

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

Ecological Indicators

journal homepage: www.elsevier.com/locate/ecolind

Tree-related microhabitats and deadwood dynamics form a diverse and constantly changing mosaic of habitats in boreal old-growth forests

Maxence Martin^{a,b,c,*}, Nicole J. Fenton^{b,c}, Hubert Morin^{a,b}

^a Département des Sciences fondamentales, Université du Québec à Chicoutimi, 555 boul. de l'Université, Chicoutimi, Québec G7H2B1, Canada

^b Centre d'étude de la forêt, Université du Québec à Montréal, P.O. Box 8888, Centre-ville Station, Montréal, Québec H3C 3P8, Canada

^c Institut de Recherche sur les Forêts, Université du Québec en Abitibi-Témiscamingue, 445 boul. de l'Université, Rouyn-Noranda, Québec J9X 5E4, Canada

ARTICLE INFO

Keywords:

Natural forest
Biodiversity conservation
Biodiversity indicator
Forest succession
Forest dynamics
TreM
Wildlife habitat

ABSTRACT

Tree-related microhabitats (TreM) and deadwood are two forest attributes providing essential resources for biodiversity conservation and ecosystem services. Old-growth forests are generally defined by a high abundance and diversity of TreM and deadwood, but little is known about TreM and deadwood dynamics once the old-growth stage is reached, in particular in the boreal biome. In this context, knowledge on TreM and deadwood dynamics in old-growth forest stands is necessary to better understand how these forests contribute to biodiversity and ecosystem services. The aim of this study is thus to determine how TreM, and deadwood abundance and diversity vary within boreal old-growth forests. To reach this objective, we surveyed TreM and deadwood attributes, as well as structural and abiotic attributes, in 71 boreal old-growth forests situated in Quebec, Canada. We used hierarchical clustering analysis to identify TreM and deadwood abundance and diversity patterns in the studied stands. We identified five clusters of TreM and deadwood characteristics, which corresponded to three stages of old-growth forest succession: canopy break-up (beginning of the old-growth stage), transition old-growth stage (replacement of the first cohort by old-growth cohorts) and true old-growth stage (first cohort all or almost all gone). The peak in TreM richness and diversity was reached at the transition old-growth stage, whereas the peak for deadwood richness and diversity was reached at the true old-growth stage. Overall, true old-growth forests were defined by a combination of moderate to high TreM density and high deadwood volume, but these values significantly varied among stands depending on past secondary disturbances, stand structure and its composition (black spruce [*Picea mariana* Mill.] dominated vs mixed black spruce – balsam fir [*Abies balsamea* (L.) Mill.]). These results therefore underscore the importance of considering old-growth forests as dynamic rather than static ecosystems, as the composition of tree- and deadwood-related microhabitats in the same old-growth stand may markedly change over time. At landscape scale, these results also imply that the mosaic of habitats present in old-growth forests can vary greatly from one location to another, highlighting the importance of maintaining a diversity of old-growth forest structure and composition.

1. Introduction

Forest ecosystems provide vital habitats for a significant part of the world's biodiversity as well as multiple ecosystem functions and services, such as carbon storage and water provision (Forest Europe, 2015; Watson et al., 2018; Warren et al., 2019). Human activities have however significantly degraded forest landscapes over the centuries, resulting in an increasing loss and fragmentation of natural forests (Aksenov et al., 1999; Achard et al., 2009; Watson et al., 2018) as well as a simplification of stand structure and composition in managed

compared to natural forests (Winter and Möller, 2008; Bauhus et al., 2009; Puettmann et al., 2009). As a consequence, doubts have been raised about the capacity of remnant forest ecosystems to maintain their associated biodiversity and ecosystem services in a context of global change (Gauthier et al., 2015a; Franklin et al., 2016; Seidl et al., 2016). For these reasons, emphasis is now placed on alternative approaches, such as “close-to-nature” or “ecosystem based” management (e.g., Kuuluvainen, 2002; Gauthier et al., 2009; Puettmann et al., 2009). These strategies generally aim to reduce the gap between managed and natural forests in order to offset the loss of biodiversity and ecosystem services

* Corresponding author at: Département des Sciences fondamentales, Université du Québec à Chicoutimi, 555 boul. de l'Université, Chicoutimi, Québec G7H2B1, Canada.

E-mail addresses: maxence.martin1@uqac.ca (M. Martin), nicole.fenton@uqat.ca (N.J. Fenton), Hubert_Morin@uqac.ca (H. Morin).

<https://doi.org/10.1016/j.ecolind.2021.107813>

Received 22 June 2020; Received in revised form 18 May 2021; Accepted 19 May 2021

Available online 26 May 2021

1470-160X/© 2021 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

caused by human activities (Puettmann et al., 2009; Park et al., 2014). Primary forests, i.e., large forests of high naturalness almost or completely undisturbed by human activities (Sabatini et al. 2018), and old-growth forests, i.e., stands at the latest succession stage and driven by secondary disturbances (Wirth et al. 2009), are the most commonly considered references for natural forests. Primary forests are however not necessarily old-growth (e.g., primary forest recently burned by a wildfire), and old-growth forests are not necessarily primary (e.g., forests previously managed and abandoned since centuries) (Buchwald, 2005; Wirth et al., 2009). Overall, the effectiveness of management strategies strongly depends on the quality of our knowledge about the characteristics and dynamics of these ecosystems.

A common approach used to evaluate the similarity between managed and primary forests is the use of structural indicators (Angers et al., 2005; Paillet et al., 2015; Storch et al., 2018), with deadwood (standing or downed) as one of the most commonly used indicators. Deadwood abundance and diversity have a significant importance for biodiversity and ecosystem services, but it is also one of the attributes most negatively affected by forest management (Puettmann et al., 2009; Stokland et al., 2012; Winter, 2012). Moreover, there has been growing interest in tree-related microhabitats (hereafter: “TreM”), i.e., “distinct, well delineated structures occurring on living or standing dead trees, that constitute a particular and essential substrate or life site for species or species communities during at least a part of their life cycle to develop, feed, shelter or breed” (Larrieu et al. 2018). Woodpecker cavities are perhaps the best known and most studied TreM but there are actually a wide variety of types (e.g., exposed sapwood, cracks, bark pockets, dendrotelm – water-filled holes – funnel spider webs...), each defined by specific faunal, floral and/or fungal users (Michel et al., 2011; Larrieu et al., 2018; Paillet et al., 2018). Many of these TreM can be perceived as signs of a reduced longevity or a decrease in wood quality by forest managers, hence as “defects” (Martin and Raymond, 2019). For this reason, TreM density and diversity often decrease as the anthropogenic impact on forest ecosystems increases, for example through forestry practices such as thinning or short-rotation silviculture (Winter and Möller, 2008; Michel and Winter, 2009; Dieler et al., 2017).

Old-growth forests are generally expected to be the forest ecosystems defined by the highest deadwood and TreM abundance and diversity (Michel and Winter, 2009; Wirth et al., 2009; McGee, 2019). TreM and deadwood are often less abundant and diverse, if not absent, in younger and/or managed forests (Michel and Winter, 2009; Paillet et al., 2015; Martin et al., 2018). For this reason, old-growth forests are often viewed as models to be emulated for promoting naturalness and biodiversity conservation in managed stands (Bauhus et al., 2009; Puettmann et al., 2009; Keeton et al., 2019). However, recent research emphasized that the term “old-growth forest” encompasses a wide variety of changing forest structures at the stand scale (Halpin and Lorimer, 2016; Meigs et al., 2017; Kozák et al., 2020). Consequently, it is likely that the composition of TreM and deadwood will significantly vary from one old-growth structure to another. For example, an old-growth forest recently disturbed by a moderate-severity windthrow may be defined by a higher volume of early-decayed deadwood and a higher density of trees with broken branches or tops (i.e., TreM trees) than an old-growth forest that has not been significantly disturbed over the last decades. Acknowledging this diversity in deadwood and TreM composition in old-growth forests, as well as identifying the processes explaining this diversity, are therefore necessary steps to ensure sustainable forest management.

Primary and old-growth forests that can be used as models are still abundant in the boreal territories of Canada and Russia (Potapov et al. 2017). In eastern Canada, a significant proportion of primary boreal forests are also at the old-growth succession stage, due to relatively long (>200 years) fire cycles (Cyr et al., 2009; Gauthier et al., 2015b; Grondin et al., 2018). The availability of old and undisturbed forest stands made it possible to highlight the structural diversity and dynamics of old-growth forests in this region (Martin et al., 2018; Portier et al., 2018; Moussaoui et al., 2019). They can therefore help to

implement protection or restoration strategies in landscapes where these ecosystems have almost disappeared or are in decline (Watson et al. 2018). However, the complexity of secondary disturbance regimes and regeneration processes in these ecosystems suggests the existence of changing and diverse deadwood dynamics (Aakala et al., 2007; Martin et al., 2018, 2019). TreM dynamics are harder to evaluate because, except for woodpecker cavities (e.g., Tremblay et al., 2015; Andersson et al., 2018; Hardenbol et al., 2019), knowledge about TreM in boreal old-growth forests is scarce (e.g., Lilja and Kuuluvainen, 2005). This knowledge gap particularly concerns living TreM-bearing trees (hereafter, “TreM trees”). For example, cavities are generally observed on broadleaved and/or large (diameter at breast height [DBH] ≥ 20 cm) boreal trees (Martin et al., 2004; Tremblay et al., 2015), and may be scarce in boreal old-growth forests, dominated by relatively small coniferous trees (Vaillancourt et al., 2008; Cadieux and Drapeau, 2017). There is therefore an urgent need to better understand the characteristics of habitat trees other than cavity trees. Moreover, boreal old-growth forests are under increasing pressure due to the expansion of logging activities towards the north, as they are not systematically protected (Cyr et al., 2009; Grondin et al., 2018; Martin et al., 2020a). This implies a risk of losing in the coming years references of natural forests that could play a key role in the establishment of sustainable forest management strategies. In this context, a better understanding of deadwood and TreM dynamics in boreal old-growth forests of eastern Canada is therefore urgently needed to evaluate the impacts of logging on biodiversity and to propose alternative management strategies. Thus, the objective of this study is to determine how TreM and deadwood abundance and diversity vary within boreal old-growth forests of eastern Canada. We hypothesize that abundance and diversity of TreM and deadwood will progressively increase during the transition towards the old-growth stage. However, once the old-growth stage is reached, it is likely that the deadwood and TreM characteristics will vary depending on the intensity and time since the last secondary disturbance.

2. Methods

2.1. Study area

The study area (Fig. 1) is a 2200 km² area of public land south east of Lake Mistassini (from 72°15'00" W to 72°30'00" W and from 50°07'23" N to 50°30'00" N), part of the black spruce (*Picea mariana* [Mill.]) – feather moss bioclimatic domain (Robitaille and Saucier, 1998). Black spruce and balsam fir (*Abies balsamea* [L.] Mill.) are the dominant tree species in this territory. Jack pine (*Pinus banksiana* [Lamb.]), white spruce (*Picea glauca* [Moench] Voss), paper birch (*Betula papyrifera* [Marsh.]) and trembling aspen (*Populus tremuloides* [Michx.]) are also present to a lesser extent but rarely form monospecific stands. Thick glacial tills are the dominant surface deposits, forming a topography characterized by gentle hills. The altitude ranges from 350 to 750 m, mean annual temperature from –2.5 to 0.0 °C, annual rainfall (rain and snow) from 700 to 1000 mm and growing season length from 120 to 155 days. The fire cycle ranges from 200 years to 272 years (Gauthier et al., 2015b; Couillard et al., 2016), implying that old-growth forests (here defined as stands older than 100 years, *sensu* Bergeron and Harper [2009]) are abundant in this area. Timber exploitation started in 1991 at a low level until the year 2000, when harvest levels increased. All the forests on this territory that have not been harvested since the beginning of timber exploitation are therefore primary forests, even if they are not necessarily old-growth forests (e.g., forests recently burned).

This territory was chosen because of its relatively recent opening to logging activities. Many old-growth forests were therefore still present on the area and accessible by road, as they had not yet been harvested. Moreover, the presence of a forestry camp within the area also greatly simplified field sampling logistics

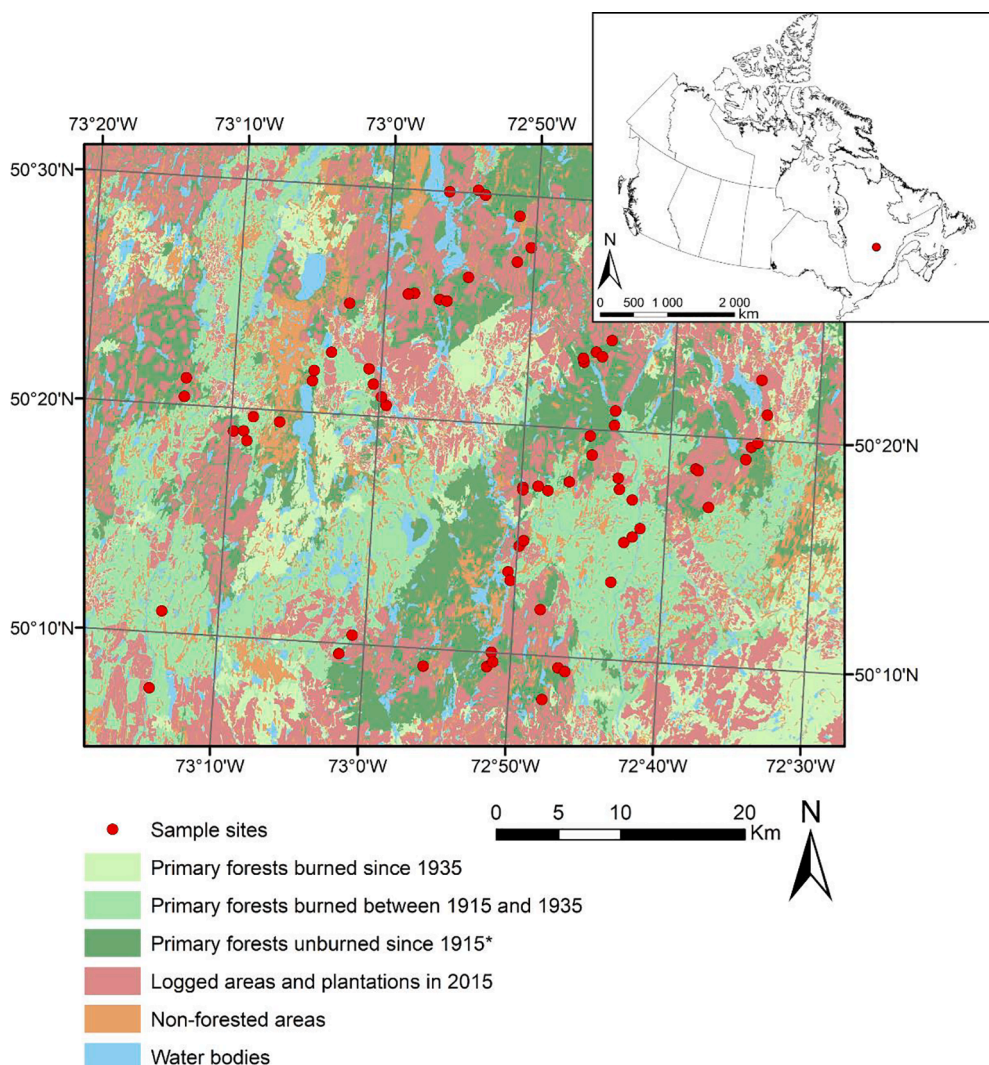


Fig. 1. Location of the sampled sites and main landscape classes in the study territory. The data used for this map – except sample site location – are made freely available by the Government of Quebec (www.donneesquebec.ca). Ancient fire maps may ignore unburned islands within a fire polygon. *: operational definition of old-growth forests, i.e., stands unburned since at least 100 years (MFFP, 2016). The insert map indicates the localization of the study territory in Canada.

2.2. Sampling

We selected 71 sites in forests unburned since 1935 within the study area, based on stratified random sampling defined according to stand age and environmental attributes (Martin et al. 2018). Five dominant and codominant trees were cored at stem base during a preliminary survey to estimate the minimum time since the last fire. The term “old-growth” can refer to stands at different successional stages, with trees from the first cohort following the last stand-replacing disturbance still being present in different proportions. For greater clarity, it is possible to distinguish “transition” old-growth forests (trees from the first cohort are still abundant) from “true” old-growth forests (trees from the first cohort have all or almost all been replaced by new shade-tolerant cohorts) (Oliver and Larson, 1996; Wirth et al., 2009). We thus defined two age classes that were most likely to discriminate the different old-growth stages in Eastern Canadian boreal forests (Uhlir et al., 2001; Bergeron and Harper, 2009; Gauthier et al., 2010): 80–200 years (most likely transition old-growth) and greater than 200 years (most likely true old-growth). Second, we used the Québec’s Ministry of Forests, Wildlife and Parks (MFWP) ecological classification to identify the dominant environmental types in the study territory, defined by the combination of stand potential vegetation, slope, surface deposit and drainage. Six of these types represented more than 72% of the forests in the study

territory and were selected for sampling (Table 1). We sampled sites belonging to the previous stand age/environmental types that were

Table 1

Number of sampled sites by environmental types and age-class combination. The age classes presented here are those measured from the ten basal discs sampled at each site; these values represent the age of the oldest tree sampled but not necessarily the age of the stand.

Environmental type	Age class					
	Potential vegetation	Slope	Surficial deposit	Drainage	80–200 years	>200 years
Balsam fir-white birch	Medium	Till	Mesic		9	3
Black spruce-feather moss	Low	Sand	Xeric		7	4
Black spruce-feather moss	Low	Till	Mesic		9	8
Black spruce-feather moss	Low	Till	Subhydric		6	7
Black spruce-sphagnum	Low	Organic	Hydric		2	5
Black spruce-balsam fir	Medium	Till	Mesic		6	5

accessible by forest road. To limit edge effects and associated bias, sampling was performed at least 125 m from the stand edge in each site.

For each site, we defined a 400 m² square plot with nested sub-plots and/or transects (Appendix A). In the 400 m² plot, we surveyed each living tree and standing deadwood (hereafter, “snags”) with a diameter at breast height (DBH) \geq 9 cm. We sampled saplings (DBH < 9 cm and height \geq 1.3 m) in two opposite 100 m² square plots within the 400 m² square plot. Downed deadwood (hereafter, “logs”) were surveyed along four 20 m-long transects following the edge of the 400 m² square plot, a methodology inspired by Clark et al. (1998). We considered only logs having a diameter \geq 9 cm at the transect intersection and not buried at a depth > 15 cm; those buried below this depth were ignored as they were difficult to sample. When a log crossed two transects, any second encounter was skipped to avoid double-counting.

We determined the presence of TreM on each living tree, using a typology adapted from Winter and Möller (2008), Michel and Winter (2009) and Vuidot et al. (2011) (Table 2). This typology was then subsequently adapted to the hierarchical TreM typology of Larrieu et al. (2018). However, due to methodological differences, TreM will be studied at the group scale (e.g., exposed sapwood and heartwood) and not at the type scale (e.g., crack). Similarly, size thresholds may differ and some classes of TreM from Larrieu et al. (2018) were not assessed (e.g. bryophytes). We have thus studied only nine groups of TreM representing six forms. Nevertheless, we have considered this adaptation to the typology of Larrieu et al. (2018) allows more coherence with current research and takes advantage of its hierarchical structure (e.g., Santopuoli et al. 2020). Asbeck et al. (2020) for example recently proposed an adaptation of the size thresholds proposed by Larrieu et al. (2018) for North American forests, partially consistent with those used in our typology (e.g., woodpecker breeding cavities, exposed sapwood only). These previously typologies have however been defined for temperate and/or mountain forests, resulting in size thresholds not necessarily adapted to the small tree dimensions in boreal forests. For each snag or log surveyed, we attributed a decay class based on Angers et al. (2005) (Table 3). The presence of TreM on snags or logs was not considered in this study first because it would have been redundant with decay classes

Table 2

TreM typology used in this study, based on Winter and Möller (2008), Michel and Winter (2009) and Vuidot et al. (2011) but subsequently adapted to the Larrieu et al. (2018) hierarchical typology.

Form	Group	Characteristics
Cavities	Woodpecker breeding cavities	Cavity with > 5 cm aperture, carved by woodpeckers
	Rot holes	Cavity with > 5 cm aperture, carved by wood decay
Tree injuries and exposed wood	Exposed sapwood only	Detached bark at least on a 5 cm \times 5 cm surface
	Exposed sapwood and heartwood	The primary stem or a large branch is broken, with diameter at breakage > 10 cm, or complete fracture of one of the two forking branches, with severe damages on the main stem, or crack with a length > 25 cm long and at least 2 cm deep in the sapwood
Crown deadwood	Crown deadwood	At least 25% of the crown is dead
	Twig tangles	Dense agglomeration of branches from a parasite or epicormic branching
Fruiting bodies of saproxylic fungi and slime mould	Burrs and cankers	Canker > 10 cm diameter
	Perennial fungal fruiting bodies (life span > 1y)	Fruiting bodies > 5 cm in diameter or occur in 10 cm long cascades of smaller fruiting bodies
Fresh exudates	Fresh exudates	Resin or sap flow at least 30 cm long or > 5 flows of sap or resin of smaller size

Table 3

Characteristics of the deadwood decay classes as defined by Angers et al. (2005).

Class	Characteristics
Class 1	Recent death or fall, buds and twigs still intact, tight bark and hard wood
Class 2	Fine parts such as buds and twigs lacking, bark loose, wood still hard
Class 3	Bark mostly gone, bole periphery softened; a blade can penetrate the outer layer; in snags, tree top is often broken
Class 4	Little to no bark remains, bole periphery well rotten and extends in the core; a blade can easily penetrate; in snags, bole is broken
Class 5	Well-decayed wood, incorporating into the forest floor, vegetation has colonized

(e.g., the TreM “exposed sapwood only” is a criterion for decay classes 2 to 4). Second, decay classes can be surveyed on both logs and snags, contrary to TreM, and thereby help to better understand the links between the different deadwood components. Third, decay classes have proven to be an efficient surrogate of stand biodiversity in boreal forests (Lassauce et al. 2011), while such knowledge is lacking for TreM.

To determine minimum stand age, we collected a disc from the base of ten coniferous merchantable trees and measured the number of rings along two radii. We sampled a similar number of trees per canopy layer (dominant, codominant, intermediary and oppressed) for each site. For each canopy layer, sampled trees were randomly selected from those within the plot. Trees presenting a marked root rot (pith absent) were not retained. At least three of these trees were dominant and their height was measured once the tree was felled to estimate the dominant stand height. Stand soil and topographic parameters were determined by digging a soil profile at the plot centre and measuring topographic variables with a clinometer.

2.3. Data computation and analysis

For each site, the following structural and environmental attributes were calculated by Martin et al. (2018): (i) tree density, (ii) sapling (trees with a DBH < 9 cm and height > 1.3 m) density, (iii) tree basal area, (iv) proportion of balsam fir in the basal area, (v) coarse woody debris volume using Marshall et al. (2000) for linear transect sampling, (vi) gap fraction (i.e., percentage of gaps in the canopy), (vii) Weibull’s shape parameter (Bailey and Dell 1973) of tree diameter distribution, (viii) cohort basal area proportion (i.e., frequency of trees from old-growth shade-tolerant cohorts in the basal area; Kneeshaw and Gauthier, 2003), (ix) minimum time since the last fire (i.e. age of the oldest tree), (x) slope, and (xi) depth of the organic layer (Table 4).

To evaluate the changes in abundance and diversity of deadwood (i.e., snags and logs) and TreM, we computed the following attributes: TreM tree (i.e., trees that bear at least one TreM) density, snag basal area, Shannon index of TreM classes, Shannon index of snag decay classes, and Shannon index of log decay classes (Table 4). We used these attributes, as well as the log volume calculated by Martin et al. (2018), to perform a hierarchical clustering of the studied sites. The objective of this analysis was to identify stand types defined by homogeneous TreM and deadwood attributes. We used Ward’s linkage clustering method (Ward, 1963) and Euclidian distances to perform the clustering, with data that were preliminarily normalized (margin sum of squares equal to one) and standardized (mean equal 0 and standard deviation equal to 1) using the *decostand* function of the *vegan* R package (Oksanen et al. 2018). These transformations aimed to limit the influence of outliers and give each variable the same importance for clustering. We next performed a principal component analysis (PCA) to highlight how the studied attributes were distributed in the clusters. The distribution of the clusters and of the explanatory variables were then observed along the first and second dimensions (Dim1 and Dim2, respectively) of the PCA. We also compared these attributes among the clusters with permutation based partial ANOVA (PERMANOVA; Anderson, 2001; McArdle and

Table 4

Attributes sampled for each site, adapted from [Martin et al. \(2018\)](#). TreM: tree-related microhabitat. “*” indicates attributes used for Ward’s clustering.

Category	Attribute	Unit	Description
TreM and deadwood attributes	TreM tree density*	n/ha	Density of merchantable trees bearing at least one TreM per hectare
	Shannon Index of TreM groups*	–	TreM index of diversity, calculated using the Shannon and Weaver (1949) formula and frequency of TreM classes
	Mean TreM frequency on TreM trees	n	Mean number of TreM classes observed on TreM trees
	TreM richness	n	Total number of TreM classes observed within the plot
	Large TreM trees density	n/ha	Number of TreM trees per hectare defined by a dbh \geq 20 cm
	Large living trees density	n/ha	Number of trees per hectare defined by a dbh \geq 20 cm
	Mean DBH of TreM trees	cm	Mean DBH of the sampled TreM trees
	Mean DBH of living trees	cm	Mean DBH of the sampled trees
	Snag basal area*	m ² /ha	Snags basal area per hectare
	Snag density	n/ha	Density of snags per hectare
	Large snag density	n/ha	Density of snags per hectare defined by a dbh \geq 20 cm
	Shannon index of snag decay classes*	–	Snag decay classes index of diversity, calculated using the Shannon and Weaver (1949) formula and frequency of snag decay classes
	Log volume*	m ³ /ha	Coarse woody debris volume per hectare, computed by Martin et al. (2018)
	Shannon index of log decay classes*	–	Log degradation classes index of diversity, calculated using the Shannon and Weaver (1949) formula and frequency of log decay classes
	Other attributes computed by Martin et al. (2018)	Tree density	n/ha
Saplings density		n/ha	Number of living saplings per hectare
Basal area		m ² /ha	Basal area of the living merchantable trees per hectare
Balsam fir proportion		%	Proportion of balsam fir in the basal area
Gap fraction		%	Percentage of the canopy under gaps
Maximum height		m	Mean height value of the dominant trees
Weibull’s shape parameter		–	Calculated using Weibull’s function of diameter distribution (Bailey and Dell 1973). This equation is characterized by the shape parameter a, identified in our study as Weibull’s shape parameter (WSP), and the scale parameter b. WSP \geq 1.5 represents a Gaussian distribution of diameters, $1 \leq$ WSP $<$ 1.5 an irregular distribution and WSP $<$ 1 a reverse J-shaped distribution
Cohort basal area proportion		–	Replacement index of the even-aged cohort by old-growth cohorts, defined by Kneeshaw and Gauthier (2003) and ranging from 0 to 1. CBAP = 0 indicates a stand with one single even-aged cohort and

Table 4 (continued)

Category	Attribute	Unit	Description
			CBAP = 1 a stand where old-growth cohorts replaced all the even-aged cohort
	Minimum time since last fire	years	Minimum stand age, defined by age of the oldest tree sampled
	Slope	%	Mean slope value along the plot
	Depth of the organic layer	cm	Mean depth of the organic layer

[Anderson, 2001](#)), using Euclidean distances and 10,000 permutations for each analysis. When the analyses were significant, we then performed pairwise PERMANOVA based on the method of [Martinez Arbizu \(2017\)](#) as a post-hoc test. The pairwise PERMANOVA were also based on Euclidean distances and with 10,000 permutations for each pairwise comparison.

To gain a better understanding of clusters’ characteristics, we then computed attributes of TreM trees and deadwood for each cluster: mean DBH of TreM trees, mean DBH of living trees, density of large (DBH > 20) TreM trees, density of large living trees, TreM richness, mean TreM frequency on TreM trees, snag density and large (DBH > 20 cm) snag density ([Table 4](#)). We also computed the frequencies of the different TreM classes, and deadwood decay classes for all the studied sites. All these attributes, as well as those computed by [Martin et al. \(2018\)](#) that were not used for the clustering, were then compared among the clusters using PERMANOVA, based on Euclidean distances and 10,000 permutations. As before, we performed pairwise PERMANOVA as a post-hoc test when the results of the PERMANOVA were significant.

Statistical analyses were completed using R-software, version 3.6.1. ([R Core Team, 2019](#)), using the *vegan* ([Oksanen et al. 2018](#)), *FactoMineR* ([Lê et al. 2008](#)) and *pairwiseAdonis* ([Martinez Arbizu, 2017](#)) packages applying a *p* threshold of 0.05.

3. Results

3.1. Cluster structural and environmental attributes

The studied sites were divided in 5 distinct clusters, with an even number of sites per cluster ranging from 11 (Cluster 3) to 20 (Clusters 5). All structural and environmental attributes differed significantly among the clusters, except tree density, basal area, broadleaved species proportion, gap fraction and Weibull’s shape parameter ([Table 5](#)). Differences in cohort basal area proportion and minimum time since the last fire indicated that the clusters were distributed along an old-growth succession gradient. Cluster 1 grouped the younger sites with the lowest cohort basal area proportion, indicating stands at the beginning of the transition towards old-growth stage (i.e., canopy break-up). Cluster 2 grouped older stands, but from various age structures. This supposes that this cluster mainly regroups stands that are still in transition (transition old-growth stage), although true old-growth forests can be present. Finally, Clusters 3 to 5 grouped the oldest stands with the highest cohort basal area proportion, indicating true old-growth forests.

Cluster 5 presented higher values of balsam fir proportion, maximum height, and slope as well as a thinner organic layer compared to the other clusters. Results were more contrasted between the clusters for sapling density, however with an increasing gradient ranging from Cluster 1 to Cluster 5. Differences in successional stage, environmental conditions and tree species composition rather than structure (e.g. tree density or basal area) therefore characterized the identified clusters.

3.2. Attributes of TreM and deadwood clusters

The two first dimensions of the PCA explained 61.3% of the variance

Table 5

Mean values and standard deviations of the structural and environmental attributes sampled by Martin et al. (2018) for the identified clusters. Different letters indicate significant differences at $p < 0.05$ with $a > b > c$. Details of the PERMANOVA models are provided in Appendix B.

Attribute	Cluster 1 (n = 16)	Cluster 2 (n = 12)	Cluster 3 (n = 11)	Cluster 4 (n = 12)	Cluster 5 (n = 20)
Tree density (n/ha)	1017.19 ± 513.46	991.67 ± 326.54	759.09 ± 388.15	989.58 ± 354.43	856.25 ± 313.5
Sapling density (n/ha)	1762.5 ± 1194.64 b	2068.75 ± 1267.79 b	2290.91 ± 1212.55 ab	2635.42 ± 1305.08 ab	3958.75 ± 2752.77 a
Basal area (m ² /ha)	15.89 ± 8.96	20.69 ± 8.67	13.19 ± 6.16	15.98 ± 5.23	20.05 ± 6.78
Balsam fir proportion (%)	0.1 ± 0.41 c	13.18 ± 23.36 bc	0.76 ± 1.1 c	5.51 ± 7.56 b	32.58 ± 27.55 a
Broadleaved species proportion (%)	0 ± 0	9.3 ± 21.82	0 ± 0	0.21 ± 0.49	6.74 ± 15.55
Gap fraction (%)	63.17 ± 25.32	55.3 ± 30.21	70.44 ± 22.01	69.99 ± 23.83	58.55 ± 25.32
Weibull's shape parameter	1.25 ± 0.46	0.96 ± 0.36	0.95 ± 0.19	1.01 ± 0.2	0.97 ± 0.53
Maximum height (m)	15.58 ± 2.75 c	18.45 ± 3.18 b	18.7 ± 2.5 b	18.18 ± 3.15 b	20.67 ± 2.1 a
Cohort basal area proportion	0.35 ± 0.38 b	0.47 ± 0.34 ab	0.68 ± 0.31 a	0.73 ± 0.34 a	0.61 ± 0.33 a
Min. time since the last fire (years)	141.94 ± 59.4 c	198.33 ± 61.92 ab	240.36 ± 59.92 a	215.08 ± 63.74 ab	195.45 ± 37.99 b
Slope (%)	4.75 ± 4.88 b	9.08 ± 12.56 b	6.82 ± 6.18 b	6.17 ± 7.8 b	17.55 ± 9.65 a
Depth of the organic layer (cm)	28 ± 16.1 ab	36 ± 19.57 a	40.64 ± 18.83 a	35.83 ± 12.74 a	23.1 ± 10.52 b

and the clusters were separated along them (Fig. 2). The first dimension revealed a positive trend among all TreM and deadwood attributes. The second dimension revealed an opposing trend between log attributes (volume and Shannon Index) and TreM attributes (bearing tree density and diversity), while the variables related to snags presented no correlation. Cluster 1 and 5 were on opposite ends of Dim1, while Cluster 2 and 3 were on opposite ends of Dim 2. Cluster 4, however, had no precise pattern as it was dispersed along the first two dimensions of the PCA. These results indicated clear differences in TreM and deadwood abundance and diversity within the clusters.

We observed significant differences for all the attributes related to deadwood (i.e., snags and logs) abundance and diversity (Table 6). The majority of these attributes followed a similar pattern, with the lowest values for Cluster 1, intermediate in Clusters 2 to 4, and the highest in Cluster 5. The Shannon Index of snag decay classes however showed a different trend, with lower values for Cluster 1 and 4 compared to the others, but without significant differences between Clusters 2, 3 and 5. Similarly, snag density was the highest for cluster 3 compared to the others, which did not differ significantly from one another. We also observed significant differences in the frequencies of snags of decay classes 1 and 3 (Fig. 3). Snag decay class 1 was significantly more frequent in Cluster 1 in comparison to Cluster 5, with intermediate values for the other clusters. The frequency of snag decay class 3 was higher for Clusters 3 and 5 compared to clusters 1, again with intermediate values for the other clusters. In contrast to snags, we observed a significant difference in the frequency of decay class 4 logs, which was significantly lower in cluster 1 compared to the others.

All attributes related to TreM presented significant differences between the clusters (Table 6). The distribution of values of TreM-related attributes between clusters was, however, more complex than those related to deadwood. Cluster 2 presented the highest TreM tree density, large TreM tree density and Shannon Index of TreM group values. Values for the TreM-related attributes in Cluster 5 were generally similar to those of Cluster 2, at the exception of slightly lower TreM tree density and Shannon index of TreM groups values. In contrast, Cluster 1 generally showed the lowest values. Finally, Clusters 3 and 4 presented similar and intermediary values for the TreM-attributes related to tree size, but significant differences in TreM abundance and diversity. In this case, Cluster 4 was similar to Cluster 5 while Cluster 3 was similar to Cluster 1. No analysis was performed for the frequency of the following TreM because of an insufficient number of observations: woodpecker breeding cavities, rot holes, twig tangles, burrs and cankers and perennial fruiting bodies (Appendix D). For the remaining TreM, we observed a significant difference within the clusters only for the exposed sapwood group (Fig. 4). Their frequency was higher in Cluster 5 compared to Clusters 1 and 3, with intermediate values for the others.

4. Discussion

TreM and deadwood abundance and diversity presented complex and sometime divergent patterns. True old-growth stands were in general defined by a higher deadwood abundance and diversity in comparison to transition stands. In contrast, TreM abundance and richness reached their peak during the transition and then strongly varied from

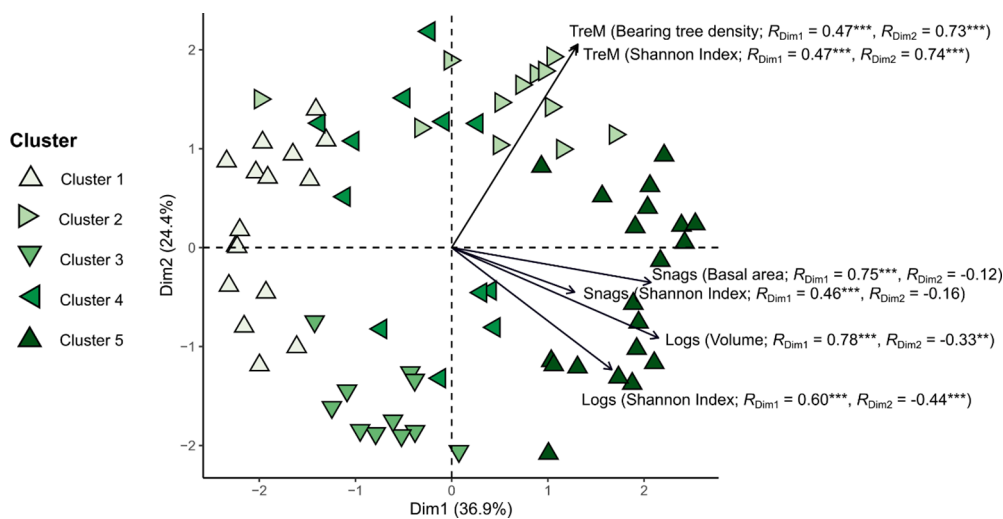


Fig. 2. PCA biplot and results of Ward's clustering for the 71 sites sampled. *R* indicates values of the correlation coefficient along the two first dimensions of the PCA (Dim1 and Dim2). "****" indicates p -values < 0.001 , "***" p -values < 0.01 and "**" p -values < 0.05 . The contribution of each dependant variable to the PCA dimensions is provided in Appendix C.

Table 6

Mean values and standard deviations of TreM and deadwood attributes within the identified clusters. Different letters indicate significant differences at $p < 0.05$, with $a > b > c$. Details of the PERMANOVA models are provided in [Appendix B](#).

Category	Attribute	Cluster 1 (n = 16)	Cluster 2 (n = 12)	Cluster 3 (n = 11)	Cluster 4 (n = 12)	Cluster 5 (n = 20)
TreM	TreM tree density (n/ha)	34.38 ± 20.16 c	133.33 ± 28.87 a	27.27 ± 26.11 c	75 ± 30.15 b	83.75 ± 40.78 b
	Shannon Index of TreM groups	0.36 ± 0.39 c	0.96 ± 0.27 a	0 ± 0 c	0.83 ± 0.31 b	0.82 ± 0.43 b
	Mean TreM frequency on TreM trees (n)	1.25 ± 0.38 ac	1.1 ± 0.12 b	1 ± 0 c	1.38 ± 0.38 a	1.35 ± 0.43 a
	TreM richness (n)	1.44 ± 0.81 b	3 ± 0.74 a	0.73 ± 0.47 c	2.58 ± 1 a	2.65 ± 1.18 a
	Mean DBH of TreM trees (cm)	14.27 ± 2.94 c	18.34 ± 3.15 ab	17.77 ± 3.87 ab	15.34 ± 4.54 bc	20.22 ± 5.8 a
	Large TreM trees density (n/ha)	3.12 ± 8.54 b	54.17 ± 41.06 a	6.82 ± 11.68 b	8.33 ± 12.31 b	33.75 ± 27.24 a
	Mean DBH of living trees (cm)	13.53 ± 1.95 c	15.42 ± 2.22 ab	14.4 ± 1.78 bc	13.82 ± 1.85 bc	16.69 ± 3.1 a
	Large living tree density (n/ha)	75 ± 97.47 b	189.58 ± 137.12 a	84.09 ± 65.45 b	85.42 ± 65.24 b	203.75 ± 115.93 a
	Snags	Snag basal area (m ² /ha)	1.65 ± 1.19 c	3.71 ± 1.69 b	3.26 ± 1.47 b	2.61 ± 1.54 bc
Shannon index of snag decay classes		0.52 ± 0.37 b	1.02 ± 0.23 a	1.01 ± 0.17 a	0.52 ± 0.28 b	0.96 ± 0.23 a
Snag density (n/ha)		107.81 ± 82.52 b	168.75 ± 84.02 b	154.55 ± 56.81 b	118.75 ± 61.35 b	242.5 ± 95.32 a
Large snag density (n/ha)		4.69 ± 10.08 c	37.5 ± 31.08 b	18.18 ± 31.8 bc	25 ± 28.2 b	118.75 ± 73.39 a
Logs	Log volume (m ³ /ha)	9.06 ± 9.74 c	41.68 ± 26.64 b	46.34 ± 20.36 b	45.8 ± 25.35 b	120.95 ± 52.78 a
	Shannon index of log decay classes	0.34 ± 0.44 c	1.03 ± 0.26 b	1.21 ± 0.23 ab	1.19 ± 0.29 ab	1.32 ± 0.17 a

one true old-growth structure to another. Our hypothesis, that TreM and deadwood abundance and diversity will progressively increase during the transition towards the old-growth stage, reaching their maximum at the true old-growth stage, was therefore only partially supported by our results. Similarly, at the true old-growth stage, many interrelated factors such as disturbance history, topography and tree species composition influenced TreM and deadwood characteristics. Rather than a straight line, TreM and deadwood dynamics seem to follow sinuous paths in the boreal old-growth forests of eastern Canada.

4.1. TreM dynamics along boreal old-growth forest succession

TreM dynamics observed in the study territory was unexpected, because TreM tree density significantly increased at the old-growth transition to eventually drop down once the true old-growth stage was reached. This was particularly striking in black spruce-dominated stands. The peak in TreM trees observed in transition old-growth stands was probably due to the high abundance of old and senescent trees from the pioneer cohort that appeared following the last stand-replacing disturbance. Indeed, the longevity of trees in the eastern Canadian boreal forest is generally relatively low (i.e., less than 200 years; Burns and Honkala, 1990) and the presence of TreM can be an indicator of tree senescence (Martin and Raymond, 2019; Martin et al., 2021). It is thus likely that an important proportion of the even-aged cohort trees become senescent and develop TreM before dying and being replaced by new cohort trees. Then, once the true old-growth stage is reached, stand structure becomes more complex, with trees of various ages and sizes, and therefore fewer susceptible to developing TreM.

The divergence in TreM tree density and richness between Clusters 3 to 5 highlighted how differences in structural attributes within true old-growth forests may influence their habitat diversity. In comparison to Cluster 3 and 4, Cluster 5 was defined by a higher density of large trees as well as a greater frequency of balsam fir and broadleaved species. TreM presence is generally linked to tree diameter, with larger trees more susceptible to bear TreM than smaller ones (Michel and Winter, 2009; Asbeck et al., 2019; Paillet et al., 2019). Similarly, broadleaved species are more prone to developing TreM than coniferous species (Paillet et al., 2019). Moreover, the higher sensitivity of balsam fir to root rot or windthrow in comparison to black spruce (Basham, 1991; Ruel, 2000) may increase the frequency of senescent and/or wounded trees in stands where balsam fir is abundant. As a result, the frequency and severity of secondary disturbances is often higher in old-growth stands where black spruce and balsam fir are mixed in comparison to pure black spruce stands (De Grandpré et al., 2018; Martin et al., 2018, 2019). This is consistent with our results, as Cluster 5 is defined by a higher snag basal area and higher log volume than Clusters 3 and 4. TreM abundance and diversity were however equivalent between Clusters 4 and 5, while they were very low in Cluster 3. Interestingly, there were no differences

in the density or in the size of living as well as TreM trees between Clusters 3 and 4, implying that the differences observed in TreM abundance and diversity were not influenced by tree dimensions. Further, Cluster 2 may also contain some true old-growth forests. This suggests that TreM characteristics can vary markedly from one old-growth stand dominated by black spruce to another. Martin et al. (2020b) highlighted a cyclicity in the mortality and regeneration dynamics of black spruce. TreM may thus appear periodically in old spruce forests as they approach to a senescence phase. Overall, these results underscore that TreM richness and diversity are more related to tree species composition and disturbance regime than to specific structural attributes in true old-growth forests.

Old-growth forests in the boreal biome are generally defined by smaller trees and a predominance of coniferous species compared to old-growth forests from other biomes (Bergeron and Harper, 2009). As TreM are generally more abundant on hardwood species compared to coniferous species, as well as on large trees compared to the smaller ones (Paillet et al., 2019), trees in boreal forests may be less susceptible to develop TreM. Thus, the density of TreM trees (from 34.3 to 133.3 TreM trees/ha in the different clusters) observed in our study was unsurprisingly lower than that observed by Kozák et al. (2018) in primary forests dominated by European beech (*Fagus sylvatica* L.) in Europe (277.8 trees/ha). However, Jahed et al. (2020) surveyed around 100 TreM trees/ha in primary forests dominated by broadleaved species in Ukraine and Iran and found densities similar to those observed in clusters 2 and 3. TreM density and mean TreM frequency on trees are hard to compare to other studies as we used a simplified typology (9 TreM groups). For example, the typology of Michel and Winter (2009) contains 19 TreM classes. This high number of classes may inflate the TreM density observed on Northeastern American Douglas fir (*Pseudotsuga menziesii* var. *menziesii* [Mirbel] Franco) in the study of Michel and Winter (2009) (around 750 TreM/ha) in comparison to ours. Admittedly, the trees studied by Michel and Winter (2009) were much larger than ours (all trees sampled defined by a DBH > 20 cm) and this factor certainly significantly contributed to their results. Similarly, the typology of Larrieu et al. (2018) defines 47 TreM types that can be regrouped in 15 groups or seven forms. In comparison, our typology included nine groups and six forms. The exhaustiveness of new reference TreM typologies can therefore help to better identify the differences in habitat tree characteristics between different forests.

Nevertheless, considering the intrinsic limits to TreM development in boreal forests (i.e., coniferous composition and small trees), the richness observed in the studied stands was often high. As these stands are primary forests, it is likely that this result was mainly due to their naturalness. Moreover, we chose to not include the TreM observed on dead standing trees in this study, as it would have been redundant with snag decay classes. As TreM density is in general far higher on snags in comparison to living trees (Paillet et al., 2019), it is therefore likely that

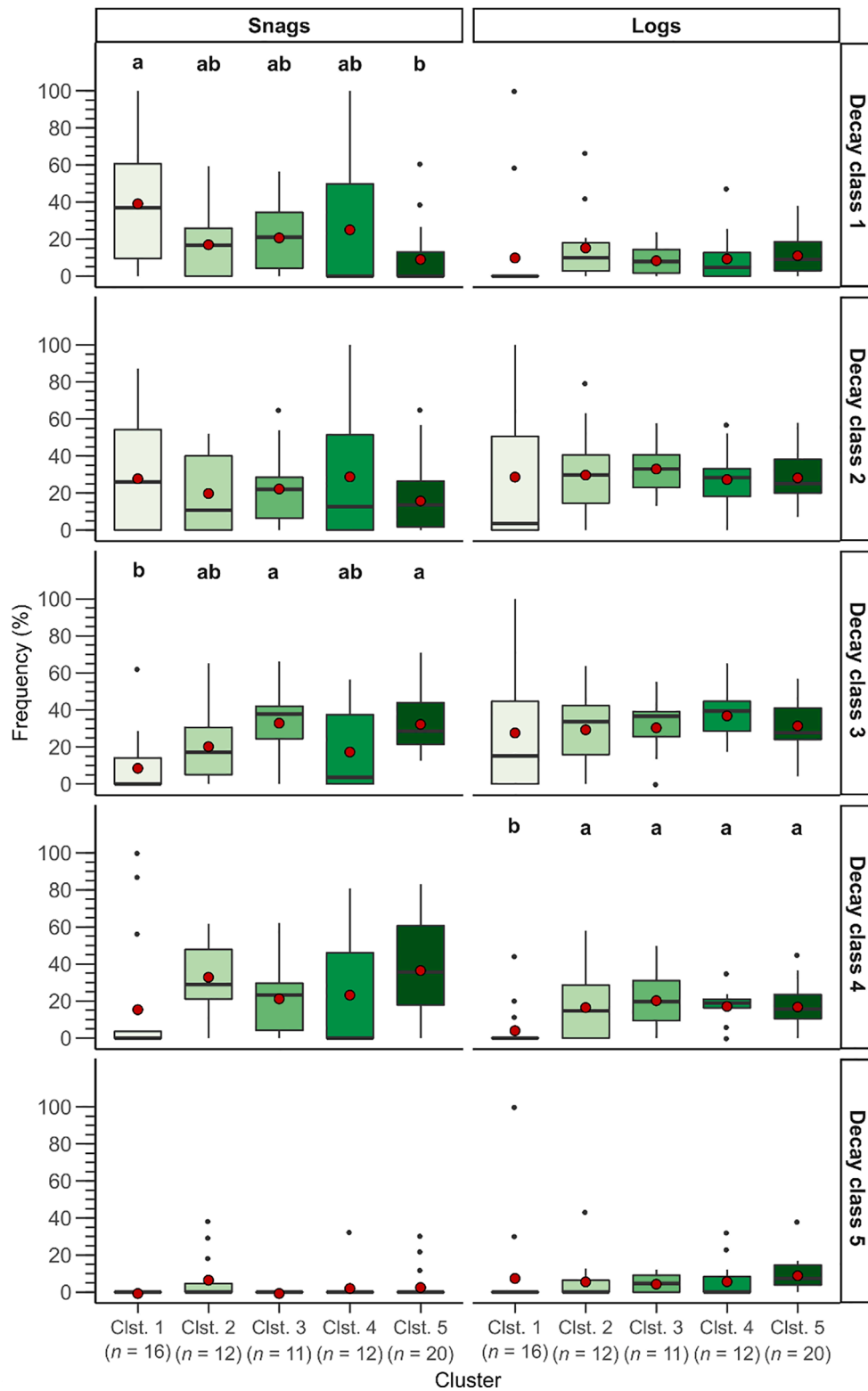


Fig. 3. Boxplot of deadwood decay class frequencies for the identified clusters. Different letters indicate significant difference at $p < 0.05$, with $a > b > c$. Red dots indicate mean values. Clst.: cluster. Details of the PERMANOVA models are provided in [Appendix B](#). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the total density in the studied stands was higher. Finally, broadleaved species were uncommon in the studied stands, particularly aspen. This pioneer boreal species can quickly reach large diameters and is favoured by woodpeckers for carving cavities (Martin et al., 2004; Remm and Löhmus, 2011; Blanc and Martin, 2012). In eastern Canada, mixedwood

forests hence play a key-role in the provision of nesting and feeding sites for avifauna (Cadieux, 2017; Cadieux and Drapeau, 2017). As a consequence, further research should be performed on mixedwood boreal stands containing trembling aspen to determine if they are defined by a higher TreM richness and diversity in comparison to coniferous boreal

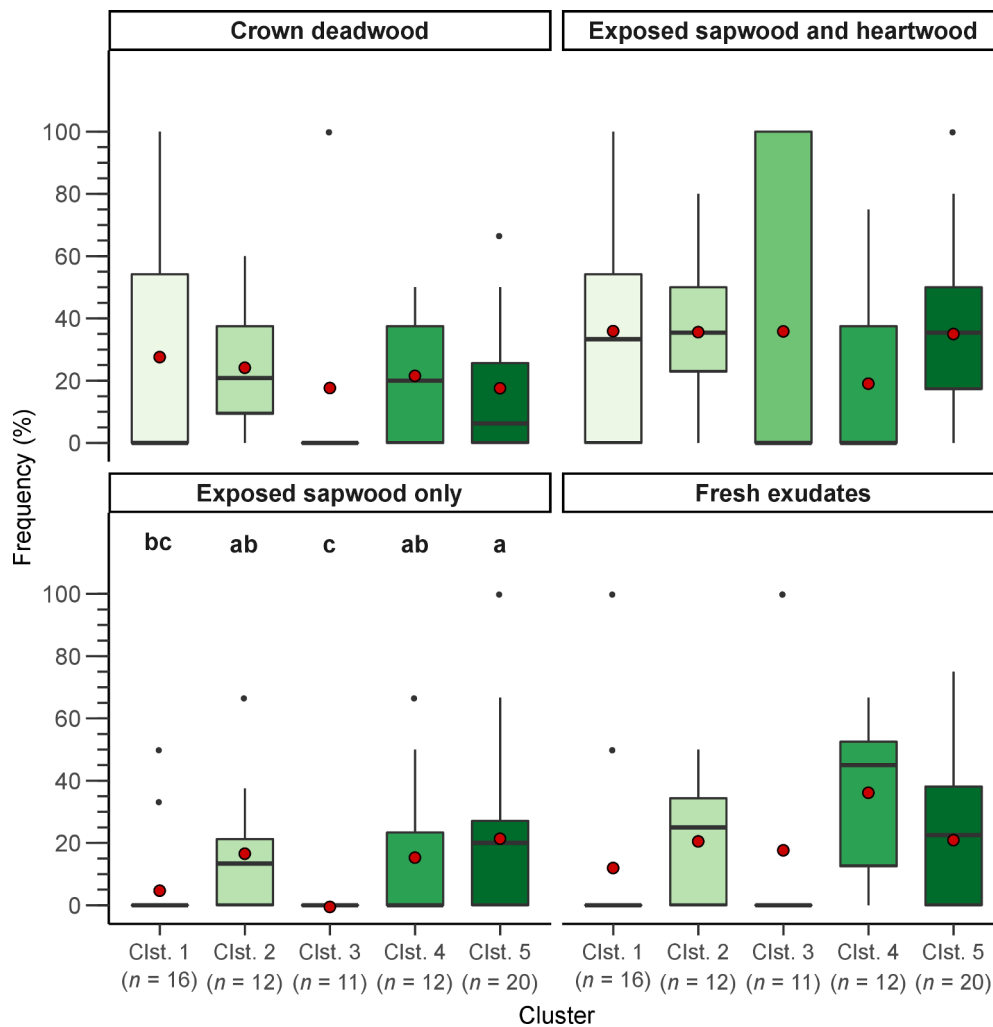


Fig. 4. Boxplot of TreM classes' frequencies for the identified clusters. Different letters indicate significant difference at $p < 0.05$, with $a > b > c$. Red dots indicate mean values. Clst.: cluster. Details of the PERMANOVA models are provided in [Appendix B](#). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

stands.

4.2. Deadwood dynamics along boreal old-growth forest succession

Once the old-growth stage is reached, it is often assumed that deadwood continues to accumulate or reaches a plateau ([Brassard and Chen, 2006](#)). However, our results underscored that the dynamics of deadwood in old-growth forests are more complex, depending on the succession process, progressive changes in species composition and the action of secondary disturbances. Even if we observed an increase in snag basal area and log volume between the canopy break-up and transition old-growth stages, the deadwood pattern then diverged depending on the true old-growth forest type. Specifically, snag basal area and log volume were similar between transition old-growth forests and true old-growth forests dominated by black spruce, while they were significantly higher for true old-growth forests with a mixture of black spruce and balsam fir. These results are consistent with the literature review performed by [Bergeron and Harper \(2009\)](#), who observed similar trends between pure black spruce and mixed black spruce – balsam fir old-growth forests. Indeed, mixed black spruce – balsam fir stands are subject to higher and more frequent deadwood inputs in comparison to pure black spruce stands because of the higher severity of the secondary disturbance regime ([Martin et al., 2019, 2020c](#)). However, the abundance of balsam fir in true old-growth stands may vary significantly over

time because of the action of secondary disturbances ([Pham et al., 2004; De Grandpre, 2009](#)). This implies changes in deadwood dynamics over time in boreal true old-growth forests of eastern Canada, depending on the change in tree species composition over time.

The pattern of deadwood diversity along old-growth succession was also slightly different to that of deadwood abundance. The diversity in snag decay classes reached its maximum at the transition old-growth stage and remained unchanged thereafter. In contrast, the richness in log decay classes reached its maximum at the true old-growth stage, independently of stand composition (i.e., black spruce dominated or black spruce – balsam fir). For the snags, this increase in diversity along forest succession is probably due to the gradual addition of new standing dead trees, where new early decayed snags (decay class 1) appear while the older snags continue to rot (decay classes 3 and 4). For logs, however, we observed a significant difference in frequency over time for only one decay class (class 4), compared to two classes for snags. It is therefore more difficult to reconstruct the debris dynamics, although we can expect it to be broadly similar to that of snags, albeit with a slight lag ([Brassard and Chen, 2006](#)). Several factors may explain the absence of clear differences in frequency of log decay classes among the clusters. First, canopy break-up is a progressive process ([Oliver and Larson, 1996; Pesklevits et al., 2011](#)), which may have started decades ago even in the cluster grouping the youngest stands (cluster 1), meaning that some snags and logs are already in advanced decay stages. Remnant

deadwood originating from the last stand-replacing disturbance can also still be present, providing well-decayed logs in even-aged stands (Maser et al., 1979; Brassard and Chen, 2006). Second, the half-lives of black spruce and balsam fir snags are often short (around 20 years; Angers et al. 2010) and these species are also sensitive to stem breakage because of windthrows (Whitney et al., 2002; Wilson and MacLean, 2015). This is consistent with the high frequency of the “broken stem or branch” TreM type in the studied sites. Windthrow or breakage may result in sudden inputs of logs from both well-decayed snags that finally broke and formerly living black spruce that underwent stem breakage. Third, multiple factors other than the time since tree death drive wood decay speed, such as tree species, degree of contact with the ground, stand environmental conditions, tree vitality when decay started (i.e., before or after tree death) as well as decaying fungi species or community (Pioli et al., 2018; Přívĕtvý et al., 2018; Shorohova et al., 2019). Finally, in boreal forests, deadwood is often buried in the organic layer before it completes decay, with intermediate to highly decayed logs being the most susceptible to burial (Moroni et al., 2015; Stokland et al., 2016). Deadwood diversity therefore results from complex interactions among decay speed, deadwood inputs from varying decay classes and log burying, explaining the scarcity of significant changes in log decay class frequency during old-growth succession.

4.3. TreM and deadwood dynamics in boreal old-growth forests: a conceptual model

By focusing on old-growth forest stands, our study revealed unexpected and complex TreM and deadwood dynamics in these ecosystems (Fig. 5). However, our results are mostly restricted to black spruce dominated forests on gentle to moderately steep slopes. Further research on mixedwood boreal forests and on stands on steep slopes are needed to complete a landscape level portrait. Yet, old-growth forests may commonly alternate over time between black spruce and mixed black spruce - balsam fir forests in eastern Canada (Pham et al., 2004; De Grandpre, 2009; Martin et al., 2018). For this reason, shifts from Cluster 3 or Cluster 4 to Cluster 5 are still possible if the abiotic conditions are favourable for balsam fir. TreM and deadwood dynamics in regenerating and even-aged stands were not addressed in this study. The pathways related to these two forest types presented in Fig. 5 are therefore hypothetical and complementary research would be necessary to assess our predictions. Nevertheless, previous studies highlighted that stands recently disturbed by primary disturbances in boreal forests were defined by a very large (up to > 100 m³/ha) deadwood volume, which progressively decreased with stand age until increasing again at the old-growth stage (Harper et al., 2003; Brassard and Chen, 2006). Considering the almost complete absence of surviving trees in stands recently

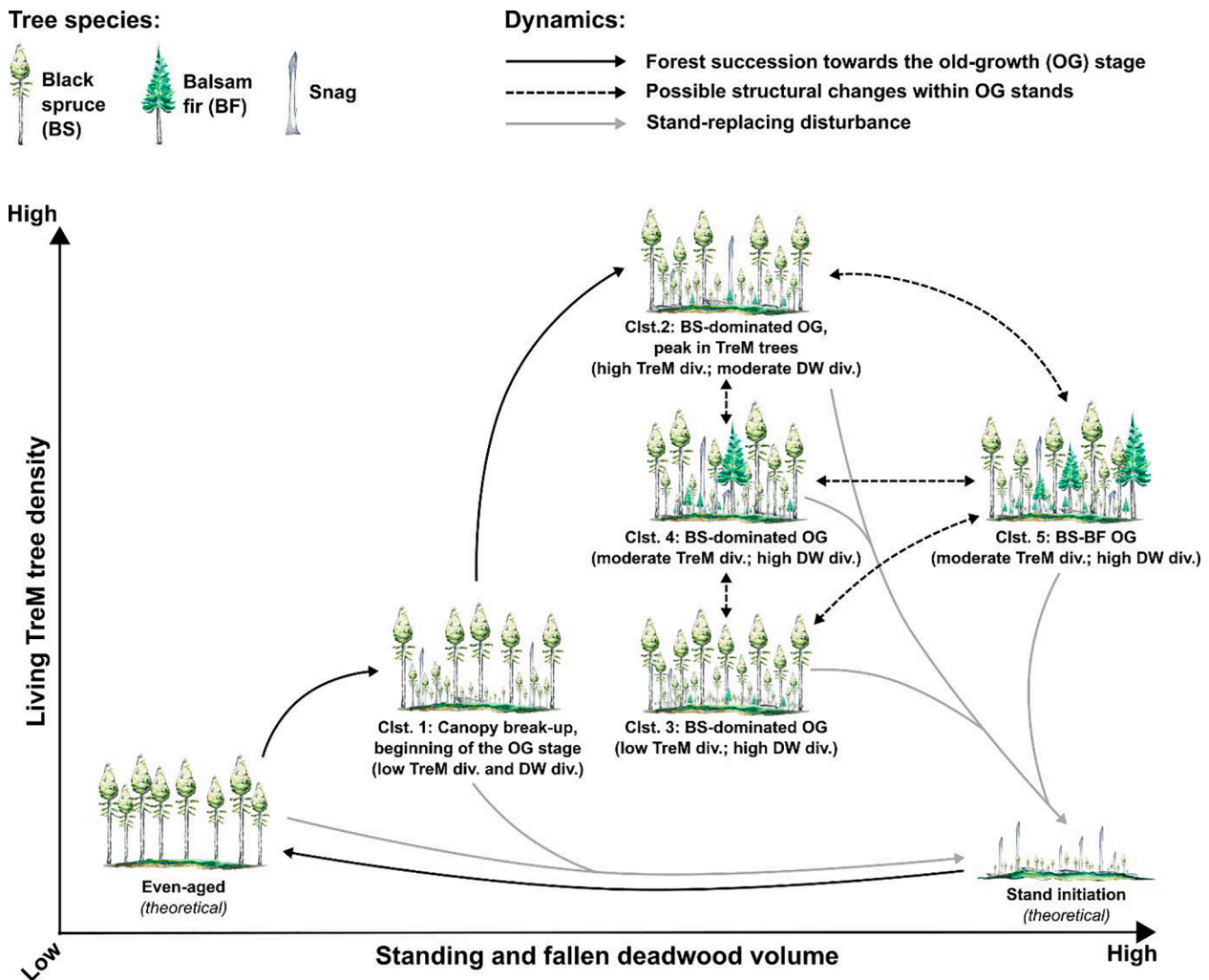


Fig. 5. Conceptual model of TreM and deadwood dynamics in black spruce dominated boreal forests. Black arrows indicate forest succession, while dotted arrows indicate possible structural changes once the true old-growth stage reached. Grey arrows indicate stand-replacing disturbance. BF: balsam fir, BS: black spruce, Clst.: cluster, Div.: diversity, DW: deadwood, OG: old-growth, TreM: tree-related microhabitats. “Theoretical” indicate succession stages that have not been studied in this article.

burned by severe crown fires, we expect TreM trees to be scarce. The presence of TreM is strongly linked to tree DBH and vigour (Paillet et al. 2019), we also hypothesize that TreM trees will be rare at the beginning of the even-aged stage. However, their density would gradually increase over time as trees from the post-fire cohort become taller and larger (Larrieu et al. 2017), to eventually reach its maximum at the transition old-growth stage, as highlighted by our results.

4.4. Implications for management

Current forest management guidelines in the boreal forests in Québec aim to maintain at least 30% of preindustrial old-growth forest areas, here defined as stands ≥ 100 years, in boreal managed landscapes (MFFP, 2016). Our study underscores that very different TreM and deadwood characteristics may define boreal old-growth forests in eastern Canada. In these landscapes, the peak in wood volume is generally reached at 150 years after the last fire (Garet et al., 2009; Portier et al., 2018), corresponding to the age of cluster 1. As underscored by Martin et al. (2020a), logging activities generally target the most economically profitable old-growth forests. There is therefore a risk that among old-growth forests, those corresponding to cluster 1, i.e., stands at the canopy break-up stage, may be the most harvested. This implies that, in the short term, forests with the highest abundance and diversity of deadwood or TreM may not be directly threatened by logging activities, but that their recruitment could become difficult in the medium term. Current aerial forest surveys, however, hardly differentiate between forests at canopy break-up stage, transition old-growth forests and true old-growth forests, especially when black spruce is the dominant species (Martin et al. 2020d). New effective remote sensing tools must therefore be developed to ensure effective and large-scale monitoring of the impact of forest management on deadwood and TreM.

The use of continuous cover forestry practices (e.g., stem-selection cut or partial cut) has been widely recommended as an alternative to clearcuts to maintain old-growth attributes and the biodiversity associated (Kuuluvainen and Gauthier, 2018; Eyvindson et al., 2021). The small size of TreM trees and the almost exclusive use of heavy machinery for logging however complexifies the identification of highly-valuable habitat trees in boreal forests. Rather than aiming at the conservation of individual habitat trees, it would be therefore preferable to maintain large retention levels within the logged forests. This approach has proven to be efficient to maintain high TreM and deadwood abundance and diversity (Fenton et al., 2013; Martin and Raymond, 2019; Santopuoli et al., 2019), as well as the biodiversity associated with old-growth forests (Fenton et al., 2013; Franklin et al., 2019).

4.5. Limitations of the study

The sampling for this study was completed in the publication year of the homogenized typology of Kraus et al. (2016), then adapted by Larrieu et al. (2018). As part of the sampled trees had already been felled in each of the sites studied, it was not possible to carry out new inventories. We have therefore subsequently adapted our typology to that of Larrieu et al. (2018) to allow a comparison at the scale of the TreM group. Only 9 TreM groups out of the 15 that make up the typology of Larrieu et al. (2018) have, however, been studied. Similarly, only TreM on live trees were included in this study, as we considered that decay classes were a most relevant surrogate of biodiversity on snags compared to TreM (Lassauce et al. 2011). However, snags generally bear more TreM than living trees (Paillet et al. 2019). This implies that only a part of the TreM have been studied in this study, although decay classes can to a certain extent provide information about the main TreM observed on snags. Considering the lack of information on TreM in boreal old-growth forests, this study is nevertheless an important first step to better understand the habitat diversity within these ecosystems. Further research on TreM in boreal forests should however use the TreM typology defined by Larrieu et al. (2018) rather than the typology used in this study.

Similarly, complementary research on TreM on snags and of their link with decay stages in boreal forests are necessary.

5. Conclusion

To our knowledge, this is the first time that TreM have been surveyed in the boreal forests of Canada, with the exception of cavities (e.g., Tremblay et al., 2015; Cadieux, 2017). Our results highlighted that TreM and deadwood dynamics follow complex pathways in boreal old-growth forests. Gradual changes in structure and composition due to forest succession and the action of secondary disturbances were the main factors explaining these dynamics. The peak in TreM density and diversity was reached at the transition old-growth stage while the highest deadwood volume and density were observed at the true old-growth stage. Overall, true old-growth forests were defined by a combination of moderate to high TreM density and deadwood volume, but these values varied among stands depending on secondary disturbances, stand structure and composition. These results therefore underscore the importance of considering old-growth forests as dynamic rather than static ecosystems, as the composition of tree- and deadwood-related microhabitats in the same stand may change significantly over time. Similarly, these results also imply that the mosaic of habitats present in old-growth forests can vary greatly from one location to another within an old-growth forest massif, highlighting the importance of maintaining a diversity of old-growth forest structure and composition in managed landscapes.

CRedit authorship contribution statement

Maxence Martin: Conceptualization, Methodology, Investigation, Data curation, Software, Formal analysis, Visualization, Writing - original draft. **Nicole J. Fenton:** Methodology, Validation, Supervision, Writing - review & editing. **Hubert Morin:** Methodology, Supervision, Writing - review & editing, Resources, Project administration, Funding acquisition.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

We thank Jean-Guy Girard, Émilie Chouinard, Miguel Montoro Girona, Anne-Élizabeth Harvey, Aurélie Couvelier, and Évelyn Belien for their help during field sampling. Yan Boucher and Pierre Grondin from the Ministry of Forests, Wildlife and Parks (MWFPP), Québec, Canada, shared their data collected from the study territory. We also thank Valentina Buttò for providing watercolours for our schematic figures, as well as three anonymous reviewers for their detailed and constructive comments. This research was funded by the Fonds de Recherche du Québec—Nature et Technologies (FRQNT), Ministère des Forêts de la Faune et des Parcs du Québec, and the Natural Sciences and Engineering Research Council of Canada (NSERC)—Université du Québec à Chicoutimi (UQAC) NSERC Industrial Research Chair “Industrial Research Chair on Black Spruce Growth and the Influence of Spruce Budworm on Landscape Variability in Boreal Forests.”

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2021.107813>.

References

- Aakala, T., Kuuluvainen, T., De, G.L., Gauthier, S., 2007. Trees dying standing in the northeastern boreal old-growth forests of Quebec: spatial patterns, rates, and temporal variation. *Can. J. For. Res.* 37 (1), 50–61. <https://doi.org/10.1139/X06-201>.
- Achard, F., Eva, H., Mollicone, D., Popatov, P., Stibig, H.-J., Turubanova, S., Yaroshenko, A., 2009. Detecting intact forests from space: hot spots of loss, deforestation and the UNFCCC. In: Wirth, C., Gleixner, G., Heimann, M. (Eds.), *Old-growth forests: Function, fate and value*. Ecological Studies 207. Springer-Verlag, Berlin, pp. 411–428.
- Aksenov, D., Karpachevskiy, M., Lloyd, S., Yaroshenko, A., 1999. The last of the last: the old-growth forests of boreal Europe. *Taiga Rescue Network*. 67p.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecol.* 26, 32–46.
- Andersson, J., Domingo Gómez, E., Michon, S., Roberge, J.M., 2018. Tree cavity densities and characteristics in managed and unmanaged Swedish boreal forest. *Scand. J. For. Res.* 33 (3), 233–244. <https://doi.org/10.1080/02827581.2017.1360389>.
- Angers, V.A., Messier, C., Beaudet, M., Leduc, A., 2005. Comparing composition and structure in old-growth and harvested (selection and diameter-limit cuts) northern hardwood stands in Quebec. *For. Ecol. Manage.* 217 (2–3), 275–293. <https://doi.org/10.1016/j.foreco.2005.06.008>.
- Angers, V.A., Drapeau, P., Bergeron, Y., 2010. Snag degradation pathways of four North American boreal tree species. *For. Ecol. Manage.* 259 (3), 246–256. <https://doi.org/10.1016/j.foreco.2009.09.026>.
- Asbeck, T., Basile, M., Stitt, J., Bauhus, J., Storch, I., Vierling, K.T., 2020. Tree-related microhabitats are similar in mountain forests of Europe and North America and their occurrence may be explained by tree functional groups. *Trees – Struct. Funct.* <https://doi.org/10.1007/s00468-020-02017-3>.
- Asbeck, T., Pyttel, P., Frey, J., Bauhus, J., 2019. Predicting abundance and diversity of tree-related microhabitats in Central European montane forests from common forest attributes. *For. Ecol. Manage.* 432 (June 2018):400–408. doi:10.1016/j.foreco.2018.09.043.
- Bailey, R.L., Dell, R., 1973. Quantifying diameter distributions with the Weibull function. *For. Sci.* 19 (2), 97–104.
- Basham, J.T., 1991. Stem decay in living trees in Ontario's forests: a user's compendium and guide. Information Report O-X-408, Great Lakes Forestry Centre, Forestry Canada. 64p.
- Bauhus, J., Puettmann, K., Messier, C., 2009. Silviculture for old-growth attributes. *For. Ecol. Manage.* 258 (4), 525–537. <https://doi.org/10.1016/j.foreco.2009.01.053>.
- Bergeron, Y., Harper, K.A., 2009. Old-growth forests in the Canadian boreal: the exception rather than the rule? In: Wirth, C., Gleixner, G., Heimann, M. (Eds.), *Old-growth forests: function, fate and value*. Ecological Studies 207. Springer, New York, pp. 285–300.
- Blanc, L.A., Martin, K., 2012. Identifying suitable woodpecker nest trees using decay selection profiles in trembling aspen (*Populus tremuloides*). *For. Ecol. Manage.* 286, 192–202. <https://doi.org/10.1016/j.foreco.2012.08.021>.
- Brassard, B.W., Chen, H.Y.H., 2006. Stand Structural Dynamics of North American Boreal Forests. *CRC Crit. Rev. Plant Sci.* 25 (2), 115–137. <https://doi.org/10.1080/07352680500348857>.
- Buchwald, E., 2005. A hierarchical terminology for more or less natural forests in relation to sustainable management and biodiversity conservation. *Third Expert Meet Harmon For Defn. (January):*111–127.
- Burns, R., Honkala, B., 1990. *Silvics of North America: 1. Conifers; 2. Hardwoods*. Agriculture Handbook 654. Washington D.C.: Forest Service, United States Department of Agriculture. 877p.
- Cadioux, P., 2017. *Diversité et fonction de la faune cavicole à la transition de la forêt boréale mixte et résineuse de l'Est du Canada*. Université du Québec à Montréal. 168.
- Cadioux, P., Drapeau, P., 2017. Are old boreal forests a safe bet for the conservation of the avifauna associated with decayed wood in eastern Canada? *For. Ecol. Manage.* 385, 127–139. <https://doi.org/10.1016/j.foreco.2016.11.024>.
- Clark, D.F., Kneeshaw, D.D., Burton, P.J., Antos, J.A., 1998. Coarse woody debris in sub-boreal spruce forests of west-central British Columbia. *Can. J. For. Res.* 28 (2), 284–290. <https://doi.org/10.1139/x97-208>.
- Couillard, P.-L., Frégeau, M., Payette, S., Grondin, P., Lavoie, M., Laflamme, J., 2016. Dynamique et variabilité naturelle de la pessière à mousses au nord de la région du Lac-Saint-Jean, Québec. *Ministère des Forêts, de la Faune et des Parcs, Secteur des forêts, Direction des inventaires forestiers, Québec*. 35p.
- Cyr, D., Gauthier, S., Bergeron, Y., Carcaillet, C., 2009. Forest management is driving the eastern North American boreal forest outside its natural range of variability. *Front. Ecol. Environ.* 7 (10), 519–524. <https://doi.org/10.1890/0800888>.
- De Grandpré, L., Waldron, K., Bouchard, M., Gauthier, S., Beaudet, M., Ruel, J.C., Hébert, C., Kneeshaw, D.D., 2018. Incorporating insect and wind disturbances in a natural disturbance-based management framework for the boreal forest. *Forests* 9 (8), 1–20. <https://doi.org/10.3390/f9080471>.
- De Grandpré, L., Gauthier, S., Allain, C., Cyr, D., Pérignon, S., Pham, A.T., Boucher, D., Morissette, J., Reyes, G., Aakala, T., et al., 2009. Towards an ecosystem approach to managing the boreal forest in the North Shore Region: disturbance regime and natural forest dynamics. In: Gauthier S., Vaillancourt M-A, Leduc A, Grandpré L De, Kneeshaw DD, Morin H, Drapeau P, Bergeron. *Ecosystem management in the boreal forest*. 1st edition. Québec: Presses de l'Université du Québec. p. 229–255.
- Dieler, J., Uhl, E., Biber, P., Müller, J., Rötzer, T., Pretsch, H., 2017. Effect of forest stand management on species composition, structural diversity, and productivity in the temperate zone of Europe. *Eur. J. For. Res.* 136 (4), 739–766. <https://doi.org/10.1007/s10342-017-1056-1>.
- Europe, Forest, 2015. *State of Europe's forests 2015*. In: *Ministerial Conference on the Protection of Forests in Europe, Madrid*, p. 312.
- Eyvindson, K., Du, R., Triviño, M., Blattert, C., Potterf, M., 2021. High boreal forest multifunctionality requires continuous cover forestry as a dominant management. *Land Use Policy* 100 (December 2019). <https://doi.org/10.1016/j.landusepol.2020.104918>.
- Fenton, N.J., Imbeau, L., Work, T., Jacobs, J., Bescond, H., Drapeau, P., Bergeron, Y., 2013. Lessons learned from 12 years of ecological research on partial cuts in black spruce forests of northwestern Québec. *For. Chron.* 89 (03), 350–359. <https://doi.org/10.5558/tfc2013-065>.
- Franklin, C.M.A., Macdonald, S.E., Nielsen, S.E., 2019. Can retention harvests help conserve wildlife? Evidence for vertebrates in the boreal forest. *Ecosphere* 10 (3), 1–21. <https://doi.org/10.1002/ecs2.2632>.
- Franklin, J., Serra-Diaz, J.M., Syphard, A.D., Regan, H.M., 2016. Global change and terrestrial plant community dynamics. *Proc. Natl. Acad. Sci. U.S.A.* 113 (14), 3725–3734. <https://doi.org/10.1073/pnas.1519911113>.
- Garet, J., Pothier, D., Bouchard, M., 2009. Predicting the long-term yield trajectory of black spruce stands using time since fire. *For. Ecol. Manage.* 257 (10), 2189–2197. <https://doi.org/10.1016/j.foreco.2009.03.001>.
- Gauthier, S., Vaillancourt, M.-A., Leduc, A., De, Grandpré L, Kneeshaw, D.D., Morin, H., Drapeau, P., Bergeron, Y., 2009. *Ecosystem management in the boreal forest*. Presses de l'Université du Québec, Québec, p. 572.
- Gauthier, S., Boucher, D., Morissette, J., De Grandpré, L., 2010. Fifty-seven years of composition change in the eastern boreal forest of Canada. *J. Veg. Sci.* 21 (4), 772–785. <https://doi.org/10.1111/j.1654-1103.2010.01186.x>.
- Gauthier, S., Bernier, P., Kuuluvainen, T., Shvidenko, A.Z., Schepaschenko, D.G., 2015. Boreal forest health and global change. *Science* (80). 349(6250):819–822. doi: 10.1126/science.aac6759.
- Gauthier, S., Raulier, F., Ouzennou, H., Saucier, J.-P., 2015b. Strategic analysis of forest vulnerability to risk related to fire: an example from the coniferous boreal forest of Quebec. *Can. J. For. Res.* 45 (5), 553–565. <https://doi.org/10.1139/cjfr-2014-0125>.
- Grondin, P., Gauthier, S., Poirier, V., Tardif, P., Boucher, Y., Bergeron, Y., 2018. Have some landscapes in the eastern Canadian boreal forest moved beyond their natural range of variability? *For. Ecosyst.* 5 (1), 30. <https://doi.org/10.1186/s40663-018-0148-9>.
- Halpin, C.R., Lorimer, C.G., 2016. Trajectories and resilience of stand structure in response to variable disturbance severities in northern hardwoods. *For. Ecol. Manage.* 365, 69–82. <https://doi.org/10.1016/j.foreco.2016.01.016>.
- Hardenbol, A.A., Pakkala, T., Kouki, J., 2019. Persistence of a keystone microhabitat in boreal forests: Cavities of Eurasian Three-toed Woodpeckers (*Picoides tridactylus*). *For. Ecol. Manage.* 450 (August), 117530 <https://doi.org/10.1016/j.foreco.2019.117530>.
- Harper, K.A., Boudreault, C., DeGrandpré, L., Drapeau, P., Gauthier, S., Bergeron, Y., 2003. Structure, composition, and diversity of old-growth black spruce boreal forest of the Clay Belt region in Quebec and Ontario. *Environ. Rev.* 11 (S1), S79–S98. <https://doi.org/10.1139/a03-013>.
- Jahed, R.R., Kavousi, M.R., Farashiani, M.E., 2020. A comparison of the formation rates and composition of tree-related microhabitats in beech-dominated primeval Carpathian and Hyrcanian forests. *Forests* 11 (144), 1–13. <https://doi.org/10.3390/f11020144>.
- Keeton, W.S., Lorimer, C.G., Palik, B.J., Doyon, F., 2019. Silviculture for eastern old growth in the context of global change. *Ecol. Recover East Old-Growth For.*:237–265. doi:10.5822/978-1-61091-891-6.13.
- Kneeshaw, D.D., Gauthier, S., 2003. Old growth in the boreal forest: a dynamic perspective at the stand and landscape level. *Environ. Rev.* 11 (S1), S99–S114. <https://doi.org/10.1139/a03-010>.
- Kozák, D., Mikoláš, M., Svitok, M., Bače, R., Paillet, Y., Larriou, L., Nagel, T.A., Begović, K., Cada, V., Diku, A., et al., 2018. Profile of tree-related microhabitats in European primary beech-dominated forests. *For. Ecol. Manage.* 429 (July), 363–374. <https://doi.org/10.1016/j.foreco.2018.07.021>.
- Kozák, D., Svitok, M., Wieszik, M., Mikola, M., Matula, R., Thorn, S., Buechling, A., Frankovic, M., Hora, J., Janda, P., et al., 2020. Historical disturbances determine current taxonomic, functional and phylogenetic diversity of saproxylic beetle communities in temperate primary forests. *Ecosystems*. <https://doi.org/10.1007/s10021-020-00502-x>.
- Kraus, D., Büttler, R., Krumm, F., Lachat, T., 2016. Catalogue of tree microhabitats - Reference field list. *Integrate+ Technical Paper*. European Forest Institute. 16p.
- Kuuluvainen, T., 2002. Natural variability of forests as a reference for restoring and managing biological diversity in boreal Fennoscandia. *Silva Fenn.* 36 (1), 97–125. <https://doi.org/10.1579/08-A-490.1>.
- Kuuluvainen, T., Gauthier, S., 2018. Young and old forest in the boreal: critical stages of ecosystem dynamics and management under global change. *For. Ecosyst.* 5 (1), 15. <https://doi.org/10.1186/s40663-018-0142-2>.
- Larriou, L., Cabanettes, A., Gouix, N., Burnel, L., Bouget, C., Deconchat, M., 2017. Development over time of the tree-related microhabitat profile: the case of lowland beech-oak coppice-with-standards set-aside stands in France. *Eur. J. For. Res.* 136 (1), 37–49. <https://doi.org/10.1007/s10342-016-1006-3>.
- Larriou, L., Paillet, Y., Winter, S., Büttler, R., Kraus, D., Krumm, F., Lachat, T., Michel, A.K., Regnery, B., Vandekerckhove, K., 2018. Tree related microhabitats in temperate and Mediterranean European forests: a hierarchical typology for inventory standardization. *Ecol. Indic.* 84, 194–207. <https://doi.org/10.1016/j.ecolind.2017.08.051>.
- Lassauce, A., Paillet, Y., Jactel, H., Bouget, C., 2011. Deadwood as a surrogate for forest biodiversity: meta-analysis of correlations between deadwood volume and species richness of saproxylic organisms. *Ecol. Indic.* 11 (5), 1027–1039. <https://doi.org/10.1016/j.ecolind.2011.02.004>.
- Lê, S., Josse, J., Husson, F., 2008. FactoMineR: an R package for multivariate analysis. *J. Stat. Softw.* 25 (1), 1–18. <https://doi.org/10.18637/jss.v025.i01>.

- Lilja, S., Kuuluvainen, T., 2005. Structure of old *Pinus sylvestris* dominated forest stands along a geographic and human impact gradient in mid-boreal Fennoscandia. *Silva Fenn.* 39 (3), 407–428. <https://doi.org/10.14214/sf.377>.
- Marshall, P.L., Davis, G., LeMay, V.M., 2000. Using Line Intercept Sampling for Coarse Woody Debris. Forest Service British Columbian, Vancouver Forest Region, Nanaimo, British Columbia, Canada. 34p.
- Martin, K., Aitken, K.E.H., Wiebe, K.L., 2004. Nest sites and nest webs for cavity-nesting communities in interior British Columbia, Canada: nest characteristics and niche partitioning. *Condor* 106 (1), 5. <https://doi.org/10.1650/7482>.
- Martin, M., Raymond, P., 2019. Assessing tree-related microhabitat retention according to a harvest gradient using tree-defect surveys as proxies in eastern canadian mixedwood forests. *For. Chron.* 95 (3), 157–170.
- Martin, M., Fenton, N.J., Morin, H., 2018. Structural diversity and dynamics of boreal old-growth forests case study in Eastern Canada. *For. Ecol. Manage.* 422 (April), 125–136. <https://doi.org/10.1016/j.foreco.2018.04.007>.
- Martin, M., Morin, H., Fenton, N.J., 2019. Secondary disturbances of low and moderate severity drive the dynamics of eastern Canadian boreal old-growth forests. *Ann. For. Sci.* 76 (108), 1–16. <https://doi.org/10.1007/s13595-019-0891-2>.
- Martin, M., Boucher, Y., Fenton, N.J., Marchand, P., Morin, H., 2020a. Forest management has reduced the structural diversity of residual boreal old-growth forest landscapes in Eastern Canada. *For. Ecol. Manage.* 458, 1–10.
- Martin, M., Montoro Girona, M., Morin, H., 2020b. Driving factors of conifer regeneration dynamics in eastern Canadian boreal old-growth forests. *PLoS One.* 1–27. doi:10.1371/journal.pone.0230221.
- Martin, M., Fenton, N.J., Morin, H., 2020b. Boreal old-growth forest structural diversity challenges aerial photographic survey accuracy. *Can. J. For. Res.* 50, 155–169. <https://doi.org/10.1139/cjfr-2019-0177>.
- Martin, M., Krause, C., Fenton, N.J., Morin, H., 2020c. Unveiling the diversity of tree growth patterns in boreal old-growth forests reveals the richness of their dynamics. *Forests* 11, 1–18. <https://doi.org/10.3390/f11030252>.
- Martin, M., Raymond, P., Boucher, Y., 2021. Influence of individual tree characteristics, spatial structure and logging history on tree-related microhabitat occurrence in North American hardwood forests. *For. Ecosyst.* 8 (27), 1–16.
- Martinez Arbizu, P., 2017. pairwiseAdonis: Pairwise Multilevel Comparison using Adonis. R package version 0.0.1.
- Maser, C., Anderson, R.G., Cromack, J.K., Williams, J.T., Martin, R.E., 1979. Dead and down woody material. In: Thomas JW, editor. *Wildlife habitats in managed forests, the Blue Mountains of Oregon and Washington*. USDA Agricultural Handbook. p. 78–95.
- McArdle, B.H., Anderson, M.J., 2001. Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology* 82 (1), 290–297.
- McGee, G.G., 2019. Biological diversity in eastern old growth. In: Barton AM, Keeton WS, Spies TA. 2019. Ecology and recovery of eastern old-growth forests.. Washington: Island Press, pp 197–216. doi:10.5822/978-1-61091-891-6_11.
- Meigs, G.W., Morrissey, R.C., Bače, R., Chaskovsky, O., Čada, V., Després, T., Donato, D. C., Janda, P., Lábusová, J., Seedre, M., et al., 2017. More ways than one: mixed-severity disturbance regimes foster structural complexity via multiple developmental pathways. *For. Ecol. Manage.* 406 (July), 410–426. <https://doi.org/10.1016/j.foreco.2017.07.051>.
- [MFFP] Ministère des Forêts de la Faune et des Parcs, 2016. Intégration des enjeux écologiques dans les plans d'aménagement forestier intégré de 2018-2023, Cahier 2.1 – Enjeux liés à la structure d'âge des forêts. Forestiers D de l'aménagement et de l'environnement, editor. Québec: Gouvernement du Québec. 67p.
- Michel, A.K., Winter, S., 2009. Tree microhabitat structures as indicators of biodiversity in Douglas-fir forests of different stand ages and management histories in the Pacific Northwest, U.S.A. *For. Ecol. Manage.* 257, 1453–1464. <https://doi.org/10.1016/j.foreco.2008.11.027>.
- Michel, A.K., Winter, S., Linde, A., 2011. The effect of tree dimension on the diversity of bark microhabitat structures and bark use in Douglas-fir (*Pseudotsuga menziesii* var. *menziesii*). *Can. J. For. Res.* 41, 300–308. <https://doi.org/10.1139/X10-207>.
- Moroni, M.T., Morris, D.M., Shaw, C., Stokland, J.N., Harmon, M.E., Fenton, N.J., Merganičová, K., Merganič, J., Okabe, K., Hagemann, U., 2015. Buried wood: a common yet poorly documented form of deadwood. *Ecosystems* 18, 605–628. <https://doi.org/10.1007/s10021-015-9850-4>.
- Moussaoui, L., Leduc, A., Fenton, N.J., Lafleur, B., Bergeron, Y., 2019. Changes in forest structure along a chronosequence in the black spruce boreal forest: Identifying structures to be reproduced through silvicultural practices. *Ecol. Indic.* 97 (October 2018):89–99. doi:10.1016/j.ecolind.2018.09.059.
- Oksanen J, Blanchet G, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PRB, O'Hara B, Simpson GL, Solymos P, et al. 2018. vegan: community ecology package. <https://cran.r-project.org/package=vegan>. R package version 2.4.6.
- Oliver, C.D., Larson, B.C., 1996. *Forest Stand Dynamics*, 4th ed. John Wiley & Sons, Inc, New York, p. 520.
- Paillet, Y., Pernot, C., Boulanger, V., Debaive, N., Fuhr, M., Gilg, O., Gosselin, F., 2015. Quantifying the recovery of old-growth attributes in forest reserves: a first reference for France. *For. Ecol. Manage.* 346, 51–64. <https://doi.org/10.1016/j.foreco.2015.02.037>.
- Paillet, Y., Archaux, F., du Puy, S., Bouget, C., Boulanger, V., Debaive, N., Gilg, O., Gosselin, F., Guilbert, E., 2018. The indicator side of tree microhabitats: a multi-taxa approach based on bats, birds and saproxylic beetles. *J. Appl. Ecol.* 55 (5), 2147–2159. <https://doi.org/10.1111/1365-2666.13181>.
- Paillet, Y., Debaive, N., Archaux, F., Cateau, E., Gilg, O., Guilbert, E., 2019. Nothing else matters? Tree diameter and living status have more effects than biogeoclimatic context on microhabitat number and occurrence: an analysis in French forest reserves. *PLoS One* 14 (5), 1–18.
- Park, A., Puettmann, K., Wilson, E., Messier, C., Kames, S., Dhar, A., 2014. Can boreal and temperate forest management be adapted to the uncertainties of 21st century climate change? *CRC Crit. Rev. Plant Sci.* 33 (4), 251–285. <https://doi.org/10.1080/07352689.2014.858956>.
- Pesklevits, A., Duinker, P.N., Bush, P.G., 2011. Old-growth forests: Anatomy of a wicked problem. *Forests* 2 (1), 343–356. <https://doi.org/10.3390/f2010343>.
- Pham, A.T., De Grandpré, L., Gauthier, S., Bergeron, Y., 2004. Gap dynamics and replacement patterns in gaps of the northeastern boreal forest of Quebec. *Can. J. For. Res.* 34 (2), 353–364. <https://doi.org/10.1139/x03-265>.
- Pioli, S., Antonucci, S., Giovannelli, A., Traversi, M.L., Borruso, L., Bani, A., Brusetti, L., Tognetti, R., 2018. Community fingerprinting reveals increasing wood-inhabiting fungal diversity in unmanaged Mediterranean forests. *For. Ecol. Manage.* 408 (October 2017):202–210. doi:10.1016/j.foreco.2017.10.052.
- Portier, J., Gauthier, S., Cyr, G., Bergeron, Y., 2018. Does time since fire drive live aboveground biomass and stand structure in low fire activity boreal forests? Impacts on their management. *J. Environ. Manage.* 225 (April), 346–355. <https://doi.org/10.1016/j.jenvman.2018.07.100>.
- Potapov, P., Hansen, M.C., Laestadius, L., Turubanova, S., Yaroshenko, A., Thies, C., Smith, W., Zhuravleva, I., Komarova, A., Minnemeyer, S., et al., 2017. The last frontiers of wilderness: tracking loss of intact forest landscapes from 2000 to 2013. *Sci. Adv.* 3 (1), 1–14. <https://doi.org/10.1126/sciadv.1600821>.
- Průvrtivý, T., Adam, D., Vrška, T., 2018. Decay dynamics of *Abies alba* and *Picea abies* deadwood in relation to environmental conditions. *For. Ecol. Manage.* 427 (March), 250–259. <https://doi.org/10.1016/j.foreco.2018.06.008>.
- Puettmann, K.J., Coates, K.D., Messier, C., 2009. *A Critique of Silviculture: Managing for Complexity*. Island Press, Washington D.C., p. 189
- R Core Team, 2019. R: A language and environment for statistical computing. <https://www.r-project.org/>.
- Remm, J., Löhmus, A., 2011. Tree cavities in forests – the broad distribution pattern of a keystone structure for biodiversity. *For. Ecol. Manage.* 262 (4), 579–585. <https://doi.org/10.1016/j.foreco.2011.04.028>.
- Robitaille, A., Saucier, J.-P., 1998. *Paysages régionaux du Québec méridional. Les Publications du Québec, Montréal*, p. 213.
- Ruel, J., 2000. Factors influencing windthrow in balsam fir forests: from landscape studies to individual tree studies. *For. Ecol. Manage.* 135, 169–178.
- Sabatini, F.M., Burrascano, S., Keeton, W.S., Levers, C., Lindner, M., Pötzschner, F., Verkerk, P.J., Bauhus, J., Buchwald, E., Chaskovsky, O., et al., 2018. Where are Europe's last primary forests? *Divers. Distrib.* 24 (10), 1426–1439. <https://doi.org/10.1111/ddi.12778>.
- Santopuoli, G., Di Cristofaro, M., Kraus, D., Schuck, A., Lasserre, B., Marchetti, M., 2019. Biodiversity conservation and wood production in a Natura 2000 mediterranean forest. A trade-off evaluation focused on the occurrence of microhabitats. *IForest*. 12 (1), 76–84. <https://doi.org/10.3832/ifer2617-011>.
- Santopuoli, G., Di Febraro, M., Maesano, M., Balsi, M., Marchetti, M., Lasserre, B., 2020. Machine learning algorithms to predict tree-related microhabitats using airborne laser scanning. *Remote Sens.* 12 (13), 1–19. <https://doi.org/10.3390/rs12132142>.
- Seidl, R., Spies, T.A., Peterson, D.L., Stephens, S.L., Hicke, J.A., 2016. Searching for resilience: addressing the impacts of changing disturbance regimes on forest ecosystem services. *J. Appl. Ecol.* 53 (1), 120–129. <https://doi.org/10.1111/1365-2664.12511>.
- Shorohova, E., Kapitsa, E., Ruokolainen, A., Romashkin, I., Kazartsev, I., 2019. Types and rates of decomposition of *Larix sibirica* trees and logs in a mixed European boreal old-growth forest. *For. Ecol. Manage.* 439 (December 2018):173–180. doi:10.1016/j.foreco.2019.03.007.
- Stokland, J.N., Siitonen, J., Jonsson, B.G., 2012. *Biodiversity in dead wood*. Cambridge University Press, editor. New York City. 509p.
- Stokland, J.N., Woodall, C.W., Fridman, J., Ståhl, G., 2016. Burial of downed deadwood is strongly affected by log attributes, forest ground vegetation, edaphic conditions, and climate zones. *Can. J. For. Res.* 46 (12), 1451–1457. <https://doi.org/10.1139/cjfr-2015-0461>.
- Storch, F., Dormann, C.F., Bauhus, J., 2018. Quantifying forest structural diversity based on large-scale inventory data: a new approach to support biodiversity monitoring. *For. Ecosyst.* 5 (1), 1–14. <https://doi.org/10.1186/s40663-018-0151-1>.
- Tremblay, J.A., Savard, J.P.L., Ibarzabal, J., 2015. Structural retention requirements for a key ecosystem engineer in conifer-dominated stands of a boreal managed landscape in eastern Canada. *For. Ecol. Manage.* 357, 220–227. <https://doi.org/10.1016/j.foreco.2015.08.024>.
- Uhlir, P.A., Harris, G., Craig, C., Bowling, B., Chambers, B., Naylor, B., Beemer, G., 2001. *Old-growth forest definitions for Ontario*. Ontario Ministry of Natural Resources, editor. Queen's Printer for Ontario. 27p.
- Vaillancourt, M.-A., Drapeau, P., Gauthier, S., Robert, M., 2008. Availability of standing trees for large cavity-nesting birds in the eastern boreal forest of Québec, Canada. *For. Ecol. Manage.* 255 (7), 2272–2285. <https://doi.org/10.1016/j.foreco.2007.12.036>.
- Vuidot, A., Paillet, Y., Archaux, F., Gosselin, F., 2011. Influence of tree characteristics and forest management on tree microhabitats. *Biol. Conserv.* 144 (1), 441–450. <https://doi.org/10.1016/j.biocon.2010.09.030>.
- Ward, J.H., 1963. Hierarchical grouping to optimize an objective function. *J. Am. Stat. Assoc.* 58 (301), 236–244.
- Warren, D.R., Keeton, W.S., Bechtold, H.A., Kraft, C.E., 2019. *Forest-stream interactions in eastern old-growth forests*. In: Barton, A.M., Keeton, W.S., Spies, T.A. (Eds.), *Ecology and Recovery of Eastern Old-Growth Forests*. Island Press, Washington, pp. 159–178.
- Watson, J.E.M., Evans, T., Venter, O., Williams, B., Tulloch, A., Stewart, C., Thompson, I., Ray, J.C., Murray, K., Salazar, A., et al., 2018. The exceptional value of intact forest

- ecosystems. *Nat. Ecol. Evol.* 2 (4), 599–610. <https://doi.org/10.1038/s41559-018-0490-x>.
- Whitney, R.D., Fleming, R.L., Zhou, K., Mossa, D.S., 2002. Relationship of root rot to black spruce windfall and mortality following strip clear-cutting. *Can. J. For. Res.* 32 (2), 283–294. <https://doi.org/10.1139/x01-194>.
- Wilson, E.A., MacLean, D.A., 2015. Windthrow and growth response following a spruce budworm inspired, variable retention harvest in New Brunswick, Canada. *Can. J. For. Res.* 45 (6), 659–666. <https://doi.org/10.1139/cjfr-2014-0444>.
- Winter, S., 2012. Forest naturalness assessment as a component of biodiversity monitoring and conservation management. *Forestry* 85 (2), 293–304. <https://doi.org/10.1093/forestry/cps004>.
- Winter, S., Möller, G.C., 2008. Microhabitats in lowland beech forests as monitoring tool for nature conservation. *For. Ecol. Manage.* 255 (3–4), 1251–1261. <https://doi.org/10.1016/j.foreco.2007.10.029>.
- Wirth, C., Messier, C., Bergeron, Y., Frank, D., 2009. Old-growth forest definitions: a pragmatic view. In: Wirth C, Gleixner G, Helmmann M, editors. *Old-growth forests: Function, fate and value*. Ecological Studies 207. Springer. p. 11–33.