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Using paleoecology to improve reference conditions for ecosystem-based management in western spruce-moss subdomain of Québec

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ABSTRACT

Ecosystem based management in Québec is framed by reference conditions defining percentage of old-growth forest (> 100-years-old) and forest composition characterizing pre-industrial forest landscapes. In the western spruce-moss bioclimatic subdomain (154 184 km^2) a fire cycle estimated at 150 years was used to target that 49% of the landscape has to be composed of old-growth forest. Yet, this target was developed using past (19th–20th C.) climate and vegetation data and assume that environment and ecosystem processes are homogeneous for the entire western spruce-moss bioclimatic subdomain. The wide spatial and narrow temporal windows limit the application of reference conditions under ongoing climate change.

Our aim was to classify current vegetation heterogeneity of the western spruce-moss subdomain into homogeneous zones and to study the long-term history of fire and vegetation within these zones. This approach will help to refine forest management targets that are based upon short-term records by providing a long-term perspective that is needed for the forests to be managed within their natural range of variability. Modern forest inventories data were used along with climate, physical variables, and natural and human disturbances to study the current vegetation-environment interactions among the western spruce-moss subdomain. We also used 18 published sedimentary pollen and charcoal series to reconstruct Holocene vegetation and Fire Return Intervals (FRI).

Contemporary data revealed 4 zones with homogeneous interactions between vegetation and environment. Pollen analysis revealed three long-term vegetation paths: early successional species dominance, late to early species transition and late successional species dominance. These suggest that modern forest composition results from Holocene trajectories occurring within each zone. Holocene mean FRI (mFRI) ranged from 222 to 258 years across the subdomain, resulting in old-growth forests ranging between 64% and 68%, depending upon the zone.

Paleoecological and contemporary results support that to make forest management more sustainable, current landscape heterogeneity that arises from millennial forest composition trajectories and fire cycle dynamics should be taken into account by down-scaling the previously established reference conditions.

1. Introduction

Conservation and sustainable management of ecosystems is a major concern for stakeholders and policy makers thus leading to the establishment of reference conditions used as guidelines for ecosystem restoration (Kuuluvainen, 2009, Pollock et al., 2012), conservation, and management (Goebel et al., 2005). In the province of Québec, these reference conditions consist of an average fire cycle and associated percent of old-growth forest (> 100-years-old) at the spatial scale of vegetation subdomains (average area of 77 587 km^2, Boucher et al., 2011). Old-growth forest stands, mostly composed of late successional species, shelter high biodiversity and, therefore, are valuable for conservation of vascular plants (Gauthier et al., 2000), non-vascular plants (Fenton et al., 2005), and animals (Drapeau et al., 2009). These

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reference conditions are used by forest managers as a scientific framework for measuring and bridging the gap between natural and managed forest landscapes, the main goal of which is maintaining these forests within their natural range of variability according to the pre-industrial period (19th–20th C.).

In Québec, the western spruce-moss subdomain is one of the largest subdomains (154 184 km^2) located in the northwestern portion of Québec's commercial forests (Saucier et al., 2009). Its reference conditions have been established from inventory data covering the 19th–20th centuries and showed that pre-industrial landscapes prior to the advent of industrial forestry were composed of 89% resinous species, 9% mixed stands, and 2% broadleaf stands (Boucher et al., 2011). A 150-year fire cycle for the last 200–300 years was estimated for this subdomain using dendrochronology (Bergeron et al., 2001) and the resulting percentage of old-growth forests was ~49% (Boucher et al., 2011). Old-growth forests are mostly composed of late successional species such as balsam fir (*Abies balsamea* [L.] Miller) and black spruce (*Picea mariana* [Mill.] BSP). The latter species can also be considered as early successional (Gagnon and Morin, 2001). Conversely, early-successional forest stands are composed of jack pine (*Pinus banksiana* Lambert), black spruce, trembling aspen (*Populus tremuloides* Michaux), and paper birch (*Betula papyrifera* Marshall) that eventually transit into black spruce forests in lowlands and flat topography zones, and black spruce stands mixed with balsam fir in uplands (Cogbill, 1985, Saucier et al., 2009). In this subdomain, vegetation composition and fire regime are highly spatially heterogeneous. Indeed, vegetation distribution within the region is driven by topography, coupled with climate, soil conditions and disturbance regimes (Palik et al., 2000, Grondin et al., 2014). As the main disturbance, fire interacts with age-class distribution of the stands (Bergeron, 2000), which in turn influences the percentage of old-growth forests (Cyr et al., 2005). Fire effects also display high spatial heterogeneity in southern Québec and at vegetation subdomain scales (Bergeron et al., 2004, Gauthier et al., 2015). Interestingly, mixed and coniferous zones of western Québec are characterized by different fire regimes and contrasting vegetation trajectories that were established after the retreat of the last glaciers, and persisted during the Holocene (Carcaillet et al., 2010, Blarquez and Aleman, 2015). For this subdomain, there is therefore a need to increase the resolution of landscape analyses and their associated millennial trajectories to ascertain whether the short time period that is currently used to define reference conditions is sufficient to cover the natural variability of these forest ecosystems (Landres et al., 1999).

Indeed, reference conditions are based upon data that date back to the Little Ice Age (1600–1850 CE), when climate was cooler and drier, and fire frequency was higher than what is currently observed (Bergeron and Archambault, 1993). This type of climate differs from the forecasted one since the predicted future climate of Québec is likely to be characterized by higher temperature and higher precipitation (IPCC, 2013). However, the increase in precipitation would not necessarily offset the increase in temperature, thereby leading to potentially higher fire activity (Girardin and Mudelsee, 2008). As wildfire frequency and intensity are major drivers of forest dynamics, a modification of fire regimes can deeply modify forest composition and dynamics for example by favoring the establishment of post fire early successional species (Cogbill, 1985). Thus, the choice of baseline data that are used to define management targets is critical and should provide information regarding the state of the targeted ecosystem, regardless of whether it is currently stable or transient (Gillson and Marchant, 2014). There is then a need for a higher temporal coverage of the above-mentioned reference conditions. Long-term information regarding ecosystem dynamics, therefore, can inform ecosystem range of variability according to past climate and fire regime changes (Dearing and Zolitschka, 1999). Thus, paleoecology represents an important source of data and methodological approaches for providing multi-millennial information on ecosystem functioning and improving guidelines for biodiversity conservation and management (Willis et al., 2010).

Here we used pollen analysis for long-term vegetation reconstructions in order to bring insights regarding post-glacial vegetation dynamics (Carcaillet et al., 2010) and to reconstruct regional vegetation trajectories that are followed by forests (Jamrichová et al., 2017). Charred particles that are contained in lake sediments and peatlands cores were used to reconstruct the Holocene Fire Return Interval (FRI) (Ali et al., 2012) and to calculate the long-term dynamics of old-growth forests within the landscape (Cyr et al., 2009).

We hypothesize that regional differentiation of vegetation in time and space would occur within the western spruce-moss subdomain under the multi-scalar influence of the environment, climate, and disturbances regimes. These regional differences would result from ecological legacies that have persisted after the retreat of Lake Barlow-Ojibway (i.e., ~8000 cal. years BP in the area; by convention, the present is 1950 CE). If long-term vegetation and fire dynamics explain current landscape heterogeneity, then this data will help to redefine current forest management targets that would comply with ecosystem-based management principles and objectives (Cyr et al., 2009, Bergeron and Fenton, 2012). Therefore, to inform forest managers regarding the long-term dynamics of ecosystems, the Holocene history of boreal forest ecosystems should be reconstructed. In particular, our aims are to (1) highlight and describe current landscape heterogeneity in the western spruce-moss bioclimatic subdomain forest of Québec, (2) to define and classify Holocene vegetation trajectories that have led to current vegetation heterogeneity, (3) to reconstruct FRIs to identify homogeneous fire regimes and analyze their consequences on vegetation distribution and finally (4) estimate the range of variability of the percentage of old growth forest for redefining reference conditions based on Holocene variability.

2. Material and methods

2.1. Study area

The western spruce-moss subdomain covers 154 184 km^2 of Québec, extending from 70°W to 80°W and from 48°N to 52°N (Fig. 1). This territory ranges from mixedwood boreal forest in the south to the spruce-lichen subdomain in the north (Saucier et al., 2009), which corresponds to the northwestern portion of Québec's commercial forests. Climate is characterized by low annual temperatures that range from −5 °C to 3 °C, with a clear North-South gradient. Total precipitation exhibits an East-West gradient, i.e., from 1300 mm to 600 mm, which is linked to increasing distance from the Atlantic Ocean (Grondin et al., 2007a). Elevation ranges from 15 m a.s.l. (above sea level) with a flat topography in the West to 630 m a.s.l. with a hilly topography in the East. The northwestmost region is dominated by organic deposits that diminish eastward. The Clay Belt is located in the southwest part of the study area and is characterized by a layer of clay left by the pro-glacial Lake Barlow-Ojibway. The central and eastern parts of the study area are dominated by till. Wildfires are abundant in the northern part of the study area and are less abundant elsewhere, particularly in the western part dominated by peatlands (Gauthier et al., 2015).

2.2. Contemporary zonation of the ecological districts

All modern data that are used were provided by the *Ministère des Forêts, de la Faune et des Parcs* (Ministry of Forests, Wildlife and Parks) of Québec and are defined at the district scale (Grondin et al., 2007a). Photo-interpretation of 1:60 000 scale surficial deposits and the analysis of 1:50 000 scale physiography on topographic maps permitted delineation of ecological districts (Robitaille, 1988). The study area is composed of 440 ecological districts, which have a mean surface of 300 km^2, and that have been characterized with respect to their current vegetation, climate, physical environment, and natural and human

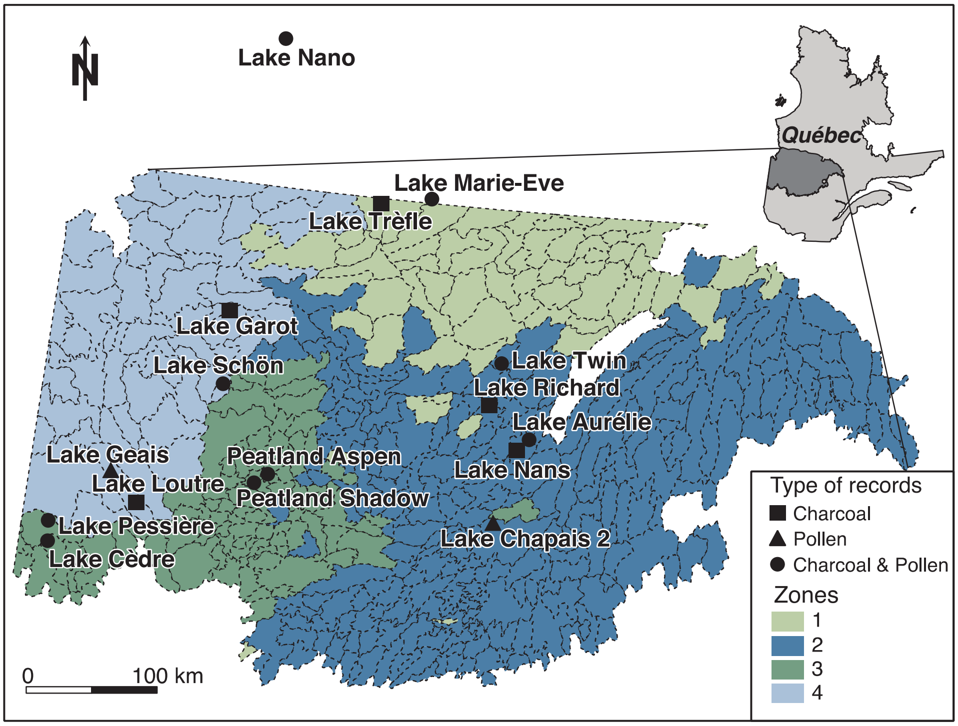

Fig. 1. Contemporary homogeneous zones (numbers 1–4 and associated colors) of the western spruce-moss subdomain obtained by RDA and *k*-means partitioning that were applied on ecological districts (n = 440). The study area (upper right hand map) represents the western spruce moss subdomain of Québec (Saucier et al., 2009), and paleosites used in this study are denoted according to the type of proxy studied, squares for charcoal, triangle for pollen and circles for both charcoal and pollen. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

disturbances. Vegetation data consist in relative importance of species basal area and forest stand cover. The two last sets of vegetation variables have been defined by using forest plot inventories and forest maps recorded during the 1980s. Climate data were generated using BioSIM 10 (Régnière and Bolstad, 1994), which interpolates climate information from stations at a cell size of 2 km^2. Climate data that were used range from 1961 to 1990. Physical environment data described surficial deposit relative abundance (percentages) and topography variables described the slope and elevation. Human disturbances referred to anthropogenic fires (Ministry archives 1938–1999) and to forest use through the creation of partial and clear-cuts, and plantations (1970–1980 cartographic data). Natural disturbances consisted of natural fires, outbreaks of spruce budworm (*Choristoneura fumiferana* (Clemens)) and windthrows, and are expressed as the percentage of a district's surface area that was affected by those disturbances during the 1980s.

2.3. Statistical analysis on contemporary data

All statistical analyses were performed in R 3.3.2 (R Core Team, 2016). Redundancy analysis (RDA) was used to analyze the relationships between the response, vegetation data (Y matrix, 26 variables), and the explanatory, environmental data (X matrix, 46 variables) of the 440 districts forming the study area. Before applying RDA, the vegetation variables were Hellinger-transformed, which is recommended when dealing with species abundance data (Legendre and Gallagher, 2001). Forward selection, using the *adespatial* package version 0.0–8 (Dray et al., 2017), was also carried out on the explanatory variables to select the most significant ones, according to two criteria, based upon their *P*-values ($P < 0.05$) and the adjusted coefficient of multiple determination (adjR2thresh = 0.54) obtained after performing a preliminary RDA on all the variables (Blanchet et al., 2008). This selection allowed for the identification of more parsimonious and therefore more interpretable links between the vegetation and explanatory environmental variables. The RDA was performed using the *vegan* package (Oksanen et al., 2014). To group the ecological districts according to their specific vegetation-environment interactions, iterative *k*-means partitioning was performed on the constrained RDA axes scores. This procedure was run for 2–12 groups (or clusters) with 100 iterations to strengthen each result and evaluate the consistency of the number of groups (Borcard et al., 2018).

2.4. Paleoecological study sites

Fourteen lakes and 2 peatlands within the study area have been studied to reconstruct long-term vegetation and fire regime dynamics (Table S2, Fig. 1). The lacustrine sites were cored with a Livingstone sampler and the water–sediment interface was sampled with a Kajak-Brinkhurst corer. Sampling of peatlands was conducted by excavating a trench with a shovel, and then cutting peat monoliths from top to bottom (mineral soil). AMS (Accelerated Mass Spectrometry) radiocarbon dating was used to date lacustrine or peat sediments (Table S3: macroremains, charcoal or gyttja samples) and to derive age-depth models. All ages were calibrated against calendar ages using the IntCal04 dataset (Reimer et al., 2004). Radiocarbon dating and age-depth models were accessed from the original publications for each studied lake or peatland, and have been listed in Table S3. Ages were expressed in calibrated years before present (hereafter: BP) with a reference year set at 1950 CE (0 BP = 1950 CE).

2.5. Paleoecological data

To reconstruct the Holocene vegetation history, only the most common tree and shrub species observed in the studied area were kept (Saucier et al., 2009) and represent the main pollen signal measured in the sediment. Overall, the objective is to guide forest managers and stakeholders that preferentially base their management plans on trees rather than on herbaceous species. These nine pollen taxa are: *1-Abies* related to pollen from *Abies balsamea. 2–3 Alnus crispa* (Current designation: *Alnus viridis* [Chaix] DC. ssp. *crispa* [Aiton] Turrill) and *A. incana* [L.] Moench, were taken individually since they are adapted to respectively dry and humid soils; this characteristic was of interest in the current study since both soil types widely typify the study area surficial deposits. 4-*Betula* encompassed pollen for *Betula papyrifera, B. glandulosa* Michaux and *B. alleghaniensis* Britton, with the latter species being rare in our study area. 5-*Picea glauca* (Moench) Voss and *P.*

mariana were combined in the taxon *Picea*, since *Picea glauca* is scarce in the study area. *6–7 Pinus strobus* and *P. banksiana* were differentiated since their autoecologies differ according to fire characteristics (surface, severity, cycle) (Pausas et al., 2004), and their geographical distributions. *Pinus strobus* is found where fires are less severe and rare, while *Pinus banksiana* dominates where fires are both more frequent and severe. 8-The taxon *Populus* refers to *Populus tremuloides* Michaux, and to a lesser extent, *Populus balsamifera* L., with no distinction being made between the two species. 9-*Thuja* and *Juniperus* are indistinguishable using pollen analysis; however, *Juniperus* is rare in the boreal forest, and as such, we can infer that the *Thuja/Juniperus* pollen type mainly corresponded to *Thuja occidentalis* L. Thus, the taxon was denoted *Thuja.* Pollen percentages were calculated to permit between-site comparisons and were used to plot pollen diagrams with the R package *rioja* (Juggins, 2015).

In the original studies, charred particles larger than 150 μm (Lynch et al., 2004) were counted for each 1 cm^3 core sub-sample to calculate the charcoal concentration, which was then multiplied by the sediment accumulation rate to obtain the charcoal accumulation rate (CHAR), which is expressed as $mm^2\,cm^{-2}\,year^{-1}$ (Higuera et al., 2010). Charcoals subsamples were taken contiguously each 0.5–1 cm depending on core length and overall sedimentation rate (Table S2). CHAR is composed of different subpopulations of signals that are related to charcoal deposition and taphonomy. To distinguish the CHAR signal that was statistically related to fires, we used CharAnalysis software (1.1) (Higuera et al., 2009) and the *Ensemble member procedure*, which is described in Blarquez et al. (2013). Briefly, we filtered CHAR raw data using 5 available filtering techniques in CharAnalysis (LOWESS, robust LOWESS, moving mean, median and mode) and associated window widths (470 different windows, from durations of 100–1500 years in 3 year increments). This procedure resulted in 5 × 470 (2350) filtered series, from which we were able to distinguish between low frequency signals ($CHAR_{background}$) that were related to charcoal taphonomy (production, transportation, deposition) and high frequency signals ($CHAR_{peak}$) that were related to fires. We used a Gaussian mixture model to define a local threshold on $CHAR_{peak}$ that discriminates fire event-related charcoal deposits ($CHAR_{fire}$) from noise ($CHAR_{noise}$). A SNI (Signal to Noise Index) greater than 3 was sufficiently to distinguish robust fire events. From this *Ensemble member procedure*, we selected fire events that occurred in at least 75% of the reconstructions; these "statistically robust" fire events were used for calculating the Fire Return Interval (FRI) as the time between two fire events.

2.6. Statistical analysis on paleoecological data

2.6.1. Pollen data

We performed PCA (Principal Component Analysis) on all pollen assemblages after performing chord-distance transformation (Legendre and Gallagher, 2001). Confidence ellipses (95%) on the taxonomic variables were then calculated to depict the position that was occupied by each site within PCA space. Pollen assemblage coordinates were aggregated using thousand-year periods, including [0–1000), [1000–2000), … [7000–8000) BP, by calculating the mean position along the first and second axes of all samples within each period. These consecutive 1000-year time window means were then connected to display long-term ecological trajectories.

2.6.2. Charcoal data

For each sedimentary sequence, mean Fire Return Intervals (mFRI) (i.e., number of years between two consecutive fire events) were calculated. To compare mFRI sequences between zones and then between sites located in the same zone, the mFRI sequences of all respective sites that were located in each zone and individual sites were fitted against a two-parameter Weibull function, and their scale parameters were compared (here we assumed that the shape parameter equals to 1) (Schafer and Sheffield, 1976). The iterative comparison of mFRI sequences for two zones or two sites relied upon calculating the difference between (1) the sum of the log-likelihood for the two zones or sites that we wanted to compare and (2) the log-likelihood of the pooled sequence. If the *P*-value of the previously calculated log-likelihood difference is less than the threshold set to $P = 0.05$, then Holocene fire dynamics for the two zones or sites were considered to be significantly different.

Forest stand age-class distributions were related to the fire return interval using a Weibull-type function:

$$A(t) = 1 - \int_{t}^{inf} exp\, -(t/b)^{c} dt$$

where A is the proportion of landscape stands that were older than *t* (years), *b* is the scale parameter and is equal to the mFRI, and *c* is the shape coefficient, which is not significantly different from 1, even between periods with different fire cycles (Johnson and Gutsell, 1994) (hereafter $c = 1$) (Cyr et al., 2009). By setting *t* to 100, the formula allowed us to calculate the proportion of old-growth forests within a landscape under a given mFRI, and the 95% confidence interval was calculated by bootstrap resampling.

3. Results

Refining the current vegetation classification of the western spruce-moss subdomain represents a spatial framework of the current vegetation heterogeneity that can be used later to analyze the regionalization of the Holocene vegetation trajectories and fire dynamics, while guiding the downscaling of reference conditions from subdomain to homogeneous zones of vegetation.

3.1. Contemporary vegetation-environment interactions to characterize homogeneous territories

When coupled with *k*-means partitioning that was applied to vegetation and environmental data for the districts of the western spruce-moss subdomain, RDA showed four zones where links between forest composition and environmental constraints are homogeneous (Fig. 1). Zone number one (Z1) concentrates 29% of *Pinus banksiana* and 63% of *Picea mariana*, which are respectively the highest and lowest proportions of these species within the western spruce-moss subdomain, on a substratum dominated by till (51%). The second zone (Z2) has a lower percentage of *P. banksiana* than zone 1 (12%), a higher proportion of *P. mariana* than zone 1 (71%), and surficial deposits are also mostly till (45%). Zone three (Z3) has a substantial proportion of *P. mariana* (73%), together with *P. banksiana* (9%) and *P. tremuloides* (7%), on clay deposit (45%). Indeed, this zone belongs to the Clay Belt. In Zone number four (Z4), forests are mostly composed of *P. mariana* on organic soil (85%). For a complete description of ecological variables that were retained by forward selection, together with the relationship between paleoecological sites and environmental variables, the reader is referred to Fig. S1 and to Grondin et al. (2014).

3.2. Holocene vegetation histories

The two first axes of the PCA that was applied to the pollen assemblages represent 44% of the variance (the first three axes represent 60%; Fig. 2). Pollen taxa are well discriminated by the PCA (Fig. 2A). Three groups can be distinguished: *Betula-Alnus incana-Thuja-Pinus strobus-Abies; Picea-Populus*; and *Pinus banksiana-Alnus crispa*. The vegetation history that was observed for Marie-Eve Z1, Nano Z1 and Twin Z2 is characterized by a dominance of the fire-prone taxa *P. banksiana* and *A. incana*. The second vegetation history is characterized by an increasing proportion of *P. banksiana* since 4000–3000 BP. The assemblages (and consequently, the ellipses) span the length of PCA1 with several taxa that can be described as light-demanding species (*Populus* and *Betula*) for sites in Zones 2 (Aurélie Z2), 3 (Aspen Z3,

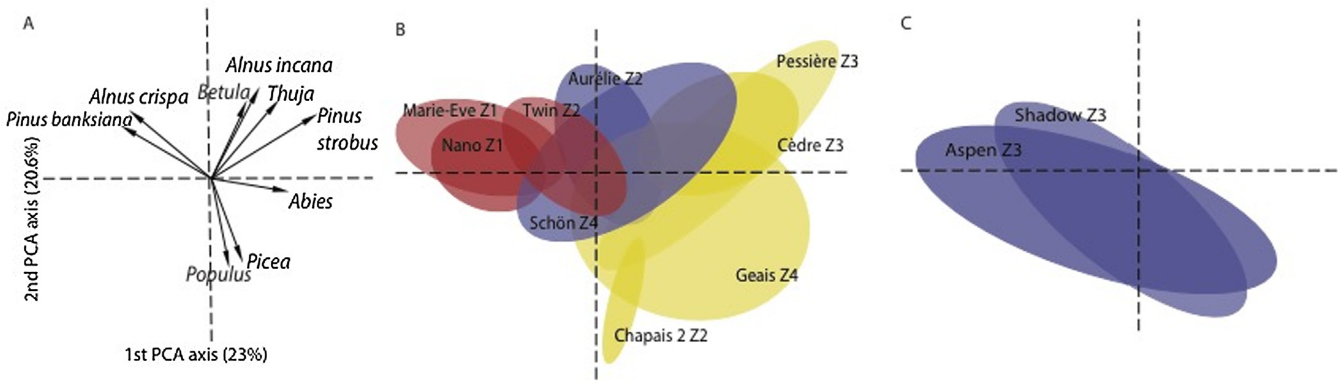

Fig. 2. Holocene vegetation histories assessed by a PCA applied to the pollen assemblages of lakes and peatlands. (A) Projection of species (pollen taxa) onto the first two axes of the PCA, using scaling 2 thus reflecting the correlation between pollen taxa. (B) 95% confidence ellipses for the lakes. (C) 95% confidence ellipses for the peatlands, using scaling 1 to observe the Euclidean distance between the pollen assemblages. Ellipse color highlights three vegetation histories: red is characterized by a forest composition dominated by *Pinus banksiana.* Blue ellipses represent sites with both late successional species and *P. banksiana;* yellow refers to vegetation that is mostly composed of late-successional species. The numbers following sites names refers to the zone in which they are located. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Shadow Z3) and 4 (Schön Z4). A third vegetation history, mostly characterized by a high abundance of late-successional species (*Thuja* and *Abies*, and to a lesser extent, *Picea*), characterizes sites on the right side of the ordination, i.e., zones 2 (Chapais Z2), 3 (Cèdre Z3, Pessière Z3), 4 (Geais Z4).

3.3. Holocene vegetation trajectories

3.3.1. 1st vegetation trajectory: dominance of jack pine over the entire Holocene

Marie-Eve (Fig. 3B) and Nano (Fig. 3C) exhibit vegetation that is dominated by *A. crispa* and *P. banksiana*. From the beginning of the Holocene to 6000–5000 BP, Marie-Eve vegetation exhibited a higher proportion of *Populus* and *Betula*, subsequently converging towards stands strongly dominated by *P. banksiana,* such as in Nano. For Twin (Fig. 3D), the early Holocene pollen assemblages reveal more mixed stands, which then converged toward Marie-Eve and Nano since 4000–3000 BP. Overall, these three sites (Marie-Eve, Nano, Twin) have their whole vegetation dynamics contained within the early successional portion of the ordination and evolved toward or have always been dominated by *P. banksiana* and *A. crispa.*

3.3.2. 2nd vegetation trajectory: increase of jack pine during the Holocene

Aurélie (Fig. 3E) and Schön (Fig. 3H) lakes present similar vegetation paths and they are both moving towards vegetation that is dominated by *P. banksiana* and *A. crispa,* such as what is observed for Aspen (Fig. 3F) and Shadow (Fig. 3G). These latter two peatlands exhibit very similar vegetation trajectories that are mainly characterized by early successional broadleaved species, even when considering that the Shadow sequence has only covered the last 4000 years.

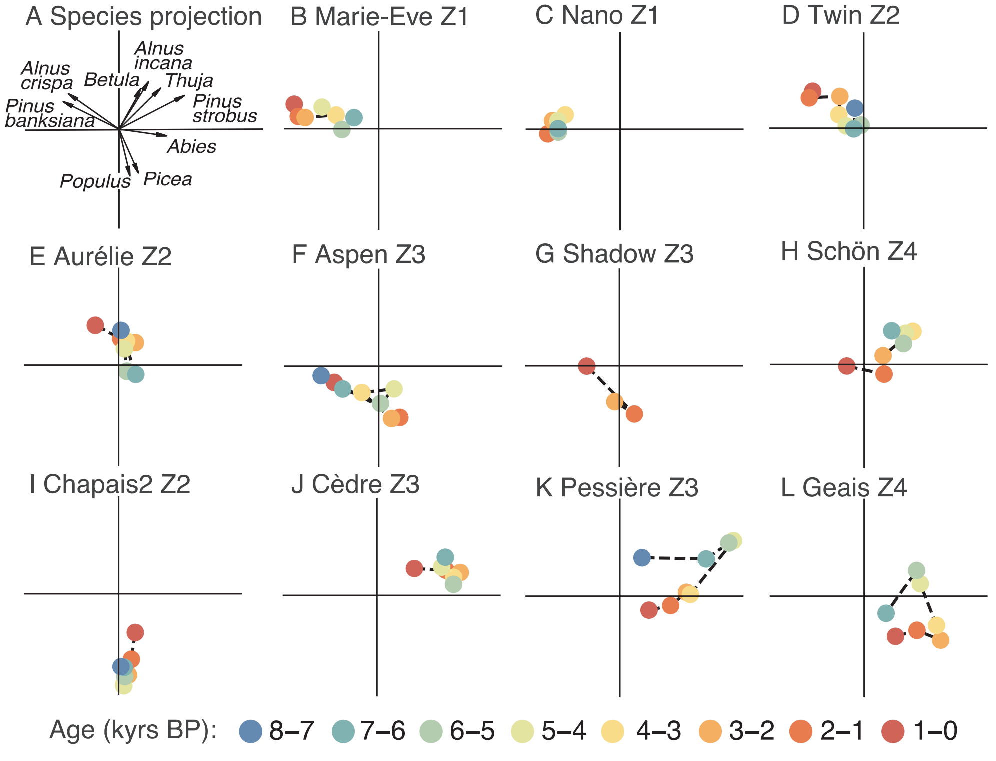

Fig. 3. Vegetation trajectories corresponding to 1000-year pollen assemblage means projected onto PCA axes 1 and 2 for each paleoecological site. Panels B to L show vegetation trajectories followed by each site, which are represented by dashed lines using scaling 1. Each millennium is represented by a dot, red for the most recent assemblages and blue for the oldest ones. Species were projected onto the PCA (Panel A) using scaling 2 (same as Fig. 2). First raw of panels corresponds to the dominance of jack pine during Holocene, the second one to the transitional trajectory (from late to early successional species) and the third row corresponds to dominance of late successional species. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

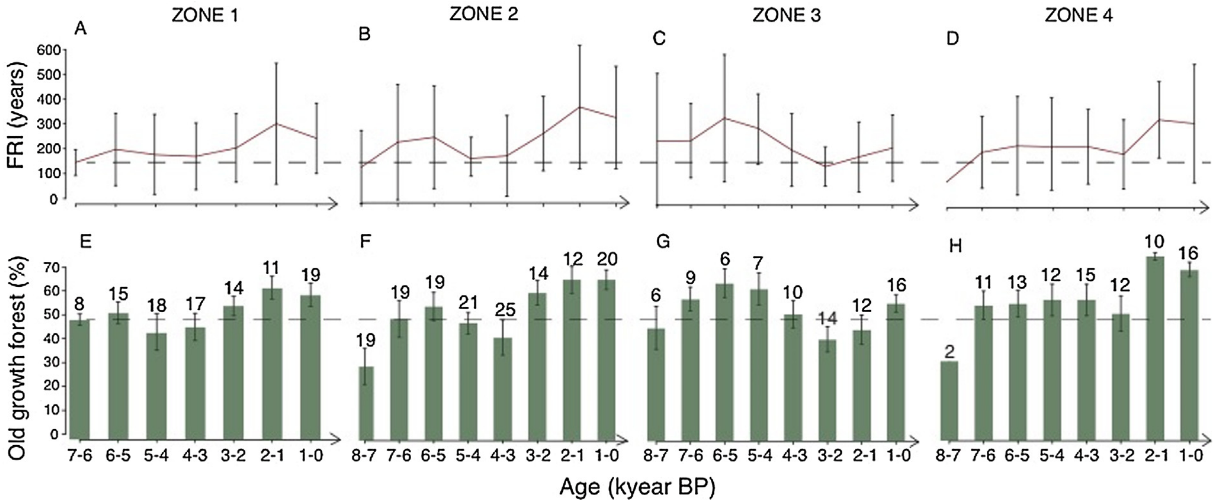

Fig. 4. Graph showing the Holocene evolution of mFRI (upper row of panels) and the evolution of old-growth forest percentage (lower row of panels). Dashed line in the first row of panels represents a fire cycle of 150 years, in the lower row it represents the 49% of old-growth forest both corresponding to the reference conditions established for the western spruce-moss subdomain. Numbers above each histogram correspond to the number of individuals used to calculate the mean and standard deviation of the data.

3.3.3. 3rd vegetation trajectory: dominance of late successional species over the Holocene

The sites Chapais 2 (Fig. 3I), Cèdre (Fig. 3J), Pessière (Fig. 3K) and Geais (Fig. 3L) have their entire vegetation dynamics contained within the late-successional portion of the ordination. Pessière and Geais have shown very variable landscape composition during the Holocene, but started to converge with Cèdre around 2000 BP. Chapais 2 vegetation composition was largely dominated by *Populus* and *Picea* until 4000–3000 BP and has been converging towards the three latter sites since 1000 BP. Most of these lakes are also characterized by the similarity of the main tree species vegetation between the late and the early Holocene.

3.4. Holocene fire regime variability

Following mFRI (mean fire return interval) reconstructions, it appears that all zones show distinct but not significantly different Holocene fire dynamics (Fig. 4). Nevertheless, it is worth noting that all zones exhibit a period from the beginning of the Holocene until 4000–3000 BP, during which the mFRI was shorter than between 3000 and 1000 BP. Since the last millennium, some zones have exhibited a slight increase in mFRI, except for Z3 sites (Fig. 4A). Consequently, the percentage of old-growth forest has also increased (Fig. 4E).

The mFRI for the entire western spruce-moss subdomain is 240 years, with a 95% confidence interval of (222, 258), which corresponds to 66% old-growth forests, with a 95% confidence interval of (64, 68) (Table 1). Comparison of the mFRI distributions did not reveal significant differences among zones. The same analysis has been led on sites FRI sequences and differences appeared between lakes that were located in the same zone (see Table S1). In Zone 2, Aurélie showed a significant difference with respect to other sites that were located in the same zone: Richard ($P = 0.00045$), and Twin ($P = 0.048$).

Table 1
Regional Holocene mFRI (mean and 95% confidence interval) and percentage of old-growth forest (hereafter OF: mean and 95% confidence interval) for each zone in the western spruce-moss subdomain.

Zone	mFRI (years)	95% CI	OF (%)	95% CI
1	227.3	(194.6, 260)	64.4	(59.8, 68.1)
2	234.9	(201.7, 268)	65.3	(60.9, 68.9)
3	226.7	(189.2, 264.2)	64.3	(58.9, 68.5)
4	266.2	(226.4, 305.9)	68.7	(64.3, 72.1)
Mean	240.1	(221.9, 258.3)	65.9	(63.7, 67.9)

4. Discussion

In this study, we showed that it is possible to (1) highlight and describe current landscape heterogeneity in the western spruce-moss bioclimatic subdomain forest of Québec, (2) to define and classify Holocene vegetation trajectories that have led to current vegetation heterogeneity, (3) to reconstruct FRIs to identify homogeneous fire regimes and analyze their consequences on vegetation distribution and finally (4) estimate the range of variability of the percentage of old growth forest for redefining reference conditions based on Holocene variability.

4.1. Current landscape heterogeneity

We demonstrated that the contemporary vegetation could be divided into four main zones where relationships between forest composition and physical characteristics, climate and disturbances regimes are homogeneous. Interestingly, this zonation shows important similarities with the third vegetation level of division that was developed for the whole southern Québec (Grondin et al., 2007b). Yet, this is not the spatial scale that is currently used for establishing management targets in Québec (Boucher et al., 2011). Developing restoration and management targets at the scale of homogeneous vegetation-environment interactions has been shown to be relevant to ecosystem restoration for identifying disturbed ecosystems and prioritizing the interventions to restore the most disturbed sites among them (Palik et al., 2000). We therefore suggest using the zonation proposed in our analysis for developing new management targets in the western spruce- subdomain.

4.2. Holocene vegetation trajectories leading to contemporary vegetation heterogeneity

The first vegetation path that corresponds to northernmost sites that were located in Zone 1 and Lake Twin (Zone 2, close to Zone 1), boreal species migration resulted in an unprecedented increase in *P. banksiana* and *A. crispa* abundance within the vicinity of the sites (Remy et al., 2017), driving the vegetation to deviate toward early-successional species. This corresponds to the first vegetation path identified in this study (Fig. 2), and is consistent with the current vegetation type observed in this region of the spruce-moss subdomain. This vegetation path is characterized by early Holocene differentiation and subsequent cyclical dynamic involving frequent fires (Gauthier et al., 2015).

The second vegetation path was found in lakes and peatlands that are located in Zones 2 and 3. Peatlands Aspen and Shadow located in Zone 3, as well as Schön located at the border between Zones 3 and 4 and Aurélie located in Zone 2. This dynamic is characterized by "transitional" vegetation dynamics for which the surrounding vegetation was initially dominated by broad-leaved species that changed towards stands with an increasing proportion of *Pinus banksiana* since 2000–1000 BP. This increase in *P. banksiana* has been noticeable for the three vegetation paths and has been more precisely dated to around 1800 BP. Its increase is usually interpreted as the development of boreal forest as currently observed or 'borealization' (Carcaillet et al., 2010) coupled with more frequent fire (Payette et al., 2017), or less frequent but larger and more severe fires (Remy et al., 2017). Since then, a diminution of *Abies balsamea* and an increase in *Pinus banksiana* (Blarquez and Aleman, 2015, Asselin et al., 2016) has been reconstructed highlighting the transition from late- to early- successional dominated landscapes (Fig. 3). The similarity of vegetation between the Late Holocene and the early Holocene has also been observed by some authors, such as Payette et al. (2017) in temperate forests.

The third vegetation path that was identified is characterized by vegetation dynamics involving late successional species that are located in the right part of the ordination (Fig. 2) and corresponds to lakes Geais located in Zones 4 and by extension to lakes Cèdre and Pessière located in Zone 3 and that represent landscapes dominated by peatlands. After the retreat of Lake Barlow-Ojibway, forest stands of southernmost sites (e.g., lakes that were located in Zone 3) were dominated by broad-leaved species, mixed with *Thuja* and *P. strobus* (Carcaillet et al., 2001). For the Clay Belt (Zone 3), *Thuja* reached a maximum extent in 6000–5000 BP and retreated around 2000 BP to its current extent. Between 5000 and 3000 BP, its relative abundance was mostly explained by low fire frequency, which overrode the effects of climate and carbonate soils. The two latter factors thus explain not only that *Thuj*a persists today in the Clay Belt (Zone 3) (Carcaillet et al., 2001, Paul et al., 2014), but also to a lesser extent around Lakes Geais and Schön located in Zone 4. *Pinus strobus* was present at 50°N latitude around 6000 BP, but this species is currently found in the southern part of the boreal forest in mature forests characterized by surface fires (Bergeron et al., 1997). With the end of the Holocene Thermal Maximum (HTM; ca. 10 000–6000 BP (Kaufman et al., 2004) and the occurrence of a less favorable climate associated with less frequent and more severe fires, *Pinus strobus* retreated to its current limits (Carcaillet et al., 2010). Interestingly, the Holocene dynamics of *Thuja* and *Pinus strobus* suggest that all site trajectories withdrew from the upper-right quadrant of the PCA ordination (Fig. 2). For Geais, Cèdre, Pessière and Chapais 2, other species, such as *Picea*, *Betula* and *Alnus crispa,* increased in abundance following the retreat of Lake Barlow-Ojibway, around 8000 BP (Carcaillet et al., 2010, Blarquez and Aleman, 2015). *Picea* became the dominant taxon, which is often associated with *Abies balsamea* (Ali et al., 2008, Remy et al., 2017). The period 7000–6000 BP is marked by the settlement of various species that enhance biodiversity (Blarquez et al., 2014), which is also consistent with variations in ROC (Rate of Change) that were observed in the study area during this period (Carcaillet et al., 2010, Remy et al., 2017).

Our results have shown that current vegetation patterns are the results of the Holocene dynamics of vegetation, particularly those of forest species. Indeed, during the Holocene, the climate underwent changes that initiated vegetation settlement and dynamics (Blarquez et al., 2015) that differ regarding their location in the western spruce-moss subdomain. In the following section, we will discuss the Holocene fire dynamics that might have influenced the previously identified vegetation trajectories.

4.3. Long-term variation of FRI

These changes in vegetation composition followed climate changes during the Holocene, but were also determined by interactions with fire dynamics. In particular, fire return intervals can strongly influence forest composition (Bergeron and Charron, 1994, Carcaillet and Blarquez, 2017), thereby determining the percentage of old-growth forest that has been retained in the landscape and its associated biodiversity (Cyr et al., 2009). Surprisingly, Zone 1 has one of the shortest mFRI, i.e., 227.3 years (95% confidence interval: 194.6, 260; Table 1), but this fire return interval is not significantly shorter than the one reconstructed for the entire western spruce-moss subdomain (240.1). However, the current fire cycle distribution is of 67.4 years as reconstructed using fire archive data ranging from 1938 to 1998 (recalculation from Gauthier et al., 2015). Interestingly, the width of the 95% confidence interval window (194.6–260 years) is no larger than the one reconstructed using archive data. Indeed, Mansuy et al. (2010) identified three different fire zones that encompassed our Zone 1, with fire cycles ranging from 90 years (95% confidence interval: 57, 208) to 149 years (95% confidence interval: 86, 257). In both instances, these estimates are among the lowest observed in southern Québec (Gauthier et al., 2015). Lakes located in Zone 1 show only one slightly significant difference, i.e., between Lakes Trèfle and Nano (Table S1), thereby revealing a relatively homogeneous long-term fire dynamic history for this zone.

The second zone has a Holocene fire mFRI of 235 years (95% confidence interval: 202, 268) for a current fire cycle of 198.1 years (recalculation from Gauthier et al. (2015)). It is located around Lake Mistassini where surficial deposits exhibit heterogeneity, leading to a wide range of fire cycles. These cycles span a range from 90 years (95% confidence interval: 57–208,) on tills to 715 years (95% confidence interval: 353, infinity) on organic soils (Mansuy et al., 2010). Lake-to-lake comparisons showed significant differences between Lake Aurélie and the other lakes that were located in the zone, i.e., Richard and Twin, thereby revealing in-between zone heterogeneity in long-term fire dynamics.

Zone 3, reconstructed FRI dynamic and mFRI (226.7, 95% confidence interval: 189.2, 264.2) were surprisingly lower than the current fire cycle, which is of 1272.3 years (recalculation from Gauthier et al., 2015). Bergeron et al. (2001) have reconstructed a fire cycle prior to 1850 with an estimate of 101 years (95% confidence interval: 79, 129) and 398 years (95% confidence interval: 302, 527) since 1920, where some sites located on till or sand deposits tended to have a shorter fire cycle. Cyr et al. (2005), who also reconstructed fire events in this area, found a fire cycle estimated to be 446 years (95% confidence interval: 190, 1047) with local differences explained by firebreaks, such as paludified areas, which can contribute to lengthening fire cycles.

Zone 4 has a reconstructed mFRI of 266.2 years (95% confidence interval: 226.4, 305.9) which is not significantly different from the current fire cycle estimated at 242.1 years (recalculation from (Gauthier et al., 2015)). Also, the site-to-site comparisons show no significant differences thus highlighting a relatively homogeneous Holocene mFRI for the zone.

Overall, our FRI values must not be taken as a strict equivalent of the fire cycle. Indeed, fire cycle, which represents the time for burning an area of interest is equivalent to FRI only if each past fire (from charcoal records) burned the entire study area, which is probably not always the case here. This conceptual difference and others, related for example to the spatial scale of paleoecological proxies, may explain the observed differences. Indeed, the spatial scale at which ecological processes had occurred in the past from lake records (Hawthorne et al., 2017), depends on local-scale effects, such as fuel load dynamics or ignition conditions (Gavin et al., 2007), vegetation (Girardin et al., 2013), and climate (Ali et al., 2012). More generally, the record of paleoecological proxies is influenced by taphonomical processes, which include transportation of particles, watershed characteristics, lake hydrographic connectivity, and physiognomy (Higuera et al., 2007, Anderson, 2014). This might explain the differences in reconstructed FRI, for example, for two lakes located in Zone 3 (Cèdre and Pessière, Table S1) that are only 20 km apart. Alternatively, the differences in reconstructed mFRI might represent real local differences in fire occurrences. Despite these differences, paleofire reconstructions from charcoal data constitute a unique way of assessing past fire regimes at a temporal scale that is not accessible by any other means (Conedera et al., 2009).

4.4. Integration of Holocene ecosystem range of variability in the definition of reference conditions for the western spruce-moss subdomain

With the combined contemporary and paleoecological approaches that were developed in this study, we aimed at defining more local (homogeneous vegetation-environment interactions) reference conditions that also would consider the long-term natural variability of boreal forest ecosystems. Our results showed that long-term fire return interval had a mean value of 240 years and a narrow 95% interval (221.9, 258.3) (Table 1), but the provincial reference conditions registry targets a fire cycle for the whole western spruce-moss subdomain at 150 years, based upon inventories that were conducted in the 1970s (Boucher et al., 2011). Our long-term approach allowed us to define a mean FRI for the entire subdomain, together with estimates for the individual zones that we defined.

Moreover, this method also provides an interval of variation that encompasses the natural multi-millennial behavior of fire dynamics. From the FRI, it is possible to reconstruct how the percentage of old-growth forests changed through time and, as for the FRI, to provide intervals of variation through time. Therefore, it is possible to assess whether current management guidelines are well adapted or whether they are leading landscapes outside their natural boundaries (Cyr et al., 2009, Bergeron et al., 2010). Indeed, Cyr et al. (2009) indicated that old-growth forests cover only 13% of the current landscape south of the western spruce-moss subdomain, while they should conservatively represent between 40% and 70%. Our results suggest that the past mean percentage of old-growth forest for the entire area was 65.9% (95% confidence interval: 63.7, 67.9) which is included in the conservative range developed by Cyr et al. (2009). This noticeable discrepancy in stand age-class distributions between the reference condition and the Holocene natural range of variability has prompted more questions regarding the use of present-day reference conditions to establish management targets. The reference conditions register actually reflects 19th and 20th century forests, a short time scale for boreal species for which life spans can exceed 200 years (Bergeron and Charron, 1994), and might not be well adapted for current and future conditions. Therefore, as percentage of old growth forest values derive from mFRI, they should be taken with perspective. Paleoecological studies can thus provide long-term variation in fire regimes and forest composition. We then suggest that management targets should be adapted to the long-term natural variability of boreal forest ecosystems.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.foreco.2018.08.007.

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