

ARTICLE

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# Contrasting current and potential productivity and the influence of fire and species composition in the boreal forest: a case study in eastern Canada<sup>1</sup>

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**Abstract:** The capacity of a forest stand to produce timber is related to the interactions that exist between its regeneration capacity, physical site characteristics (climate, surficial deposit, drainage), and disturbances. Minimally, to be sustainably managed, a forest needs to be sufficiently productive and able to regenerate after a disturbance so that its productive capacity is maintained or enhanced. To this effect, we evaluated timber productivity over a large area (175 000 km<sup>2</sup>) covering the latitudinal extent of closed-canopy black spruce (*Picea mariana* (Mill.) B.S.P) forest. Site index and relative density index were used to identify stands that cannot reach a minimum volume of trees of minimum size over one rotation. A nonparametric method was used to estimate their values for all stands within the study area. This imputation used either physical site attributes alone to assess potential productivity independent of stand history or physical and vegetation site attributes to assess current productivity. The proportion of productive stands was then estimated at the scale of landscapes ranging from 39 to 2491 km<sup>2</sup>. Physical site factors alone explain 84% of the variability in the percentage of potentially productive stands (78% for currently productive stands); their combination resulted in an abrupt transition in productivity over the study area. However, burn rate alone also explains 63% of variation in the proportion of currently productive stands and 41% of the relative difference between percentages of potentially or currently productive stands. These results have implications for strategic forest management planning at land classification stage, as timber production area is assumed to remain stable through time, whereas it is apparently related to the disturbance rate.

Key words: boreal forest, fire, timber production area, black spruce, jack pine.

**Résumé**: La capacité d'une forêt à produire du bois est en relation avec les interactions existant entre sa capacité de régénération, les caractéristiques physiques du site (climat, dépôt de surface, drainage) et les perturbations. De facon minimale, pour que son aménagement soit durable, une forêt doit être suffisamment productive et capable de se régénérer après une perturbation de façon telle à ce que sa capacité de production soit maintenue ou améliorée. À cet égard, nous avons évalué la productivité en bois d'une vaste région (175 000 km<sup>2</sup>) qui recouvre l'étendue latitudinale de la pessière noire fermée (Picea mariana (Mill.) B.S.P). L'indice de qualité de station et l'indice de densité relative ont été utilisés pour identifier les peuplements qui ne peuvent atteindre un volume minimal de bois et des dimensions minimales d'arbres en une révolution. Une méthode non paramétrique a été utilisée pour estimer leur valeurs pour tous les peuplements de l'aire d'étude. Cette imputation a été faite en utilisant soit uniquement les attributs physiques du site pour estimer une productivité potentielle indépendante de l'historique du peuplement, soit une combinaison d'attributs physiques et de végétation pour estimer une productivité actuelle. La proportion de peuplements productifs a ensuite été estimée à l'échelle de paysages de taille variant entre 39 et 2491 km<sup>2</sup>. Les facteurs physiques du site expliquent à eux seuls 84 % de la variabilité dans le pourcentage potentiel de peuplements productifs (78 % pour le pourcentage actuel de peuplement productifs) et leur combinaison cause une transition abrupte de la productivité dans l'aire d'étude. Toutefois, le taux de brûlage, lorsque considéré seul, explique 63 % de la variabilité de la proportion de peuplements actuellement productifs et 41 % de la différence relative entre les pourcentages actuels et potentiels de peuplements productifs. Ces résultats ont des implications pour la planification stratégique de l'aménagement au moment de la stratification du territoire, puisque il est supposé que la superficie productive reste constante dans le temps alors qu'elle semble être en lien avec le taux de perturbation.

Mots-clés : forêt boréale, feu, superficie productive, épinette noire, pin gris.

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## Introduction

After humid tropical forest, the boreal forest is the second most extensive forest biome in the world (Hansen et al. 2010), where fire disturbances represent the main driver of forest dynamics, particularly in North America (Johnson 1992; Potapov et al. 2008) and eastern Canada (Bergeron et al. 2001; Gauthier et al. 2009). Fire disturbances are strongly variable in space and time (Cyr et al. 2009) and, when interacting with climate and soil deposits, can generate a mosaic of forest types with species compositions (Bergeron and Dansereau 1993; Le Goff and Sirois 2004), stand structures (Lavoie and Sirois 1998; Boucher et al. 2006), and productivities (Simard et al. 2007; Girard et al. 2008) that differ from one site to another. In particular, the proportions of closed-crown forest, open woodland, and lichen heath can be related to the frequency of fire disturbances (Girard et al. 2008, 2009; Mansuy et al. 2012).

The importance of sustainable forest management has been recognized by its adoption over the last 30 years in 150 countries (98% of the world's forest) (Wijewardana 2008). Sustainability requires that some minimum conditions be fulfilled and, among these, certain minima must be met for forest productive and regeneration capacities (e.g., Montreal Process (2009) for temperate and boreal North America). With respect to timber production, forests need to be productive enough that a sufficient volume of trees of a minimum size can be expected to be produced within a reasonable period of time (one rotation). Forests also need to regenerate after natural or anthropogenic disturbance in such a way that productivity prior to disturbance is either maintained or enhanced (Montreal Process 2009). In this context, studies of forest dynamics have mostly focused on analyzing the effects of disturbance on forest composition and stand structure (e.g., for eastern Canada: Lavoie and Sirois 1998; Payette and Delwaide 2003; Bergeron et al. 2004; Girard et al. 2008, 2009). However, studies that address the effects of disturbances on timber productivity remain relatively rare (Pennanen et al. 2004). Further, conceptual models of forest dynamics still need to be translated into the quantitative framework of timber supply planning (Seymour and Hunter 1999; Bergeron et al. 2001).

Forest productivity is related to the capacity of a site to produce tree biomass (Skovsgaard and Vanclay 2008). Timber productivity is itself related to forest productivity in that the stems represent an important fraction of the aboveground tree biomass (e.g., Gower et al. 1997). "Timber" refers to that portion of the tree stem used for wood processing, which requires a minimum merchantable top diameter. Potential site productivity can differ markedly from what is actually observed on a site (Skovsgaard and Vanclay 2008). Consequently, site productivity must be evaluated using data on current productivity vs. estimates of potential productivity. Current productivity attests to the history of the trees that are growing within the stand and is estimated from the existing vegetation (Weiskittel et al. 2011). Current productivity can vary with the density of the forest cover, even for sites with similar physical site characteristics (climate, surficial deposits, drainage). As a result, current productivity does not necessarily reflect a site's potential, especially if it has a low density of stems (deficient postfire recovery, secondary succession undermined by disturbances) or if no stems are present (Girard et al. 2009; Mansuy et al. 2012). Potential productivity represents the production capacity of a site, whether it currently has trees or not. It is determined by taking into account physical site characteristics (climate, surficial deposits, drainage) based on the assumption that a forest stand of given density will develop on the site, provided that there are no impediments to growth.

Black spruce (*Picea mariana* (Mill.) B.S.P.) and jack pine (*Pinus banksiana* Lamb.) are two common overstory species in the boreal forest of eastern Canada. These two species display different adaptations to fire (Burns and Honkala 1990). Jack pine is better adapted to short fire cycles, whereas black spruce can perpetuate

itself, regardless of whether fire is present or absent. Yet, jack pine is much less abundant than black spruce in the coniferous boreal forest. A relatively low fire frequency (in comparison with its life span and life history traits; Le Goff and Sirois 2004) seems to have prevented jack pine from migrating further north and east following the last deglaciation (Desponts and Payette 1993). Soil deposits and species abundance also have an important influence on the actual geographic distribution of this species (Parisien et al. 2004). Black spruce is a slow-growing species in comparison with jack pine. Its minimum harvesting age varies between 70 and 120 years, relative to the 40 to 60 years that are required for jack pine (Pothier and Savard 1998; Gustafson et al. 2006). The presence of jack pine, even in an area that is dominated by black spruce, may thus have a controlling influence on forest productivity.

The main objective of this study was to evaluate forest timber productivity within a large area in the boreal coniferous forest of eastern Canada (175 000 km<sup>2</sup>) and to identify the key factors that explain it. This area covers a broad latitudinal extent, ranging from the closed-canopy black spruce forests to open spruce woodlands. Moreover, varying fire regimes have been observed in this area (Mansuy et al. 2010). To this end, we used a growth and yield model to evaluate whether a stand produces sufficient timber or not within one rotation. We then realized four spatial analyses to estimate the percentage of timber-productive stands by landscape unit to test the influence of jack pine on their timber production area and to analyze how differences between current and potential productivities relate to physical site variables and to the fire disturbance regime.

# Methods

# Study area

The area that was under study (175 000 km<sup>2</sup>; Fig. 1) extended from 49°N to 53°N and from 70°W to 76°W. The closed-crown black spruce – moss bioclimatic domain covers the south up to 52°N, where it is replaced by the open black spruce - lichen bioclimatic domain (Robitaille and Saucier 1998). Two climatic gradients crisscross the study area, viz., precipitation, which is linked to the distance from James Bay (from 1100 mm·year-1 in the southeast of the study area to 680 mm·year<sup>-1</sup> in the northwest) and growing degree-days above 5 °C, which is linked to elevational and latitudinal changes (from 1200 °C in the southwest to 750 °C in the northeast) (Fig. 1). Mean annual temperature varies between 1.9 °C in the southwest and -6.0 °C in the northeast (Mansuy et al. 2010). Surficial deposits are mainly composed of glacial deposits, particularly thick (>1 m) undifferentiated tills (44% of the terrestrial area), thin undifferentiated tills (21%), and organic deposits (12%) (Mansuy et al. 2010). The fire cycle (time required to burn an area of a size equal to a study area, Johnson and Gutsell 1994; estimated with fire data observed between 1940 to 2009) varies from 90 years in the northwest to more than 700 years in the southeast (Mansuy et al. 2010). The forest canopy is largely dominated by black spruce, sometimes accompanied by jack pine, and less frequently by trembling aspen (Populus tremuloides Michx.), white or paper birch (Betula papyrifera Marsh.), and balsam fir (Abies balsamea (L.) Mill.). Balsam fir is slightly more common in the southeast due to a longer fire cycle (Bouchard et al. 2008).

South of 51°N (the approximate northern limit for timber allocation on public land), the area is subdivided into forest management units in which logging and silviculture have been practiced on a large scale since about 1950 (southwest of the study area). North of 51°N, the forest is unmanaged and little affected by human activities.

#### Forest data

The source of data changes when moving from south to north of the timber allocation limit. North of 51°N, aerial photographs at the scale of 1:40 000 were used to map surface deposits and hydric **Fig. 1.** (*a*) Mean elevation and degree-days and (*b*) burn rate and precipitation within the study area. Degree-days and precipitation were generated with BioSIM (Régnière and Saint-Amant 2008). Burn rate values are taken from Mansuy et al. (2010). The northern limit of timber allocation corresponds to that set by the Ministry of Natural Resources and Wildlife (Quebec) in 2002 (MRNFQ 2000).



regimes. Landsat images from 2005 were then used to delineate forest stands (minimum area of 8 ha) and classify their vegetation and probable origin (cover type, understory vegetation, cover density class, development stage and disturbance of origin; Létourneau et al. 2008; Mansuy et al. 2012). South of 51°N, vegetation information came from interpretation of aerial photographs, which was performed during the last regular forest inventory program of the Ministère des Ressources Naturelles (MRN) (1990-2001) and updated in 2006 to account for recent stand-destroying disturbances. Minimum stand area (4 ha) and the level of detail describing physical and vegetation stand attributes were adapted to the cartographic standards applied north of the timber allocation limit (Robitaille et al. 2013). For the purposes of the present study, we have used 945 sampling plots that were dominated by black spruce or jack pine (one species had to represent >75% of the plot basal area). These sampling plots were either established in 2006 or 2007 (248 temporary sample plots essentially north of 51°30'N) or measured between 1990 and 2001 as part of the re-measurement program of the permanent sample plot network (406 plots south of 51°N; 291 plots north of 51°N). The plot dataset is evenly distributed across the study area (Supplementary

Fig. S1<sup>2</sup>). Most of the permanent sample plots that were north of the timber allocation limit are situated south of 52°N. Within each sample plot (400 m<sup>2</sup>), species and diameter at breast height (DBH, 1.3 m) were recorded for each merchantable tree (DBH > 9 cm). In each plot, three to five dominant or co-dominant trees were randomly selected to record their age (core at 1 m height) and total height. Merchantable volumes were estimated from the volume tables of Perron (1985).

## Climate data

Sum of degree-days above 5 °C, the number of frost-free days (days·year<sup>-1</sup>), growing-season length (number of days between two periods of three consecutive days with a negative minimum daily temperature, days·year<sup>-1</sup>), length of the frost-free season (longest period of year with a mean daily temperature above 0 °C, days·year<sup>-1</sup>), total yearly radiation (MJ·m<sup>-2</sup>·year<sup>-1</sup>), an aridity index (sum of the difference between Thornthwaite's potential evapotranspiration and monthly precipitation, mm·year<sup>-1</sup>; Dunne and Leopold 1978), annual precipitation (mm·year<sup>-1</sup>), and the proportion of total precipitation as snow were obtained from the BioSIM model

<sup>&</sup>lt;sup>2</sup>Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2014-0124.

#### Estimation of productivity at the plot level

To help assess the differences that may exist between potential and current productivities, productivity needs to be divided into two components: site productivity and density. This distinction forms the basis of yield tables that are used for black spruce and jack pine stands growing as far north as 51°N latitude in Quebec (Pothier and Savard 1998). The yield tables are based on two key parameters: site index (SI) and relative density index at 100 years (RDI<sub>100</sub>). SI is a measure of site potential based on the height of dominant trees in a stand at a reference age of 50 years; it remains independent of density over a wide range of densities (Skovsgaard and Vanclay 2008). RDI<sub>100</sub> refers to the density of a stand relative to that of a very dense stand of the same mean diameter size (Drew and Flewelling 1979), normalized to 100 years. These indices are intended mainly for even-aged monospecific stands, but they can also be used for more open or irregular stands (Monserud 1984).

The yield tables of Pothier and Savard (1998) correspond to a system of four equations that are used to predict dominant height, basal area, mean quadratic diameter, and merchantable volume for merchantable stems in monospecific stands (where a species represents >75% of stand basal area) from stand age, SI, and RDI<sub>100</sub>. Because these tables are empirical and were calibrated with data that were located essentially south of 51°N, a first step consisted of verifying whether these tables would also be valid north of 51°N or they should be recalibrated. The quality of the predictions for both black spruce and jack pine stands was assessed with the coefficient of determination (R<sup>2</sup>) for observed vs. predicted merchantable volumes and with the "novel test" of Klejinen et al. (1998) to detect biases. This latter procedure tests if the parameters of a linear regression between the difference and the sum of observed and predicted values are equal to zero. Sample plots that were established north of 51°N in 2006 or 2007 and, consequently, never utilized for yield table calibration were used for this purpose.

These yield tables were used to identify productive stands across the study area. Unproductive stands are stands that do not reach a harvesting threshold (minimum number of trees of a minimum size) in one rotation and are excluded from the timber production area. A double threshold was thus used: a minimum merchantable volume ( $\geq 9$  cm diameter) at the stand level (50 m<sup>3</sup>·ha<sup>-1</sup>), and a minimum stem volume (50 dm<sup>3</sup>). These harvesting thresholds are considered to be loose constraints and provide very narrow economic benefits (Liu et al. 2007).

# Estimation of productivity at the level of landscapes

The study area was divided into two by the northern limit of commercial forestry in Quebec, which was set in 2002 (Ministère des Ressources naturelles et de la Faune (MRNFQ) 2000). Areas were excluded from the timber production area because the proportion of their timber production area, relative to their total terrestrial area, was judged insufficient. Ecological districts were found to be appropriate for characterizing landscape-level species distributions as a function of the abundance of surficial deposits (Messaoud et al. 2007), for characterizing forest productivity, or for applying landscape-level guidelines for forest management (Gauthier et al. 1996). These districts corresponded to land units that are characterized by particular relief, combinations of surficial deposits, and their drainage regimes (Robitaille et al. 1989). The study area included 404 ecological districts (average size = 473 km<sup>2</sup>). Their size ranged from 38 to 2491 km<sup>2</sup>, with small-sized districts being concentrated in the southwest and large ones being concentrated in the northwest of the study area (Supplementary Fig. S1<sup>2</sup>). District sizes reflected landscape heterogeneity.

To estimate the percentage of productive stands by ecological district (Fig. 2), a nonparametric method (nearest-neighbour, NN; Moeur and Stage 1995) was used to extend the productivity results that were obtained from forest stands containing a sample plot to all other stands within the entire study area. The k-NN method estimates the desired forest attributes of a target land unit (i.e., stand) as the mean values of these attributes from the k most similar reference land units for which these attributes have been determined from forest inventory sample plots (Moeur and Stage 1995; McRoberts et al. 2007; Bernier et al. 2010). The target dataset consists of all forest stands in the study area. Similarity between a reference stand and the target stand was estimated with Gower's distance (DISTANCE procedure, SAS Institute Inc., Cary, North Carolina), which has the advantage of accepting both categorical and numeric attributes (Gower 1971). The weighted mean of the SI and  $RDI_{100}$  for the k nearest reference plots served as SI and  $RDI_{100}$ estimates for the target stands. Weights of reference plots corresponded to the inverse of the distance. The number of k nearest stands was determined by cross-validation to determine the number of k that minimized the root mean square error (RMSE) of the SI and RDI<sub>100</sub> estimates.

The variables that were most likely to be significant in determining the *k*-NN were selected using a two-step approach. Step 1 consisted of performing an initial *k*-NN analysis that considered all available mapping and climatic attributes. Step 2 served to select from among these attributes those that significantly explained the distance (with the GLMSELECT procedure in SAS), while retaining only one attribute when selected attributes showed a strong (r > 0.6) correlation between them. All *k*-NN analyses were then carried out by considering the variables that were selected in step 2 or a set of them (Table 1).

Four subsequent k-NN analyses were realized to address the effects of species composition and fire regime on forest productivity (two types of species composition × two types of productivity). We first assumed that black spruce occurs alone across the study area. To estimate potential productivity, two k-NN analyses were realized with black spruce dominated plots (712 plots), using either all variables that were considered (Table 1) to estimate current productivity or the set of variables that did not relate to vegetation. By excluding all variables pertaining to vegetation, an analysis could indeed be performed that was dependent solely on a site's physical characteristics, making it possible to estimate productivity on sites that had no trees or that have experienced deficient postfire recovery, which can be equated with potential productivity. We then assumed that black spruce or jack pine dominated stands can occur concurrently in an ecological district. The species dominance of any target stand was first estimated with two logistic models (LOGISTIC procedure in SAS), the first to estimate the probability of jack pine presence and the second to estimate the probability of jack pine dominance in any plot that included at least one jack pine tree. Strength of association was measured with the gamma coefficient (Goodman and Kruskal 1954). Either one of the plot datasets (712 black spruce and 233 jack pine plots) was then used in two subsequent k-NN analyses to estimate whether a target stand was currently or potentially productive, as a function of its species dominance. The numbers of neighbours that were used in the k-NN analyses were 14 (black spruce, potential productivity), 15 (black spruce, current productivity), and 17 (jack pine, both types of productivity).

SI and  $RDI_{100}$  values that had been assigned to all forest stands in a district by the *k*-NN method allowed stand classes to be derived (productive vs. unproductive) with the stand yield tables of Pothier and Savard (1998), thereby allowing estimation of the percentage of productive stands at the scale of ecological districts (Fig. 2). This classification cannot be performed with any certainty at the level of stands as imputation of the corresponding SI and **Fig. 2.** Flowchart describing the four *k*-NN analyses that were used to address the effects of species composition and fire regime on forest productivity (two types of species composition (black spruce alone or black spruce and jack pine concurrently) crossed with two types of productivity (potential or current)).



Table 1. List of mapping and climatic attributes used in the k-NN analyses.

Climatic variables (Régnière and Saint-Amant 2008)	Physical site variables	Historical variables (Létourneau et al. 2008)	Vegetation variables (Létourneau et al. 2008)ª
Degree-days (°C·year-1)	Elevation (m)	Disturbance of origin (burn, clear cut, severe defoliation, windthrow) <sup>b</sup>	Cover type (hardwood, mixed, conifer) <sup>b</sup>
Growing season length (days·year <sup>-1</sup> )	Slope exposure (°)	Partial disturbance (partial burn, partial defoliation, partial windthrow) <sup>b</sup>	Cover density (more than 60%, 40%–60%, 25%–40%, and 10%–25% of ground area covered by trees) <sup>b</sup>
Length of the frost-free season (days-year-1)	Soil surficial deposit (Robitaille and Allard 2007)	······,	Ecological type (Robitaille and Saucier 1998) <sup>b</sup>
Total radiation (MJ·m <sup>-2</sup> ·year <sup>-1</sup> )	Drainage (hydric, subhydric, mesic, and xeric)		Understory vegetation (lichen, moss, and moss and lichen) <sup>b</sup>
Aridity index (mm·year <sup>-1</sup> ) (Dunne and Leopold 1978)			Developmental stage (mature, young, regenerated, not regenerated) <sup>b</sup>
Proportion of total precipitation as snow			

<sup>*a*</sup>Variables used only to estimate current productivity.

<sup>b</sup>Categorical variables.

RDI<sub>100</sub> values from mapping attributes is adversely affected by considerable variability (e.g., Ung et al. 2001; Bernier et al. 2010). To reduce the risk of obtaining an incorrect (especially an overestimated) percentage of productive stands in each district, the first decile (rather than the median value) of the cumulative frequency

distribution of the percentage of productive stands was selected as an estimate of district productivity.

Cumulative frequency distributions of the proportion of productive stands per district were consequently constructed to address the effects of this variability, which has been detailed as **Fig. 3.** Coefficient of variation (CV) for the first decile of the cumulative probability distribution of the percentage of potentially productive stands by ecological district (solid grey circles). The dark lines and solid black circles represent, respectively, the first and last quartiles and the median of the cumulative probability distribution of this CV when districts are regrouped by classes of percentages of productive stands. The histogram bars denote the number of districts by percentage class of productive stands.



follows. Because each stand is allocated *k* sample plots to estimate its current or potential productivity, random sampling with replacement (bootstrapping) of *k* plots among the *k* plots for each stand in a district was repeated 100 times to calculate each type of productivity. Given the mean number of stands per district (2380 forest stands), this number of repetitions ensured that the coefficient of variation for the first decile was maintained below 5% for most ecological districts (88% of the districts, 73% of the study area; Fig. 3). Almost all of the districts for which this coefficient of variation was greater than 5% had a very low percentage of productive stands (below 10%; Fig. 3).

The use of a nonparametric imputation technique such as the *k*-NN method makes it much more difficult to interpret the results. The results were therefore synthesized to explain the percentage of productive stands using variables that were estimated at the district scale or, more specifically, dominant relief (plain, hill-ocks, hills, mountains, or valleys; Robitaille and Saucier 1998), dominant surficial deposit, and climatic variables. General linear models were used for this purpose (GLM procedure in SAS). The objective of this synthesis was not to replace the imputation method; rather, it identified the four or five factors that best explained the percentages of potentially and currently productive stands in each district.

# Results

## Validation of yield tables north of 51°N

North of the timber allocation limit, Pothier and Savard's (1998) yield tables provide very accurate but significantly biased estimates of stand merchantable volume (Fig. 4). For both species, the novel test rejected the hypothesis of strict equality between observed and predicted volumes ( $F_{obs} = 11.6 > F_{[0.9,2,197]} = 2.3$  for black spruce and  $F_{obs} = 5.2 > F_{[0.9,2,46]} = 2.4$  for jack pine). Despite this result, we tolerated (sensu Freese 1960) the presence of biases, as they average less than 3% for both species.

# Estimation of site index and relative density index with *k*-NN

Biases in the estimates of SI with the training dataset for current or potential productivity are low for both species (between -0.5% and 0.3%). Biases for RDI<sub>100</sub> are slightly higher (between -3.2% and -4.8%), with no particular trend appearing as a function of species or type of productivity. Mean quadratic errors, however, are much higher, exhibiting a great deal of residual variability (Fig. 5), and, indeed, largely exceed their respective biases, with

**Fig. 4.** Observed vs. predicted merchantable volumes for (*a*) black spruce and (*b*) jack pine monospecific sample plots (more than 75% of basal area), which were established in 2006 or 2007 north of the existing timber allocation limit.



values between 1.8 to 1.9 m for SI (15% to 17%) and between 0.2 and 0.4 for  $RDI_{100}$  (44% to 212%). The fit to observed values was relatively acceptable, with coefficients of determination between 24% and 32% for SI and between 11% and 28% for  $RDI_{100}$  (Fig. 5). The lowest coefficients of determination and highest biases are observed for the  $RDI_{100}$  of jack pine (Figs. 5g and h). This is attributable to lower variability in observed  $RDI_{100}$  values for jack pine when compared with black spruce and to the fact that most (64% of the plots) jack pine stands have a cover density (mapping attribute, Table 1) below 40%.

# Estimation of probability of occurrence and dominance of jack pine over black spruce

Probability of occurrence of jack pine is well explained by logistic regression, with a measure of association (gamma) of 0.81. Occurrence probability increases in areas of low elevation within the study area, especially on sites with xeric or mesic drainage, a developmental stage of the vegetation that is qualified as "regenerated" (merchantable stems are rare) or "young" (most stems are merchantable), and where the understory vegetation is dominated by lichens (Table 2). Globally, jack pine is not scattered across the study area but is concentrated in the northwestern region (Fig. 6a), where the burn rate is the highest (Fig. 1b). In contrast, the probability of occurrence of stands that are dominated by jack pine is more difficult to predict with a logistic regression (gamma value of 0.39). Dominance of jack pine is associated with particular surficial deposits (mostly outwash materials with sandy to sandy silt texture and disintegration moraines; see Mansuy et al. 2010, their appendix 1) or specific hilly terrain in the northwestern part of the study area, where surficial deposits are mainly composed of stony and sandy textured glacial deposits (Mansuy et al. 2010) (Fig. 6b).

## Contrasting current and potential productivities

In terms of potential productivity, when the *k*-NN analysis only considers black spruce dominated plots, the study area is clearly subdivided into two sections north of Lake Mistassini, with the

**Fig. 5.** Observed vs. predicted site and relative density indices for (*a*, *b*, *e*, *f*) black spruce and (*c*, *d*, *g*, *h*) jack pine. Predicted values are imputed with a *k*-NN method considering either a mix of physical and vegetation site attributes (current productivity: *b*, *d*, *f*, *h*) or one considering physical site attributes only (potential productivity: *a*, *c*, *e*, *g*). A list of attributes is presented in Table 1.



**Table 2.** List of variables that were selected with logistic regression to explain the probability of presence and the probability of dominance of jack pine.

Probability of oc	curi	ence	Probability of dominance		
Variables	df	Wald $\chi^2$	Variables	df	Wald $\chi^2$
Elevation	1	309.6	Surficial deposit	15	31.6
Drainage	3	72.8	Understory vegetation	3	14.2
Developmental stage	3	68.5	Relief	3	13.2
Understory vegetation	3	40.1			
Disturbance of origin	5	29.1			
Proportion of precipitation as snow	1	18.8			

northern and northeastern parts often having less than 10% and sometimes less than 25% of their terrestrial area covered with productive stands (Fig. 7*a*). A relatively abrupt shift between occasional and frequent productive stands by ecological district is apparent for the eastern part of the study area, and this shift is linked with the change of elevation and a decrease in degree-days. This shift occurs at about 1000 degree-days·year<sup>-1</sup> (Fig. 1*a*). Over the whole study area, however, the combination of degree-days and dominant surficial deposit, together with dominant relief and the Julian date of the first autumnal frost, explains 84% of the variability in the percentage of potentially productive stands by ecological district, as measured with the coefficient of determination in PROC GLM.

The percentage of currently productive stands, when still considering only black spruce plots in the *k*-NN analysis, is lower than the percentage of potentially productive stands (Fig. 8), most especially west of Lake Mistassini (Figs. 7*b* vs. 7*a*). This difference is related to the heterogeneity in the burn rate across the study area (Figs. 1*b*, 8*b*;  $R^2 = 0.41$ ). Indeed, the burn rate alone explains 63% of the variability in the percentage of currently productive stands. When burn rate is combined with degree-days, surficial deposits, and the percentage of the area of ecological districts that has recently been burned, the coefficient of determination for the relationship between percentage of currently productive stands and these attributes increases to 0.91.

Considering both black spruce and jack pine in the analysis affects the estimation of the percentage of potentially productive stands, most notably in the areas where jack pine dominated stands tend to occur more frequently (Figs. 6*b* and 7*c*). The effect of considering both species, however, is smaller for the percentage of currently productive stands, except for a few ecological districts in the northwestern part of the study area (Fig. 7*d*). The attributes that best explain the variability in the percentage of potentially ( $R^2 = 0.84$ ) or currently ( $R^2 = 0.90$ ) productive stands when black spruce is considered in combination with jack pine are the same as those when black spruce is considered alone.

# Discussion

## Estimation of productivity at the plot level

To our knowledge, this is the first study to relate relative density index with mapping attributes; therefore, the present analysis of results is essentially limited to the SI. Although moderate ( $R^2$  values between 24% and 32%), the explanatory power that was obtained for black spruce SI is greater than that estimated by Ung et al. (2001; R<sup>2</sup> = 0.25), Boucher et al. (2006; R<sup>2</sup> = 0.11), and Beaulieu et al. (2011;  $R^2 = 0.21$ , for black spruce plantations). For jack pine, it is lower than that estimated by Beaulieu et al. (2011;  $R^2$  = 0.35, for jack pine plantations). Root mean square errors are high but are of the same order of magnitude (±2 m) as those estimated in other studies regarding the spatial distribution of productivity (McKenney and Pedlar 2003). With the k-NN method, a trade-off exists between prediction variance and bias, which is linked to the selected number of neighbours (Hastie et al. 2009). For the estimation of both SI and RDI<sub>100</sub>, the numbers of neighbours are fairly high (greater than 13 in all cases), and because predicted values are averages, extremely low and high values could be over- and under-estimated, respectively. This type of bias is not apparent in our case (Fig. 5), given the low predictive capacity of the models, so that instead of observing a bias for extreme values, predicted values seem to be bounded (for example, site indices between 9 and 14 m; Figs. 5a to 5d).

There are many possible explanations for such an important residual variability. The first factor relates to shade tolerance of black spruce. Trees that are currently dominant may have been

**Fig. 6.** Probability of (*a*) presence of jack pine and (*b*) abundance of forests dominated by jack pine (with a probability greater than 66%) per ecological district. The northern limit of timber allocation corresponds to one set by the Ministry of Natural Resources and Wildlife (Quebec) in 2002 (MRNFQ 2000). Values originate from two logistic models (Table 2) and were categorized according to the following abundance classes: <10%, rare; 10%–25%, occasional; 25%–50%, frequent; and 50%–100%, common or abundant.



suppressed in the past, which would alter the relationship between SI and the variables that explain site productivity (Weiskittel et al. 2011). A second factor relates to the types of attributes that were used, as the present study is limited to mapping attributes. Ung et al. (2001) showed that inclusion of an index describing stand structure greatly improves the explanatory power of this type of model for black spruce. The depth of the organic matter horizon, which is not included in the list of mapping attributes, also has considerable influence on black spruce productivity (Simard et al, 2007) and stand density (e.g., Belleau et al. 2011).

The size of the inventory sample plots (400 m<sup>2</sup>), relative to the level of allocation of the mapping attributes, is also a major source of additional variability (McKenney and Pedlar 2003). In addition, the calculation of climatic variables represents yet another source of error, given that the density of weather stations is much lower in the study area than farther south in Quebec (Girardin et al. 2012, for the same study area). In a study on trembling aspen, Lapointe-Garant et al. (2010) also showed that observed variability in a growth index that was comparable to SI could be explained not only by differences in variables that were compared between sites (fixed effects such as physical site factors, including climate, and type of surficial deposit), but also by (just under 50%) intrasite factors, which could not be predicted from these variables (random effects such as stand history or population genetics).

Given that stand history is particularly important in areas where the burn rate is highest within the study area (Mansuy et al. 2012) and where jack pine is the more common species (Fig. 6), we suspect that these factors explain our inability to predict more accurately the relative density index of jack pine stands ( $R^2 = 0.11$  to 0.14 for jack pine vs. 0.25 to 0.28 for black spruce). The range of site index values was also more limited for jack pine (mostly between 10 and 12 m at 50 years; Figs. 5*c*, 5*d*). Finally, Ung et al. (2001) discussed the concept of the site index, which involves circular reasoning that cannot easily be extrapolated to other unobserved sites; stands with a greater measured dominant height will necessarily have a higher volume yield (Eichhorn's rule, Skovsgaard and Vanclay 2008). Despite all of these elements, Ung et al. (2001) and Beaulieu et al. (2011) showed that by replacing the SI estimated from forest inventory sample plots with an index of productivity, which was estimated from mapped attributes, it is possible to predict the main mensuration parameters that are required for forest planning with only a slight loss of precision, particularly for merchantable volume.

# Estimation of productivity at the scale of landscapes

The percentage of productive timber area by district is protected against overestimation by using the first decile of its cumulative probability distribution at the scale of ecological districts. However, the bootstrap approach that we used to estimate this cumulative distribution might not have captured all of the expected variability (Mario Haché, Institut de la Statistique du Québec, personal communication, 2012). Part of the missing variability could originate from errors that are incurred in the estimation of SI and RDI<sub>100</sub> for the k neighbours of each stand with the k-NN imputation method (McRoberts et al. 2007). This error can be estimated per plot with leave-one-out cross-validation (Fig. 5). The main problem in the present study lies in the curse of dimensionality (McRoberts et al. 2011) that we face when estimating spatial autocorrelation between stands, as we had around 961 000 forest stands across the study area. To circumvent this problem and to obtain similar variance estimates, McRoberts et al. (2011) recently proposed a bootstrap procedure that involves bootstrapping the whole training sample-plot dataset to compute a variance of the bootstrap samples for each target stand. Such an approach relies upon the concept that "the variance of a single k-NN imputation is approximately the variance of the Y values of the k nearest reference elements" (Magnussen 2013, p. 13). The

**Fig. 7.** Percentage of (*a*, *c*) potentially or (*b*, *d*) currently productive stands by ecological districts, considering either the presence of (*a*, *b*) black spruce alone or (*c*, *d*) black spruce and jack pine combined. The northern limit of timber allocation corresponds to that set by the Ministry of Natural Resources and Wildlife (Quebec) in 2002 (MRNFQ 2000). Values were categorized according to the following abundance classes: <10%, rare; 10%–25%, occasional; 25%–50%, frequent; and 50%–100%, common or abundant.



bootstrap procedure that has been used here relies on the same assumption but was much faster to execute (15 times) as it did not require the recomputation of distances between target and reference stands or the selection of different neighbours at each bootstrap iteration. A preliminary comparison of these two procedures with a random sample of 24 ecological districts showed no difference in estimates of the percentage of potentially productive stands by district (average median difference of 1.3% per district, with first and last deciles of the difference estimated, respectively, as -6.7% and 17.7%). However, the first decile of the percentage of productive timber area by district was underestimated by 7% (Supplementary Fig. S2<sup>2</sup>), on average, and its value corresponded more to the first quartile of the cumulative distribution functions that were estimated with the McRoberts' bootstrap procedure. Thus, the results presented here have a lower level of protection against overestimation than that which was expected.

## Productive or potentially productive districts

An area's timber production capacity depends on permanent environmental factors, the disturbance history, forest dynamics, **Fig. 8.** (*a*) Relationship between the percentages (Perc.) of potentially and currently productive stands by ecological district. (*b*) The relative difference between percentages, which are expressed here as box-and-whisker plots, is related to the burn rate. Burn rates were regrouped by classes of 0.25%-year<sup>-1</sup>. Solid dots correspond to maximum and minimum values, vertical bars (whiskers) correspond to the first and last deciles, boxes correspond to the first and last quartiles, and the bar between the boxes corresponds to the median.



and postdisturbance reproductive conditions. It is intimately linked to the resilience of the region that is concerned, albeit at different spatial and temporal scales (Girard et al. 2008). The proportion of terrestrial area of an ecological district that currently exceeds the double productivity threshold is, therefore, a contextual indicator of forest productivity. It could be considered contextual because it does not separate the effects of disturbance history, postdisturbance reproductive conditions, or permanent environmental factors that would explain an area's potential productivity. Thus, it is necessary to introduce a second (theoretical) productivity indicator, more specifically, the proportion of terrestrial area that could potentially be productive under ideal density conditions.

The difference between these two indicators provides information on the effect of deficient postfire forest recovery on the productivity of a reference unit (Fig. 8a). Important differences emerge when the mean burn rate exceeds 0.25%-year-1 (fire cycles less than 400 years) (Fig. 8b), and deficient forest recovery may predominate over the potentially productive area when burn rates exceed 0.50%·year<sup>-1</sup> (fire cycles less than 200 years). Because deficient postfire forest recovery may occur anywhere within the black spruce forest, from closed-crown stands to open woodlands (Girard et al. 2008, 2009), the vulnerability of productive timber forest to fire is not only related to the probability that productive stands may burn before they attain their merchantable maturity (Gauthier et al. 2015), but also to the occurrence of deficient recovery. Vulnerability of these forests, therefore, is possibly linked to a potential change in the timber-production area, should the fire regime change through time (Balshi et al. 2009; Bergeron et al. 2010)

Despite these theoretical concepts and concurrent results, *k*-NN analyses remain empirical and their results depend on the dataset that is used for their training. The very clear difference between current and potential productivity estimates (Fig. 8) emerges from the contrasting conditions that exist in the present study area, with various disturbance regimes, patterns of postdisturbance canopy recovery (Mansuy et al. 2012), and growing conditions (surficial deposits and climate). Therefore, it is expected that should the study area be enlarged (Gauthier et al. 2015) or reduced, results could be different.

The presence and abundance of jack pine is related to the fire regime (Figs. 1b and 6), either because of the climate or the drying potential of the surficial deposits (Mansuy et al. 2010) or because black spruce is less well adapted to these conditions. Girardin et al. (2012) concluded that a dynamic feedback between boreal forest productivity and fire regime might exist through a change in forest age structure and the maintenance of jack pine stands. They supported this conclusion mostly with tree ring data and simulations from a carbon exchange model. In contrast, the present study shows that even if jack pine abundance increases together with the burn rate, jack pine stands having a lower density tend to grow (Figs. 5 and 6) and occur in areas where deficient postfire forest recovery is more frequent (Fig. 8b; Van Bogaert et al. 2015). These results are consequently more consistent with those of Girard et al. (2008), who contrasted the potential shift between closed-crown forests and open woodlands with a change in the fire regime. In fact, such a shift is related to a substantial change in forest productivity.

# Conclusion

The distinction between potential and current productivity has helped demonstrate the importance of the fire regime in determining the proportion of terrestrial area that may produce timber, especially at the transition between closed-crown black spruce stands and open spruce-lichen woodlands. Despite the effects of fire, however, there is an abrupt transition in productivity due to the interaction between climate and surficial deposits. The effect of the disturbance regime on the timber production area, even south of the current northern limit of timber allocation in the Province of Quebec, has important implications for strategic forest management planning. Strategic planning needs to demonstrate that sustainability is maintained over a very long time horizon (one and a half centuries in Quebec) and that the timber-production area is assumed to remain constant during the whole planning horizon. This last assertion does not seem to be valid everywhere within the closed-crown black spruce forest, especially when burn rates exceed 0.25%-year-1. In such cases, fire not only directly affects any expected timber supply by burning stands before they become harvestable, but also exerts indirect effects through deficient postfire forest recovery.

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