection based on AIC Criteria to explain the pattern of structural types distribution

Candidate models	Model ID	K	LL	AIC	Δ AIC	W_i
Age*SI+DD+RichSp+DensRoad15Km+DistRoad+FC	Mod1	8	-1256.54	2529.16	0.00	0.53
Age*SI+DD+RichSp+DensRoad15Km+DistRoad+Lat	Mod2	8	-1256.67	2529.42	0.26	0.42
Age*SI+DD+RichSp+Long	Mod3	6	-1260.53	2533.12	3.96	0.07
Age*SI+DD+RichSp+DensRoad15Km+FC	Mod4	7	-1260.25	2534.58	5.41	0.03
Age*SI+DD+RichSp+DensRoad15Km	Mod5	6	-1262.53	2537.11	7.95	0.01
Age*SI+DD+RichSp+FC	Mod6	6	-1264.03	2540.12	10.95	0.00
Age*SI+DD+RichSp	Mod7	5	-1268.38	2546.79	17.63	0.00
Age*SI+DD+AI	Mod8	5	-1269.00	2548.04	18.88	0.00
Age*SI+DD+FC	Mod9	5	-1272.43	2554.90	25.73	0.00
Age*SI	Mod10	3	-1295.56	2597.14	67.98	0.00

Note: Models are ranked based on their AIC scores, where the smallest AIC represents the best model (in bold).

K = Number of estimated parameters included in the model; LL = log-likelihood value of the model; AIC = Akaike's Information Criterion value; Δ AIC = delta AIC, a measure of the model relative to the best model; W_i = AIC model weight, representing the ratio of the Δ AIC of the model relative to the whole set of candidate models.

Table 6 Model-averaged estimates of the explanatory variables of the parsimonious model (Mod1) and their 95% confidence intervals (CI), as well as their variance partitioning

Covariates	Estimate	Lower 95% CI	Upper 95% CI	P value	Variance (%)
Age*SI	0.0065	0.0060	0.00703	<0.000	N/A
DD	0.0021	0.0014	0.00283	<0.000	42.5
RichSp	0.2226	0.1205	0.32471	<0.000	23.8
DensRoad15Km	-0.0012	-0.0019	-0.00040	0.003	11.8
DistRoad	-0.0386	-0.0670	-0.01024	0.008	9.5
FC	-0.0001	-0.0002	-0.00003	0.009	9.1

Note: All variables are significant at $P < 0.05$, based on the z test. Variance is the proportion of variability explained by variable in the model, as defined in Equations (1) and (2). In the estimation of variances, the interaction Age*SI was considered as the parameter of the null model because Age and SI are co-factors unrelated to our study assumptions, and which we want to control the effect. N/A = not applicable.

The effect of the Age*SI interaction was stronger than the individual effects of these two covariates. Apart from this local effect (expressed by Age*SI), regional climate (DD, 42.5%), stand species richness (RichSp, 23.8%), anthropogenic impact (DensRoad15km, 11.8%; DistRoad, 9.5%) and fire regime (FC, 9.1%) also contributed significantly to the observed structural variability.

Discussion

Our results indicate that the structural distribution of aspen stands can be thought of as a product of forest dynamics and biophysical processes, with regional differences observed across the Canadian boreal mixedwood. We first discuss the local and regional factors explaining stand structure, before comparing the stand structure across Canada.

Local and regional factors influencing stand structure and composition

Locally, the synergy between stand age and site productivity was established as an important factor of variation in structure

types of aspen-dominated stands within the Canadian mixedwood. Stand age or site productivity alone did not adequately predict the structure types in aspen stands. This finding corroborates studies conducted in other forest types which observed that structural changes do not depend solely on stand age or site productivity (Bergeron, 2000; Boucher et al., 2006b). This is clearly illustrated in Table 1, for example when the average stand age in BC (69.2 years) is higher than in AB (35.3 years), however, average tree diameter is larger in AB (DBH = 18.9 cm) due to better growth conditions (SI = 23.2 m) than in BC (DBH = 16.8 cm) where tree growth is slower (SI = 17.9 m). Figure 3 does not assume that the SI decreased with stand age, but it just shows the SI effect on the structural maturation rates and life expectancy of the stand. Aspen-dominated stands found on productive sites would become mature and uneven sized earlier, resulting in a more rapid emergence of shade-tolerant species within gaps, thus creating a more diverse stand than those found on less productive sites. Boucher et al. (2006b) argue that this is due in part to (1) a higher growth rate in more productive stands, which likely induces earlier senescence and thus leads to a more rapid shift to an uneven-sized structure, and (2) a scarcity of resources in poor stands, which in turn reduces both the diversity of tree diameters as well as the

maximum diameter that can be attained, even after the stand begins to breakup.

Besides this local effect, we also observed a strong regional effect of climate on the distribution of structural types, both directly (degree-days) and indirectly (fire cycle). The number of degree-days has an impact on tree growth duration and by extension the structural maturation of the stand. The fact that lengthening of fire cycle is associated with the juvenile structure type (i.e. negative effect of FC) in the best predictive model (Table 6) seemed counter-intuitive. This does not mean that longer fire cycles are positively related to juvenile structures necessarily but it could be due to a predominance of juvenile structures in the eastern aspen forests although this region is subjected to longer fire cycles which were supposed to promote more of mature structure types. In fact, the eastern boreal of Canada has experienced a longer history of timber harvesting (Paillé, 2012). The majority of juvenile structures in aspen forests in QC and ON would reflect forest landscapes that are largely shaped or affected by anthropogenic disturbances in this portion of the study area. This assumption is corroborated mainly by the higher road density in QC and ON compared with the other provinces (Table 1), suggesting an increasing pressure from human activities and their effects on forest ecosystems. The combined effects of harvesting and fire led to the simplification of forest structure (Laquerre et al., 2009; Terrail, 2013) in the eastern boreal forest. Road density was also high in AB, but it would be more related to oil exploration rather than to forest exploitation (Arienti et al., 2010; Latham et al., 2011). The distance of a stand to a road (DistRoad: another proxy for human activities) also affects forest structure but its negative effect given in Table 6 could be related to the sampling design of SK where aspen stands were mostly selected due to their proximity to road but show a mature structure generally. Finally, 'advanced' structure type was positively associated with tree species richness, since the occurrence of companion species in tree stratum appears later in aspen stand maturation. This is due partly to inherent differences in growth rates between tree species (Varga et al., 2005). In Table 5, the latitudinal gradient (Lat) in Mod2 also reflects a fire regime gradient, i.e. that wildfire events are more common in the northern part of the Canadian boreal forest compared with the southern part (Girardin et al., 2013). This explains why FC in Mod1 is replaced by the Lat in Mod2 (Table 5), thus, ultimately these two models are similar.

Comparison between regions

As expected, juvenile aspen stands were proportionally more abundant in the western and middle portions of the study transect, due to a relatively short regional fire cycle (Table 1). The Chi-squared test revealed no significant differences in the structural pattern between AB and BC. Although the average fire cycles are short, many mature aspen stands found in SK were found at the ecotone between the boreal forest and the prairie grasslands, an area infrequently exposed to fire (fire cycle >1000 years, Table 1).

Conversely, the observed low proportion of mature aspen stands in QC and ON cannot be explained by the regional fire regime (Table 1). It is likely the result of a long history of human colonization and forest management practices in the region

(Paillé, 2012) that has resulted in a reduction of a large part of the old, often structurally complex natural forest across the landscape (Gauthier et al., 2009; Bose et al., 2014). Human activities have contributed to the transformation of eastern forest landscapes since the early twentieth century by rejuvenating and altering the forest composition in the affected areas (Boucher et al., 2006a; Laquerre et al., 2009; Terrail, 2013). Forest management and human colonization may thus explain the low impact of the existing fire regime in the eastern boreal forest, by creating a distribution pattern more typical of one found under a shorter fire cycle, dominated by younger stands rather than old forests.

Cumming et al. (2009) report that the canopies of upland mesic sites in the boreal mixedwood forests of western Canada are dominated by some combination of *Populus* species (typically trembling aspen, but at times balsam poplar) and white spruce. Like these authors, we also found that white spruce and balsam poplar are the main companion tree species associated with the least pure aspen stands category in western Canada (Figure 6). Balsam fir and paper birch (mainly on coarse deposits) were their equivalent in east (Bergeron et al., 2014).

High proportions of pure aspen stands observed in SK and MB (Figure 5 and Table 4) are the result of low conifer recruitment in this region (Nlungu-Kweta et al., 2014). This is probably due to severe drought conditions that reduce the growth and survival of conifer seedlings, and intense competition from bluejoint grass (*Calamagrostis canadensis* [Michx.] P.Beauv.).

Overall, a small proportion of observed mature, old aspen forests have evolved into a multi-layered (uneven-sized) structure without compositional change. This phenomenon of multi-cohort pure aspen forests was observed throughout the entire Canadian boreal mixedwood forest (Table 4) supporting observations made by Cumming et al. (2000) in British Columbia and LeBlanc (2014) in Manitoba. The theory of gap dynamics is highlighted by suggesting a mechanism whereby old, uneven-aged aspen stands could develop and persist in the absence of shade-tolerant and other hardwood competitors (Moulinier et al., 2011). Most aspen regeneration is clonal via root suckers that can be subsidised by canopy trees (Peterson and Peterson, 1992; Frey et al., 2004). Therefore when even a small gap is created in the canopy, and there is an absence of competitors, aspen will fill the openings by root suckering to form a new cohort, generating an uneven-sized and spatially heterogeneous age structure.

Conclusion

This study revealed that the distribution pattern of aspen-dominated stand characteristics was similar between western and eastern portions of the Canada's boreal mixedwood, despite a marked contrast in climatic conditions and fire regime.

The effects of regional climate and associated disturbance regimes affect variously the forest ecosystem under study along an east-west transect. The western aspen forests remained mainly shaped by frequent wildfires, while the distribution of stand structural types of eastern aspen forests does not correspond with the dominant fire regime (long FC) in this region. The finding in eastern Canada suggests that human activities can decouple the link between natural disturbance regime and the

ecosystem by superimposing a new disturbance regime upon the pre-existing natural one. The potential effects of altered fire regime due to climate change on forest characteristics could be more significant in the eastern aspen forests, whereas the cumulative effects of fire and forest harvesting have already simplified stand structure to similar proportions as fire alone does in the western aspen forests. Besides the effects of fire regime and human activities, the site's richness appeared as a significant factor affecting the forest structural maturation rate.

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Conflict of interest statement

None declared.

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References

- Anyomi, K.A., Lorenzetti, F., Bergeron, Y. and Leduc, A. 2015 Stand dynamics, humus type and water balance explain aspen long term productivity across Canada. *Forests* **6**, 416–432.
- Arienti, M.C., Cumming, S.G., Krawchuk, M.A. and Boutin, S. 2010 Road network density correlated with increased lightning fire incidence in the Canadian western boreal forest. *Int. J. Wildland Fire* **18**, 970–982.
- Baldwin, K.A., MacKenzie, W.H., Pfalz, J., Meades, W.J., Meidinger, D.V., Robitaille, A., et al. 2012 *Level 4 Map, Version 1, Canadian Component of the Circumboreal Vegetation Map (CBVM); Canadian regional team of the Circumboreal Vegetation Map Project*. Natural Resources Canada, Canadian Forest Service, Great Lakes Forestry Centre.
- Bergeron, Y. 2000 Species and stand dynamics in the mixed woods of Quebec's southern boreal forest. *Ecology* **81**, 1500–1516.
- Bergeron, Y., Chen, H.Y., Kenkel, N.C., Leduc, A.L. and Macdonald, S.E. 2014 Boreal mixedwood stand dynamics: ecological processes underlying multiple pathways. *For. Chron.* **90**, 202–213.
- Bergeron, Y., Gauthier, S., Flannigan, M. and Kafka, V. 2004 Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. *Ecology* **85**, 1916–1932.
- Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P. and Lesieur, D. 2001 Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. *Can. J. For. Res.* **31**, 384–391.
- Borcard, D., Gillet, F. and Legendre, P. 2011. *Numerical Ecology with R*. Springer, New York, USA. 306 pp.
- Bose, A.K., Harvey, B.D., Brais, S., Beaudet, M. and Leduc, A. 2014 Constraints to partial cutting in the boreal forest of Canada in the context of natural disturbance-based management: a review. *Forestry* **87**, 11–28.
- Boucher, Y., Arseneault, D. and Sirois, L. 2006a Logging-induced change (1930–2002) of a preindustrial landscape at the northern range limit of northern hardwoods, eastern Canada. *Can. J. For. Res.* **36**, 505–517.
- Boucher, Y., Arseneault, D., Sirois, L. and Blais, L. 2009 Logging pattern and landscape changes over the last century at the boreal and deciduous forest transition in Eastern Canada. *Landscape Ecol.* **24**, 171–184.
- Boucher, D., De Grandpré, L. and Gauthier, S. 2003 Développement d'un outil de classification de la structure des peuplements et comparaison de deux territoires de la pessière à mousses du Québec. *For. Chron.* **79**, 318–328.
- Boucher, D., Gauthier, S. and De Grandpré, L. 2006b Structural changes in coniferous stands along a chronosequence and a productivity gradient in the northeastern boreal forest of Québec. *Ecoscience* **13**, 172–180.
- Boulanger, Y., Gauthier, S., Burton, P.J. and Vaillancourt, M.-A. 2012 An alternative fire regime zonation for Canada. *Int. J. Wildland Fire* **21**, 1052–1064.
- Burnham, K.P. and Anderson, D.R. 2002 *Model Selection and Multimodel Inference: A Practical Information - Theoretic Approach*. 2nd edn. Springer-Verlag, New York, USA.
- Chen, H.Y.H. and Popadiouk, R.V. 2002 Dynamics of North American boreal mixedwoods. *Environ. Rev.* **10**, 137–166.
- Chen, H.Y.H., Vasiliauskas, S., Kayahara, G.J. and Ilisson, T. 2009 Wildfire promotes broadleaves and species mixture in boreal forest. *For. Ecol. Manag.* **257**, 343–350.
- Cumming, S., Schmiegelow, F. and Burton, P. 2000 Gap dynamics in boreal aspen stands: is the forest older than we think? *Ecol. Appl.* **10**, 744–759.
- Cumming, S., Trindade, M., Greene, D. and Macdonald, S.E. 2009 Canopy and emergent white spruce in 'pure' broadleaf stands: frequency, predictive models, and ecological importance. *Can. J. For. Res.* **39**, 1997–2004.
- Environment Canada. 2013 *National Climate Data and Information Archive*. <http://climate.weatheroffice.gc.ca/> (accessed on 23 September, 2013).
- Field, C.B., Mortsch, L.D., Brklacich, M., Forbes, D.L., Kovacs, P., Patz, J.A., et al. 2007 North America. In: *Climate Change 2007: Impacts, Adaptation and Vulnerability*. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. M.L. Parry, O.F. Canziani, J.P. Palutikof, P.J. van der Linden and C.E. Hanson (eds). Cambridge University Press, Cambridge, UK. pp. 617–652. Available from http://www.ipcc.ch/publications_and_data/ar4/wg2/en/ch14.html (accessed on 8 August, 2014).
- Frey, B.R., Liefers, V.J., Hogg, E.H. (Ted) and Landhäusser, S.M. 2004 Predicting landscape patterns of aspen dieback: mechanisms and knowledge gaps. *Can. J. For. Res.* **34**, 1379–1390.
- Gauthier, S., Bernier, P., Burton, P.J., Edwards, J., Isaac, K., Isabel, N., et al. 2014 Climate change vulnerability and adaptation in the managed Canadian boreal forest. *Environ. Rev.* **22**, 256–285.
- Gauthier, S., Leduc, A., Bergeron, Y. and Le Goff, H. 2009. Fire frequency and forest management based on natural disturbances. In *Ecosystem Management in the Boreal Forest*. S. Gauthier, M.A. Vaillancourt, A. Leduc, L. De Grandpre, D.D. Kneeshaw, H. Morin, P. Drapeau and Y. Bergeron (eds.). Presses de l'Université du Québec, pp. 39–56.
- Girardin, M.P., Ali, A.A., Carcaillet, C., Blarquez, O., Hély, C., Terrier, A., et al. 2013 Vegetation limits the impact of a warm climate on boreal wildfires. *New Phytol.* **199**, 1001–1011.
- Hart, S.A. and Chen, H.Y.H. 2006 Understorey vegetation dynamics of North American boreal forests. *Crit. Rev. Plant Sci.* **25**, 381–397.

- IPCC. 2007 *Climate Change 2007 – The Physical Science Basis*. Working Group I Contribution to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Edited by S. Solomon. Vol. 4. Cambridge University Press. Available from http://www.ipcc.ch/publications_and_data/publications_ipcc_fourth_assessment_report_wg1_report_the_physical_science_basis.htm (accessed on 11 August, 2014).
- Johnson, E.A. 1996 *Fire and Vegetation Dynamics: Studies from the North American Boreal Forest*. Cambridge University Press, Cambridge, UK.
- Kneeshaw, D.D. and Bergeron, Y. 1998 Canopy gap characteristics and tree replacement in the southeastern boreal forest. *Ecology* **79**, 783–794.
- Kneeshaw, D. and Gauthier, S. 2003. Old growth in the boreal forest: a dynamic perspective at the stand and landscape level. *Environ. Rev.* **11**, 99–114.
- Kuuluvainen, T. 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fenn.* **36**, 97–125.
- Lähde, E., Laiho, O., Norokorpi, Y. and Saksala, T. 1999 Stand structure as the basis of diversity index. *For. Ecol. Manag.* **115**, 213–220.
- Laquerre, S., Leduc, A. and Harvey, B.D. 2009. Augmentation du couvert en peuplier faux-tremble dans les pessières noires du nord-ouest du Québec après coupe totale. *Ecoscience*. **16**, 483–491.
- Latham, A.D.M., Latham, M.C., McCutchen, N.A. and Boutin, S. 2011 Invading white-tailed deer change wolf–caribou dynamics in north-eastern Alberta. *J. Wildl. Manag.* **75**, 204–212.
- LeBlanc, P.A. 2014 Incorporating multi-cohort old aspen and mixedwood dynamics into a long-term forest management plan. *Forest. Chron.* **90**, 50–58.
- Legendre, P. and Legendre, L. 2012 *Numerical Ecology*. 3rd edn. Elsevier, Oxford, UK. 990 pp.
- Mazerolle, M. 2006 Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. *Amphibia-Reptilia*. **27**, 169–180.
- Mazerolle, M. 2011. AICcmodavg: model selection and multimodel inference based on (Q)AIC(c). R package version 1.17. <http://cran.r-project.org/web/packages/AICcmodavg/index.html>.
- McCarthy, J. 2001 Gap dynamics of forest trees: a review with particular attention to boreal forests. *Environ. Rev.* **9**, 1–59.
- Moss, I. 2012. *Stand Structure Classification, Succession, and Mapping Using LiDAR*. Dissertation, University of British Columbia, Vancouver, BC. 170 pp.
- Moulinier, J., Lorenzetti, F. and Bergeron, Y. 2011 Gap dynamics in aspen stands of the clay belt of northwestern Quebec following a forest tent caterpillar outbreak. *Can. J. For. Res.* **41**, 1606–1617.
- Nigh, G.D., Krestov, P.V. and Klinka, K. 2002. Trembling aspen height-age models for British Columbia. *Northwest Sci.* **76**, 202–212.
- Nlungu-Kweta, P., Leduc, A. and Bergeron, Y. 2014. Conifer recruitment in trembling aspen (*Populus tremuloides* Michx.) stands along an East–West gradient in the boreal mixedwoods of Canada. *Forests* **5**, 2905–2928.
- Paillé, G. 2012 *Histoire forestière du Canada*. Les Publications du Québec. 436 pp.
- Perala, D.A. 1990 *Populus tremuloides* Michx. Quaking aspen. In *Silvics of North America. Vol. 2. Hardwoods*. R.M. Burns and B.H. Honkala (Technical Coordinators). USDA, Forest Service. Washington, DC. Agriculture Handbook No. 654. pp. 555–569.
- Peterson, E.B. and Peterson, N.M. 1992 Ecology, Management, and Use of Aspen and Balsam Poplar in the Prairie Provinces, Canada. Forestry Canada, Northwest Region, Northern Forestry Centre, Edmonton, AB. Special Report 1. p. 252.
- R Development Core Team. 2013 *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. Available from <http://www.R-project.org/> (accessed on 6 December, 2013)
- Règnière, J. and Saint-Amant, R. 2008 BioSIM 9—Manuel de L'utilisateur. Ressources Naturelles Canada, Service Canadien des Forêts. Centre de Foresterie des Laurentides. <https://cfs.nrcan.gc.ca/publications?id=28769> (accessed on 4 February, 2012).
- Shorohova, E., Kuuluvainen, T., Kangur, A. and Jöggiste, K. 2009 Natural stand structures, disturbance regimes and successional dynamics in the Eurasian boreal forests: a review with special reference to Russian studies. *Ann. For. Sci.* **66**, 1–20.
- Stocks, B.J., Mason, J.A., Todd, J.B., Bosch, E.M., Wotton, B.M., Amiro, B.D., et al. 2002 Large forest fires in Canada, 1959–1997. *J. Geophys. Res. Atmos.* **107**, 8149.
- Terrail, R. 2013 *Influence de la colonisation sur les transformations du paysage forestier depuis l'époque préindustrielle dans l'Est du Québec (Canada)*. Dissertation, Université du Québec à Rimouski, Rimouski, QC.
- Varga, P., Chen, H.Y.H. and Klinka, K. 2005 Tree-size diversity between single- and mixed-species stands in three forest types in western Canada. *Can. J. For. Res.* **35**, 593–601.