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An indicator species highlights continuous deadwood supply is a key ecological attribute of boreal old-growth forests

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Citation: Martin, M., J. A. Tremblay, J. Ibarzabal, and H. Morin. 2021. An indicator species highlights continuous deadwood supply is a key ecological attribute of boreal old-growth forests. Ecosphere 12(5):e03507. 10.1002/ecs2.3507

Abstract. Old-growth forests are optimal habitats for many woodpeckers, which are often themselves excellent indicators of deadwood-associated biodiversity. Old-growth forests are, however, heterogeneous ecosystems in terms of structure, composition, and deadwood characteristics, thus implying a varied use of these forests by woodpeckers. In boreal landscapes, old-growth stands are threatened by forest harvesting; however, there is little information in regard to the consequences for biodiversity with the loss of specific types of old-growth forests. This study aimed to assess how the black-backed woodpecker (*Picoides arcticus*), a biodiversity indicator species associated with old-growth forest attributes, uses different types of old-growth forests for its foraging needs. We identified woodpecker foraging marks in 24 boreal old-growth forest stands in eastern Canada that were dominated by black spruce (*Picea mariana*), located within the home range of eight black-backed woodpeckers. We identified the various old-growth forest types using a typology based on the structural attributes of old-growth stands. We classified the sampled stands into four old-growth forest types, corresponding to different successional stages (recent or old, relative to the onset of the old-growth stage), composition (pure black spruce or mixed black spruce–balsam fir [*Abies balsamea*]), and productivity (ongoing paludification or not). The black-backed woodpecker foraged in all types of old-growth forests, but favored dense old-growth forests that were not paludified and that showed a high temporal continuity (i.e., old-growth dynamics probably started more than a century ago). The temporal continuity of the old-growth state allows for the continuous supply of large, slightly decayed snags, the preferred foraging substrates of the black-backed woodpecker. The old-growth forest type most favored by this woodpecker is, however, also the forest type most often targeted first by logging operations. Protecting the biodiversity associated with recent deadwood in managed areas thus requires maintaining a sufficient area and density of dense, old-growth black spruce-dominated forests in managed areas.

Key words: biodiversity; black-backed woodpecker; conservation; indicator species; old-growth forest; *Picoides arcticus*; saproxylic community; typology.

Received 2 December 2020; revised 15 December 2020; accepted 12 January 2021; final version received 11 March 2021. Corresponding Editor: Paige S. Warren.

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Introduction

Over the last centuries, anthropogenic activities have directly and indirectly degraded and fragmented global forest ecosystems (Curtis et al. 2018, Watson et al. 2018). These significant and increasing changes to forest structure, composition, dynamics, and connectivity now threaten biodiversity and a wide range of ecosystem services (Betts et al. 2017, Watson et al. 2018). Specifically, anthropogenic activities, such as industrial-scale forest management, have led to a marked disappearance of old-growth forests—stands at the final stage of forest succession, composed of shade-tolerant species and driven by secondary disturbances—in almost all forest biomes (Achard et al. 2009, Frank et al. 2009, Grondin et al. 2018). Old-growth forests are defined by structural attributes that are either absent or less abundant in younger and/or managed forests. These attributes include an irregular structure and a large volume of deadwood, found either as standing dead trees (i.e., snags) or as fallen logs (i.e., coarse woody debris; CWD) in various stages of decay (Schulze et al. 2009, Paillet et al. 2015). Consequently, old-growth forests offer specific habitats for a diverse range of species (Ohlson et al. 1997, Schulze et al. 2009, Fenton and Bergeron 2011, Schowalter 2017). The ecological continuity of these ecosystems is also vital for many low-dispersal or disturbance-sensitive species (Jonsson et al. 2005, Frank et al. 2009, Barbé et al. 2017). These particular attributes and characteristics of old-growth forests also provide important ecosystem services, such as carbon sequestration as well as water storage and filtration (Watson et al. 2018, Warren et al. 2019).

Maintaining large and continuous areas of old-growth forest, or at least emulating their characteristics in managed stands, has therefore become a major forest management issue (Bauhus et al. 2009, Freibauer 2009, Gauthier et al. 2009). Recent studies have, however, emphasized that rather than being homogeneous entities, old-growth forests consist of a mosaic of stands that vary in their composition and structure, a pattern dependent on both stand conditions and disturbance history (Halpin and Lorimer 2016, Meigs et al. 2017, Martin et al. 2018). Knowing many species are related to old-growth forest attributes (Rheault et al. 2009, Fenton and Bergeron 2011, Kozák et al. 2021), it is essential to distinguish the relative importance of heterogeneity within old-growth forests.

Much of the large remnant tracts of old-growth forest are currently found in the boreal biome because anthropogenic activities are relatively recent in these territories compared with other global biomes (Boucher et al. 2017, Watson et al. 2018, Svensson et al. 2019). Nonetheless, industrial-scale forest management is provoking a rapid decline and fragmentation of boreal old-growth forest (Östlund et al. 1997, Aksenov et al. 1999, Bergeron et al. 2017, Svensson et al. 2020). As a result, old-growth forests have almost completely disappeared in Fennoscandia (Östlund et al. 1997, Shorohova et al. 2012, Halme et al. 2013); in Canada and Russia, remnant old-growth forests remain, but they are rapidly declining within managed areas (Aksenov et al. 1999, Bouchard and Pothier 2011, Grondin et al. 2018). In general, managed territories have experienced a shift from a more heterogeneous forest mosaic under a fire-driven regime to a younger homogeneous forest landscape (Schmiegelow and Mönkkönen 2002, Boucher et al. 2017). For instance, Fennoscandian forests have been managed very intensively over the last century (Angelstam et al. 1997), and their loss of biodiversity lies in sharp contrast with that found in adjacent natural Russian forests. This loss of biodiversity is mainly related to the homogenized forest structure, changes in forest composition, and the reduced number of large snags and amount of large woody debris left behind in managed forests (Berg et al. 1994, Angelstam et al. 1997, Rassi et al. 2010). It is estimated that from 30% to more than 50% of the red-listed species in Scandinavia depend on old-growth elements such as deadwood (Tikkanen et al. 2006, Tingstad et al. 2018). Deadwood characteristics (e.g., volume, decay) in boreal old-growth forests can vary markedly even at a small spatial scale (Aakala et al. 2007, Aakala 2011, Martin et al. 2018). This variation in the characteristics of deadwood depends on complex and interrelated processes, including secondary disturbance history and stand abiotic characteristics, which shape the structural diversity of old-growth forests (Jonsson and Siitonen 2012, Martin et al. 2018, 2020*b*). However, Martin et al. (2020*a*) highlighted that in eastern Canada, the most economically profitable old-growth forests are generally logged first and are therefore less abundant in the remnant forests of managed territories compared with natural forests. There is therefore a risk that a loss of structural diversity in old-growth forests will compound the general loss of old-growth areal extent in managed landscapes. This loss could then aggravate the risks to those species that depend on deadwood characteristics specific to certain old-growth forest types.

Many woodpecker species have been frequently proposed as indicator species for deadwood-associated biodiversity in forested landscapes (Angelstam and Mikusiński 1994, Drapeau et al. 2009, Tremblay et al. 2015*b*) because these species require a certain amount of deadwood within their territories (Angelstam et al. 2003, Butler et al. 2004, Tremblay et al. 2009, 2015*b*). In the boreal forests of eastern Canada, black-backed woodpecker (*Picoides arcticus*) is known to numerously invade recently burned forests (Nappi and Drapeau 2011, Tremblay et al. 2015*a*, Tingley et al. 2018), but the species is also associated with old-growth stands in unburned forests (Setterington et al. 2000, Thompson et al. 2009, Tremblay et al. 2015*b*).

In unburned forests, this species forages almost exclusively in coniferous forest stands that are more than 90 yr old (Tremblay et al. 2009), and preferentially on recent snags (Tremblay et al. 2010, 2020*a*, Nappi et al. 2015). As noted for other woodpecker species (Drever et al. 2008, Roberge et al. 2008), the presence of black-backed woodpeckers within a given area likely indicates the presence of other vulnerable species related to old-growth forests, where secondary disturbances, such as windthrows, produce early-decay snags. Accordingly, in the province of Québec, the black-backed woodpecker has been selected as an indicator species to address ecosystem-based management issues related to the proportion of remnant old-growth forest stands or old-growth structural attributes (e.g., deadwood, microhabitats) in managed landscapes (Bujold 2013, Cheveau 2015). Research related to the black-backed woodpecker has mainly considered old-growth forests through the use of age thresholds to characterize forest stands (Drapeau et al. 2003, Tremblay et al. 2009, Cadieux and Drapeau 2017). This approach may not accurately describe how old-growth forest dynamics influence deadwood availability for this specific woodpecker as these ecosystems can undergo a wide variety of structural changes over time (Martin et al. 2018, 2020*b*, Moussaoui et al. 2019) and at different timings (Uhlig et al. 2001). Moreover, tree age ceases to be a reliable indicator of stand age at around 150 yr of age in the boreal forests of eastern Canada due to the relatively low (<200 yr) tree longevity (Garet et al. 2012). Once this threshold is reached, the use of chronosequences to discriminate old-growth forest types or successional stages must be therefore interpreted with caution.

To address this issue, Martin et al. (2018) proposed a typology based on variations in structural attributes, including basal area, CWD volume, the proportion of balsam fir in the basal area, and gap fraction, to discriminate old-growth forest types in eastern Canada and identify potential losses of structural diversity in managed territories. This approach makes it easier to understand how forest succession and secondary disturbances shape old-growth forest structures. The use of this typology may also improve our understanding of black-backed woodpecker ecology in large tracts of old-growth forest by acknowledging the structural diversity and dynamics of these old-growth forests. Accordingly, Tremblay et al. (2009) observed that foraging black-backed woodpeckers repeatedly visit specific forest stands while showing no interest in other apparently similar patches within their home range. This pattern of use can help identify the most vital old-growth forest types for this species and thus contribute to better target forests that need to be protected. Furthermore, foraging activities by woodpeckers, especially while excavating to attack preys (Tremblay et al. 2020*a*), produce marks on trees that remain for a long period of time. Hence, surveying foraging marks is an efficient way to assess woodpecker habitat use (Cadieux and Drapeau 2017, Dufour-Pelletier et al. 2020). To limit the risk of false positives (e.g., mark from a woodpecker species different to the target species), this approach nevertheless requires a good knowledge of the woodpecker populations in the study area. Similarly, to avoid false negatives (e.g., marks not surveyed because hidden at the top of the tree), it is better to rely on standardized approach where only the lower part of the trunk is considered.

In this study, we evaluate how different old-growth forest types may sustain habitats for the black-backed woodpeckers, an indicator species of biodiversity associated with old-growth forest attributes. Specifically, we classified sampled old-growth forest stands within the home ranges of black-backed woodpeckers using the Martin et al. (2018) old-growth forest typology, and woodpecker foraging marks served as proxies of the use of old-growth forests by this species. Old-growth forest types are classified by their specific structural attributes that may vary in their ecological value for our indicator species. Thus, we predicted that old-growth forest types with a sufficient amount of deadwood would offer greater foraging opportunities to the black-backed woodpecker, and those with a continuous supply of deadwood would be of greater value on the long term. Our research offers an original perspective by integrating both the study of the diversity of boreal old-growth forests at a fine scale and the use of these stands by an indicator species. Our results could provide effective tools for evaluating the ecological value of different old-growth forest types in boreal ecosystems and the importance of conserving this diversity.

Materials and Methods

Study territory and field sampling

The study area is located within the black spruce–moss forest bioclimatic domain in Québec, Canada (Saucier et al. 1998). The main tree species are black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and, less commonly, jack pine (*Pinus banksiana*), tamarack (*Larix laricina*), and trembling aspen (*Populus tremuloides*). The main natural disturbance in this ecological domain is fire, although spruce budworm (*Choristoneura fumiferana*) outbreaks may affect smaller areas. Within the study area, commercial timber harvesting began in the 1990s (Boucher et al. 2017), and most of the area has been logged under a mosaic harvesting pattern, where logged and equivalent residual forested blocks are interspaced across the landscape (Fig. 1).

We conducted vegetation sampling during summer 2007 within eight home ranges of black-backed woodpecker delineated in Tremblay et al. (2009). Briefly, woodpeckers have been caught and radio-tracked in 2005 and 2006 and GPS locations of birds were obtained by homing method (Mech 1983). Individual home ranges were calculated using all independent locations, and minimum convex polygons (100% MCP; Hayne 1949) were estimated. Habitat types were classified into eight classes based on data from the most recent provincial forest survey (barren lands, defoliated by spruce budworm, recently burned, old coniferous (>90 yr old), old cuts (>5 yr old), young coniferous (<90 yr old), and young cuts (<5 yr old) based on forest maps published by the province of Quebec. Vegetation sampling plots were randomly distributed within the different home ranges at a ratio of one plot for every 20 ha of home range area stratified by habitat types within individual woodpecker home ranges.

In this study, we focused only on old forest stands sampled (between one and five old forest stands sampled per home range). We established 0.04-ha circular plots (11.3 m radius), and for each standing tree having a diameter at breast height (DBH) $\geq$ 5.0 cm, we noted the following physical characteristics: (1) tree species, (2) height, (3) DBH, and (4) decay stage, the latter based on the percentage of needles and remaining bark as well as the tree-top condition (see Table 1 in Tremblay et al. 2009). To evaluate the CWD volume, we counted the number of unburied, fallen logs along three 20-m transects starting at one meter from the plot center (Böhl and Brändli 2007). We then noted the log length and DBH at the line/log intersection. We used the Böhl and Brändli (2007) equation to estimate CWD volume for each plot.

During sampling, we also noted the presence of woodpecker foraging marks, that is, physical signs made by the woodpecker when excavating tree trunk to feed, within 0–3 m height, and whether marks were recent (yellowish wood or sharp, defined holes) or relatively older (grayish wood and a smoother hole; Fig. 2). Such excavated foraging marks are characteristic of the black-backed woodpecker when individuals forage for wood-boring beetles from within dying or recently dead coniferous trees (Tremblay et al.

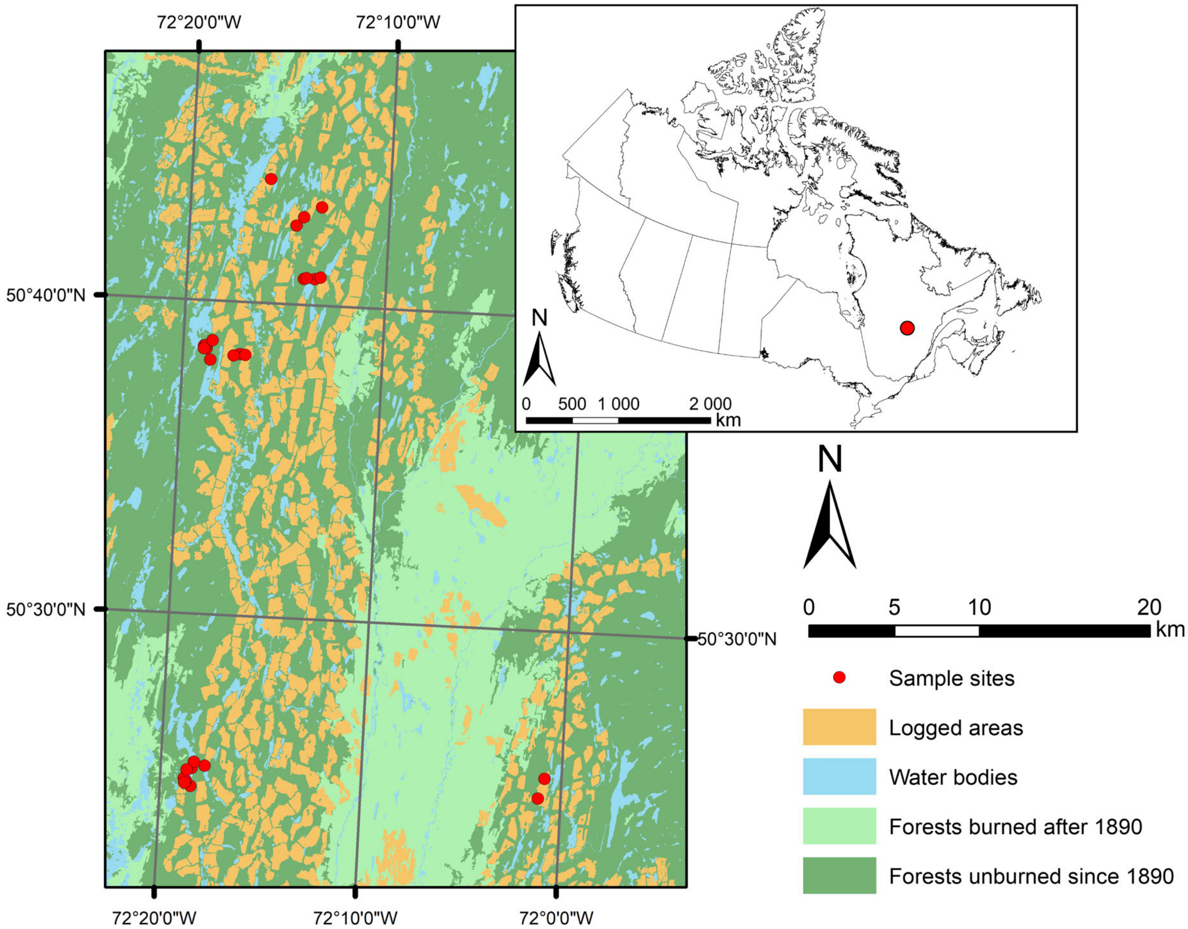

Fig. 1. Location of the 24 forest stands sampled (red circles) in the black spruce–moss forest domain in eastern Canada (see Tremblay et al. 2009 for more details). The inset map indicates the location of the study territory in Canada (red circle).

2010, 2020*a*). The American three-toed woodpecker (*Picoides dorsalis*) is the other woodpecker species that is a specialist to conifers in the study area; however, this species may also forage by excavation, but would most of the time remove bark scales to feed on bark beetles (Nappi et al. 2015, Tremblay et al. 2020*b*). The hairy woodpecker (*Leuconotopicus villosus*) can create foraging marks by excavation somewhat similar to the black-backed woodpecker. However, this species is uncommon in the study area and mainly forage on broadleaved, further by sampling marks only on the first three meters of the trunk to limit the influence of variations from one tree to another on the detection of feeding marks. Hence, we are confident that most, if not all, observed woodpecker foraging marks (excavated holes) were associated with the black-backed woodpecker, especially our vegetation sampling occurred only within individual black-backed woodpecker breeding home ranges. Our aim is therefore to propose a standardized approach for assessing the use of the studied forests by the black-backed woodpecker, which is little influenced by stand and tree characteristics. We consider this approach more suitable than trying to achieve an exhaustive census of its foraging marks, which can lead to omission errors due to foraging marks hidden at the top of the trees.

Based on field observations made during radio-tracking (Tremblay et al. 2009, 2010), we estimated that recent foraging marks are less

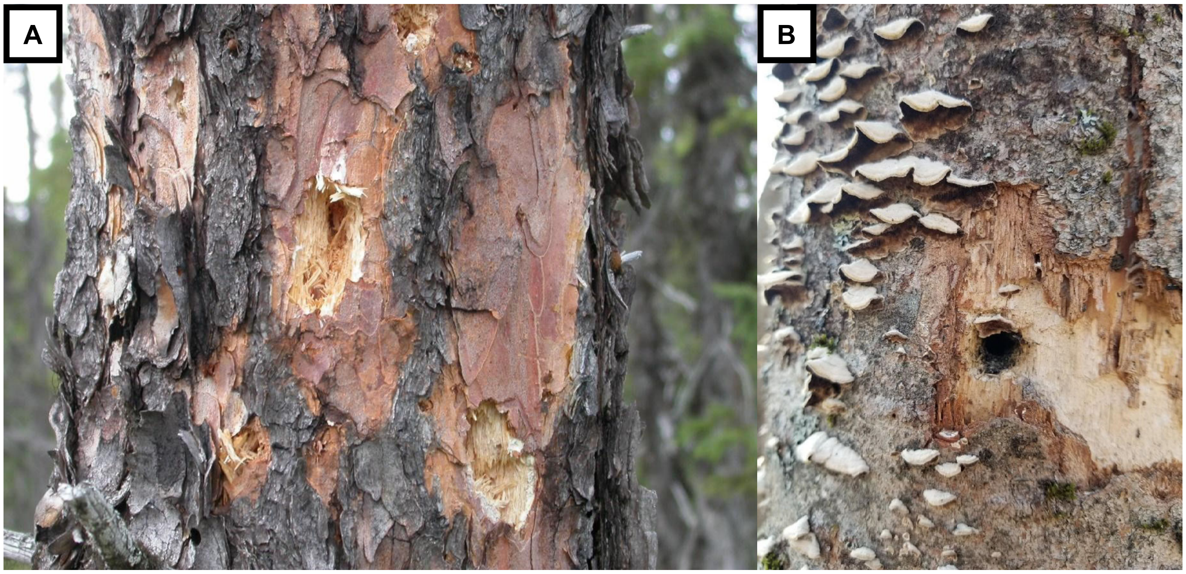

Fig. 2. Photography of a recent (A) and an old (B) foraging marks.

than 1 yr old, while old foraging marks are older than a year. Direct observations made during radio-tracking studies allow documenting the use of old-growth forests by tracked animals only over years of the field sampling, while indirect observations as feeding marks on trees offer a historical use of old-growth forests by woodpeckers. The differentiation between recent and old foraging marks also makes it possible to differentiate between short- and long-term uses, which is not possible with radio-tracking studies. However, indirect observations may not rely on the species of interest or may be unobserved due to visual obstruction or degradation of marks and trees through time.

Identification of the old-growth forest types

A preliminary study of a map of ancient fires (1890–1970) on the study territory highlighted that all the surveyed stands had not burned for at least 117 yr. This age exceeds the common age threshold of the old-growth stage used in this region (100 yr; Bergeron and Harper 2009). However, canopy breakup, that is, the beginning of gap dynamics and thus the old-growth stage, Kneeshaw and Gauthier (2003), generally occurs between 70 and 200 yr following the last stand-replacing fire in the boreal forests of eastern Canada (Uhlig et al. 2001, Bergeron and Harper 2009, Gauthier et al. 2010). Therefore, stands that are at least 117 yr old can be either (Martin et al. 2018) an even-aged forest (gap dynamics have yet to start), transition old-growth forest (gap dynamics have begun, but the even-aged cohort remains dominant), or true old-growth forest (gap dynamics have begun, and almost all of the even-aged cohort has disappeared).

Stands of the same successional stage can nonetheless be defined by very different structural attributes; these differences depend on natural disturbance dynamics, soil characteristics, and topography (Martin et al. 2018). To better understand the diversity of old-growth structures and to determine how these structures change over time, Martin et al. (2018) developed an old-growth forest typology. This typology is based on old-growth stands sampled close to the current study area (within 20–100 km) and relies on CWD volume, the proportion of balsam fir in the basal area (BFP), the basal area of living trees (BA), and the gap fraction (GF; the percentage of gaps in the canopy). As we did not measure GF in our studied stands, we based our identification of old-growth types solely on CWD, BFP, and BA. Five of the 11 old-growth types identified by Martin et al. (2018) could be identified using only CWD, BFP, and BA. For the remaining types, GF only served to discriminate pairs of old-growth types having similar CWD, BFP, and BA values. For this reason, we could use the Martin et al.'s typology despite the absence of GF values for our studied stands.

To identify the old-growth forest types, we first performed hierarchical clustering based on the CWD, BFP, and BA values for each of the studied stands—values were first standardized and normalized to homogenize their mean and variance. We used Ward's linkage clustering method (Ward 1963) and the Euclidean distances to perform clustering via the vegan package (Oksanen et al. 2018). We determined the optimal number of clusters using the average silhouette width method (Rousseeuw 1987). To facilitate subsequent analyses, we also aimed for an equivalent number of stands and a minimum of three stands per cluster. For each cluster, we calculated the mean values of CWD, BFP, and BA to determine the old-growth type, following the Martin et al.'s (2018) typology. If it was impossible to determine the old-growth type for a specific cluster, we considered this type to be a novel old-growth type, not identified by Martin et al. (2018). We then compared the structural attributes of the studied stands between the clusters using permutation-based analysis of variance (PERMANOVA; Anderson 2001). Analyses were performed with the vegan package (Oksanen et al. 2018), using the Euclidean distances and 10,000 permutations. We then performed pairwise PERMANOVA with the Bonferroni adjustments, using the pairwiseAdonis package (Martinez Arbizu 2020).

Foraging selection of woodpeckers and marks in old-growth forest types

To better understand those forest characteristics that most influence the recent and old woodpecker foraging marks in the studied old-growth forest stands, we fit linear models using the lme4 package (Bates et al. 2015) in R. The explained variable was the proportion of total snag basal area presenting recent or old foraging marks on the sampled snags. We compared models using Akaike's information criterion for small samples (AIC_c; Burnham and Anderson 2002). Due to our limited sample sizes, we reduced our candidate models to six single models and an intercept-only model for the analysis of both recent and old foraging marks. We also ensured that variables included in model selection were not correlated; for this, we used an $R < 0.7$ (Pearson's correlation) threshold running the pairs.panel function from the psych package (Revelle 2020). We based our selection of variables by choosing forest attributes that characterize old-growth forest types (Martin et al. 2018) and foraging selection by the black-backed woodpecker (Tremblay et al. 2010, 2020*a*, Nappi et al. 2015). As a complement to the linear model selection, we also performed a bootstrapped linear regression (Davidson and Hinkley 1997) to determine the confidence interval of the obtained R^2 value. Each bootstrapped linear regression was performed using the boot package and running 10,000 iterations (Canty and Ripley 2021). Bootstrapped linear regressions were not performed for the null models.

To compare the woodpecker use of each old-growth forest type, we first compared the density and the basal area of snags presenting foraging marks, depending on their age class (i.e., recent or old marks), between the clusters. As large snags (DBH ≥ 20 cm) and recent snags (decay categories 4 and 5; early decay) are used significantly more for foraging relative to the smaller and older snags (decay classes 6, 7, and 8; late decay, Tremblay et al. 2009, 2010), we also compared the density in snags presenting recent or old foraging marks between clusters. Finally, we compared the frequency of recent foraging marks among all foraging marks (i.e., recent and old) between clusters. As above, we performed PERMANOVA tests to compare the clusters, using pairwise PERMANOVA tests with the Bonferroni adjustments when the previous tests were significant. All PERMANOVA tests were based on the Euclidean distances and were run with 10,000 iterations.

All the analyses were performed using R software, version 3.6.1 (R Core Team 2019), and we applied a significance threshold of $P < 0.05$.

Results

Determination of old-growth forest types

Cluster 1 grouped forests composed almost exclusively of black spruce (mean ± standard deviation for all results presented below; 98.3% ± 2.6% of the basal area) with a low basal area (9.7 m^2/ha), snag basal area (4.0 ± 1.9 m^2/ha), and large-snag density (16.7 ± 25.8 large snags/ha) where late-decay snags are dominant (72.4% ± 30.4% of snag basal area; Table 1). Cluster 2 differed from the other clusters mainly because of its high proportion of early-decay snags (70.7% ± 19.4%), but low snag basal area, large-snag density, and CWD volume (3.4 ± 2.9 m^2/ha, 25.0 ± 22.4 large snags/ha, and 12.1 ± 6.4 m^3/ha, respectively; Table 1). Cluster 3 contained the highest proportion of balsam fir (13.2% ± 6.5% of the basal area), a high snag basal area (7.5 ± 1.7 m^2/ha), mostly at a late-decay stage (85.1% ± 8.2% of snag basal area), and a high density of large snags (60.0 ± 22.4 large snags/ha; Table 1). Finally in cluster 4, we observed the highest basal area (20.6 ± 3.3 m^2/ha), large-snag density (96 ± 68 large snags/ha), and CWD volume (46.3 ± 15.4 m^3/ha), as well as a dominance of late-decay snags (72.1% ± 15.9% of snag basal area; Table 1).

Three of the clusters corresponded clearly to the identified old-growth structures of the Martin et al.'s (2018) typology (Fig. 3): clusters 1, 2, and 4. Cluster 2 grouped black spruce-dominated stands that are considered as young old-growth stands, that is, transition old-growth–gap dynamics have begun; however, the even-aged cohort still dominates. Cluster 4, on the other hand, groups black spruce-dominated stands at the true old-growth stage—gap dynamics have begun, and almost the entire even-aged cohort has disappeared. Cluster 1 grouped low-productivity stands, which can be even-aged, transition old-growth, or true old-growth forests. Cluster 3, the cluster that stood apart from the typology of Martin et al. (2018), was similar to cluster 2, except for a higher balsam fir abundance, highest balsam fir abundance of all clusters, and higher CWD values. These characteristics suggested that cluster 3 grouped transition old-growth forests of mixed black spruce and balsam fir stands.

Forest characteristics influencing woodpecker foraging marks in old-growth stands

The proportion of early-decay snags drove the abundance of recent foraging marks of the black-backed woodpecker (w_i = 0.94, Table 2A). Forest stands characterized by a greater proportion of early-decay snags presented higher proportions of recent foraging marks. An increase of 10 early-decay snags/ha is related to an increase in the proportion of recent foraging marks of 2.0% (P = 0.002; Fig. 4A). Similarly, we observed the highest bootstrapped R^2 value for this attribute (0.35 ± 0.16) and a 95% confidence interval ranging from 0.05 to 0.65. On the other hand, the basal area of trees drove the abundance of old foraging marks of the black-backed woodpecker (w_i = 0.70) and, to a lesser extent, CWD volume (w_i = 0.11) and snag basal area (w_i = 0.08; Table 2B). However, only the basal area of trees

Table 1. Structural and deadwood attributes (mean ± standard deviation) of the clustering of old-growth forest types.

Attribute	Cluster 1 (n = 6)	Cluster 2 (n = 6)	Cluster 3 (n = 5)	Cluster 4 (n = 7)	df	F-stat	P
Tree density (n/ha)	1158.3 ± 405.5	1662.5 ± 666.5	2130.0 ± 478.4	1789.3 ± 669.4	3	2.73	0.07
Basal area (m^2/ha)	9.7 ± 4.1 c	16.4 ± 2.8 b	16.2 ± 3.6 ab	20.6 ± 3.3 a	3	10.74	<0.001
Percentage of black spruce	98.3 ± 2.6 a	98.7 ± 3.3 a	86.7 ± 6.5 b	97.7 ± 3.9 a	3	10.17	<0.001
Percentage of balsam fir	0.8 ± 2.2 b	0 ± 0 b	13.3 ± 6.5 a	2.3 ± 3.9 b	3	14.32	<0.001
Snag density (n/ha)	279.2 ± 153.6	262.5 ± 213.8	450.0 ± 81.0	353.6 ± 109.4	3	1.77	0.191
Large-snag† density (n/ha)	16.7 ± 25.8 c	25.0 ± 22.4 bc	60.0 ± 22.4 ab	96.4 ± 68.4 a	3	4.82	<0.001
Snag basal area (m^2/ha)	4.0 ± 1.9 b	3.4 ± 2.9 b	7.5 ± 1.7 a	7.4 ± 4.4 ab	3	3.02	0.038
Percentage of early-decay snags‡	27.6 ± 30.4 b	70.7 ± 19.4 a	14.8 ± 8.1 b	27.8 ± 15.9 b	3	8.31	0.001
Percentage of late-decay snags‡	72.4 ± 30.4 a	29.3 ± 19.4 b	85.2 ± 8.2 a	72.2 ± 16.0 a	3	8.31	0.001
CWD volume (m^3/ha)	21.3 ± 10.5 bc	12.1 ± 6.4 c	27.5 ± 5.3 b	46.4 ± 15.4 a	3	12.08	<0.001

Notes: CWD, coarse woody debris. n indicates the number of stands per cluster and letters indicate significant differences, with a > b > c. The terms df, F-stat, and P indicate, respectively, the degrees of freedom, the F-statistic, and the P-value obtained from each PERMANOVA test.

† Diameter at breast height >20 cm.

‡ Percentage calculated using the basal area of all snags.

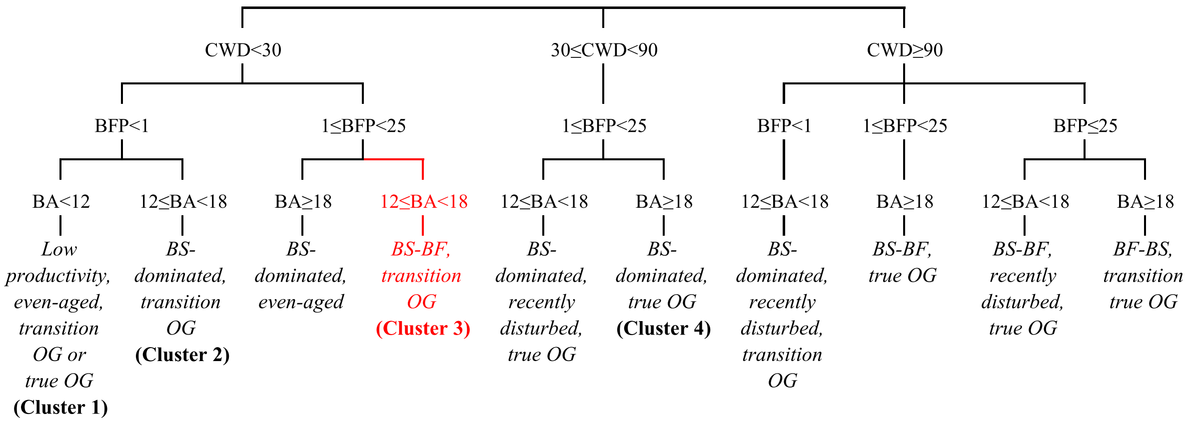

Fig. 3. Old-growth forest typology for the 24 old-growth forest stands surveyed in the black spruce–moss forest domain in eastern Canada (adapted from Martin et al. 2018). Bold text indicates the clusters identified in the study, and the red text/lines indicate novel old-growth forest types. Abbreviations are BA, basal area; BF, balsam fir; BFP, balsam fir proportion; BS, black spruce; CWD, coarse woody debris volume; Even-aged, even-aged successional stage; Transition OG, transition old-growth successional stage; True OG, true old-growth successional stage.

had a significant effect (P = 0.008), where a 1 m^2/ha increase in tree basal area increased the proportion of old foraging marks by 1.1% (Fig. 4B). The effect of CWD volume and snag basal area was, however, not significant (P = 0.11 and P = 0.08, respectively). Similarly, the confidence intervals observed for basal area, CWD volume, and snag basal area were defined by values close to zero. The influence of the structural attributes was therefore less marked for the frequency of old foraging marks than for the frequency of recent foraging marks.

Woodpecker foraging marks within the different types of old-growth forests

Overall, the basal area of snags having recent foraging marks varied slightly, and not significantly, between the clusters of old-growth forests (from 0.8 ± 0.5 to 1.9 ± 1.6 m^2/ha for clusters 3 and 4 respectively; Fig. 5A). We observed most recent foraging marks in cluster 4 on large snags (1.6 ± 1.7 m^2/ha), a significantly greater amount than cluster 3 (0 m^2/ha; Fig. 5C). Interestingly, cluster 4 also presented significantly higher snag basal areas having old foraging marks (2.1 ± 1.5 m^2/ha) than in clusters 1 and 2 (0.7 ± 0.6 m^2/ha and 0.3 ± 0.4 m^2/ha, respectively; Fig. 5B); this pattern was most related to the basal area of large snags (Fig. 5D). When we considered only the basal area of snags that presented feeding marks, cluster 2 had the highest proportion of snags with recent foraging marks (85.2% ± 16.7%), a value significantly higher than that of clusters 1 and 4 (41.9% ± 28.3% and 50.9% ± 12.4%, respectively; Fig. 5E).

Discussion

Old-growth forests are often presented as being homogeneous entities; however, our results support that boreal old-growth forest stands are not homogeneous, but rather they are defined by specific structural attributes that correspond to particular old-growth types and exhibit differential use by foraging woodpeckers. Overall, one of our identified clusters grouped low-productivity forests, two clusters reflected transition old-growth forests distinguished from each other by the relatively high presence of balsam fir in the basal area, and a fourth cluster grouped true old-growth forests, that is, stands at the end of forest succession, dominated by black spruce. All old-growth forest types presented evidence of woodpecker foraging, but the abundance of these foraging marks varied over time. Our results demonstrate that even if woodpeckers forage within all types of old-growth forest, specific old-growth forest types provide a

Table 2. Model selection of the linear mixed-effect models and bootstrapped linear regressions related to the influence of forest stand attributes on recent (A) and old (B) foraging marks of black-backed woodpeckers in 24 old black spruce forest stands.

Attribute	df	LogLik	AIC_c	ΔAIC	W_i	*P*	Bootstrapped R^2 Mean ± SD	Bootstrapped R^2 CI
(A) Recent foraging marks								
Percentage of early-decay snags	3	−82.53	172.3	0	0.94	0.002	0.35 ± 0.16	0.05–0.65
Intercept	2	−87.72	180.0	7.74	0.02	...	...	...
Snag basal area (m^2/ha)	3	−86.90	181.0	8.73	0.01	0.22	0.07 ± 0.13	0.00–0.36
Tree density (*n*/ha)	3	−87.06	181.3	9.05	0.01	0.27	0.05 ± 0.09	0.00–0.34
Basal area (m^2/ha)	3	−87.37	181.9	9.68	<0.01	0.42	0.03 ± 0.10	0.00–0.27
CWD volume (m^3/ha)	3	−87.63	182.5	10.19	<0.01	0.68	0.01 ± 0.07	0.00–0.08
Percentage of balsam fir	3	−87.69	182.6	10.31	<0.01	0.81	0.00 ± 0.09	0.00–0.02
(B) Old foraging marks								
Basal area (m^2/ha)	3	−87.50	182.2	0	0.70	0.008	0.27 ± 0.17	0.01–0.62
CWD volume (m^3/ha)	3	−89.35	185.9	3.69	0.11	0.059	0.15 ± 0.11	0.01–0.38
Snag basal area (m^2/ha)	3	−89.64	186.5	4.28	0.08	0.082	0.13 ± 0.14	0.00–0.48
Intercept	2	−91.33	187.2	5.02	0.06	...	...	...
Tree density (*n*/ha)	3	−91.24	189.7	7.48	0.02	0.69	0.01 ± 0.06	0.00–0.08
Percentage of balsam fir	3	−91.31	189.8	7.61	0.02	0.85	0.00 ± 0.05	0.00–0.02
Percentage early-decay snags	3	−91.32	189.8	7.64	0.02	0.91	0.00 ± 0.06	0.00–0.00

Notes: df, degrees of freedom; logLik, log-likelihood; AIC_c, corrected Akaike information criterion for small sample sizes; W_i, Akaike weight; R^2, coefficient of determination; SD, standard deviation; CI, 95% confidence interval; CWD, coarse woody debris. “. . .“ indicates no results for intercepts.

significantly greater temporal value to this species. The most suitable forest types for woodpecker foraging, that is, high snag density, including large snags of all decay stages, are the denser and older old-growth forests, dominated by black spruce. Large tracts of old-growth forest comprise a mosaic of various forest types, and their specific ecological value for a given species varies across these larger areas of old-growth forest. Our results thus highlight the importance of considering the internal diversity of old-growth forest types, defined by differences in structural attributes and tree species.

Diversity in old-growth forest types implies different uses by woodpeckers for foraging

The different woodpecker foraging patterns distinguished the various old-growth forest types from each other. The abundance of early-decay snags in the snag basal area greatly influenced the proportion of observed recent foraging marks, whereas the proportion of old foraging marks was mostly explained by the basal area of living trees. Hence, old-growth forest stands having an excess of decayed deadwood may not be more attractive for active foraging by black-backed woodpeckers, as these birds select mainly recent deadwood for foraging purposes (Tremblay et al. 2010, 2020*a*, Nappi et al. 2015). Forest stands that exhibit a relatively continuous supply of recent deadwood may, however, be visited regularly by foraging woodpeckers; hence, such stands likely contain both recent and old foraging marks. This pattern is congruent with a study of the foraging behavior of the Magellanic woodpecker (*Campephilus magellanicus*), which reported that individuals made foraging decisions based on visual clues from the immediate vicinity to select individual trees (Vergara et al. 2016) and forest stands characterized by more favorable foraging substrates are therefore used more intensively or more frequently by this woodpecker. An experimental study also supports this behavior; clustered girdled trees contained a greater abundance of woodpecker (*Picoides* sp.) marks than girdled trees having a uniform distribution across a stand (Dufour-Pelletier et al. 2020).

This foraging pattern of woodpeckers is supported by the Martin et al.’s (2018) old-growth typology. Stands at the true old-growth stage and dominated by black spruce (cluster 4) presented evidence—mostly through the high

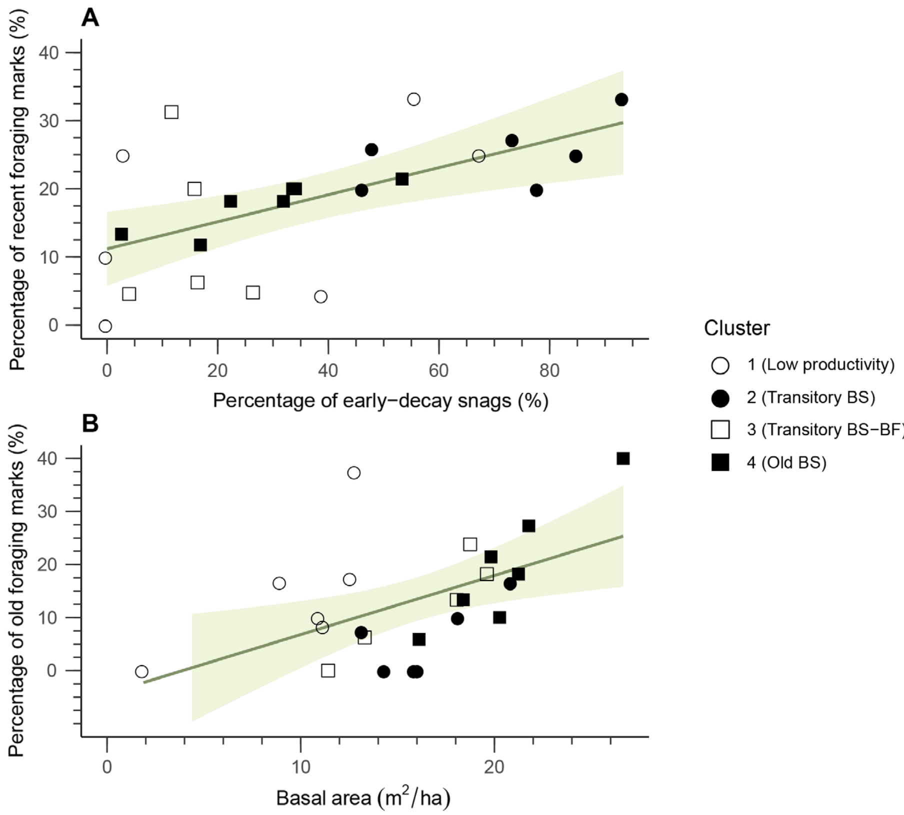

Fig. 4. Influence of (A) percentage of early-decay snags (%) in relation to the percentage of recent foraging marks and (B) basal area of trees (m^2/ha) in relation to the proportion of old foraging marks of black-backed woodpeckers in 24 old-growth forest stands in the black spruce–moss forest domain in eastern Canada (dark green line represents the linear regression, and the green-shaded zone represents the 95% confidence interval). For brevity, we present only for the top model of each type of foraging mark (i.e., recent and old; see Table 2). Abbreviations are BF, balsam fir; BS, black spruce.

proportion of either recent or old foraging marks—for a continuous use by foraging woodpeckers. In these old-growth forests, the dynamics shaping the structural characteristics and complexity of these stands began decades, if not centuries, ago (Oliver and Larson 1996, Wirth et al. 2009). Secondary disturbances therefore ensure a continuous input of recent snags (Harper et al. 2005, Aakala et al. 2007, Martin et al. 2019), which is the preferred foraging substrate of the black-backed woodpecker (Tremblay et al. 2010, 2020*a*, Nappi et al. 2015). Similarly, we observed a high density of large snags, having either recent or old foraging marks. Thus, these stands continually provide new and attractive substrates for woodpecker foraging and represent a high conservation value for deadwood-associated species with early-decay but also late-decay snags.

Our results differ for the transition old-growth stands (clusters 2 and 3). For cluster 2, that is, black spruce-dominated stands, old foraging marks were scarce; snags were mainly small and were at the earlier decay stages. This pattern suggests a recent canopy breakup, and all snags related to the last stand-replacing disturbance had fallen (Brassard and Chen 2006, Aakala et al. 2008, Angers et al. 2010). Thus, black-backed woodpeckers may have just begun to use these stands for foraging. In contrast, black spruce–balsam fir mixed stands (cluster 3) approached those of cluster 4. This similarity is likely related to the balsam fir composition in cluster 3 being similar to that in cluster 4 (true old-growth stage). Forest

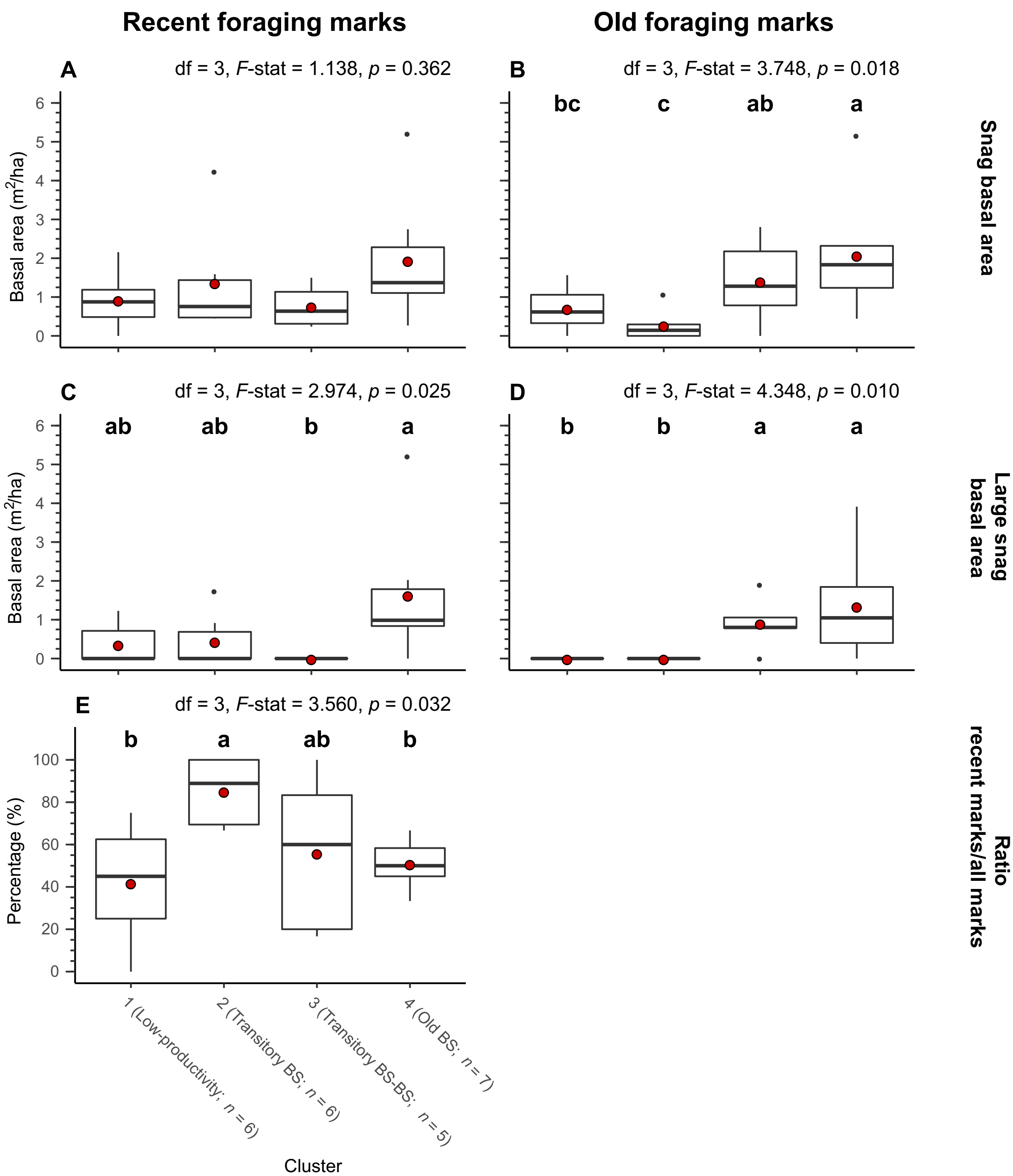

Fig. 5. Boxplots of basal area of snags with recent foraging marks (A), and old foraging marks (B), basal area of large snags (diameter at breast height > 20 cm) with recent foraging marks (C), and old foraging marks (D). The ratio of snags having recent foraging marks in relation to snags having old foraging marks (E) in 24 old-growth forest stands within the black spruce–moss forest domain in eastern Canada (red dots indicate mean values, thick horizontal lines indicate median values, box extremities indicate first and third quartiles, thin vertical lines indicate first and ninth deciles, points indicate outliers, letters indicate significant differences, with a > b > c). Abbreviations are df, degrees of freedom; *F*-stat, *F*-statistic; *P*, *P*-value; BF, balsam fir; BS, black spruce.

stands that have a mix of black spruce and balsam fir present generally more recurrent and severe disturbances than black spruce-dominated forests where balsam fir is scarce (Pham et al. 2004, Grandpré et al. 2018, Martin et al. 2018). Furthermore, canopy breakup generally begins earlier in stands favorable to balsam fir development (Uhlig et al. 2001). Snags may therefore have appeared much earlier in cluster 3 than in cluster 2. This earlier appearance would explain the advanced snag decay stage, highly variable basal area, and a higher proportion of old foraging woodpecker marks in the cluster 3 stands. Values for these properties were quite similar to those observed in cluster 4. Old-growth dynamics were not sufficiently advanced, however, to produce new large snags at an early-decay stage, as most of these snags likely originated from canopy breakup. The abundance and diversity of foraging substrates were, therefore, lower in the transition old-growth forests than in the true old-growth forests.

The high proportion of black spruce and the relatively high tree density and CWD volume of cluster 1 show that this cluster groups black spruce-dominated stands undergoing paludification rather than even-aged stands where black spruce is often mixed with jack pine (respectively, groups 11 and 1 as defined by Martin et al. 2018). As paludification is a progressive process that generally only starts after 200 yr following the last high-severity fire (Fenton et al. 2005, Lecomte et al. 2006), it is, therefore, likely that these stands were mostly true old-growth types. The low productivity of these stands, however, limits the abundance of large snags (Harper et al. 2003). In our study, paludified true old-growth stands presented the lowest abundance of large snags (16.7 ± 25.8 large snags/ha), albeit with a marked variability. Yet, the proportion of snags having recent foraging marks was similar for cluster 1 (paludified true old-growth stand) and cluster 4 (dense true old-growth stands), suggesting that paludified stands continue to be visited by foraging woodpeckers. Regardless, these paludified stands likely provide fewer foraging opportunities over the long term than dense and productive old-growth forests (cluster 4), which contain a greater basal area of snags—mostly larger snags with old foraging marks. Hence, the paludified true old-growth stand type may appear more like barren lands (mostly wetlands), which are habitats that are used proportionally to their availability by the black-backed woodpecker in the region (Tremblay et al. 2009).

Black-backed woodpecker as an indicator species for boreal old-growth forest-related biodiversity

Dense and productive true old-growth forests were the most favorable old-growth forest type for black-backed woodpeckers. The recurrent and significant inputs of new and often large snags in these stands ensure the temporal stability of foraging resources (sensu Tremblay et al. 2010). In contrast, stands entering into an old-growth stage (i.e., transition old-growth forests) and low-production stands lacked at least one of these structural attributes. These results imply that the abundance of black-backed woodpeckers in boreal forest stands that have not been recently burned may indicate the presence of true old-growth forests that have remained productive over the centuries (Pollock and Payette 2010, Ward et al. 2014). Temporal continuity of the old-growth stage is important for many disturbance-sensitive and/or low-dispersal species, such as some arthropod, bryophytes, or lichen species (Fenton and Bergeron 2011, Nordén et al. 2014, Boudreault et al. 2018). Similarly, balsam fir may require several decades or centuries to recolonize a stand after a fire as, unlike black spruce, this species is not fire-adapted (Harvey et al. 2002). Further, richness in deadwood-related species is dependent on deadwood abundance and diversity, in terms of both decay stages and tree species (McMullin et al. 2010, Stokland et al. 2012, Wagner et al. 2014). Long-term successional processes observed in true old-growth forests hence allow the development of a multicohort age structure and a continuous secondary disturbance regime, which provide diverse and abundant deadwood habitats (Brassard and Chen 2006, Aakala 2011, Ruokolainen et al. 2018). The complex structure observed in the oldest stands is also important for some arthropod or bird species (Drapeau et al. 2003, Schowalter 2017) while, at a larger scale, the continuous temporal presence of old-growth forests in contiguous landscapes is vital for endangered mammal species such as woodland caribou (*Rangifer tarandus caribou*; Schaefer 2003, Vors et al. 2007). Our study therefore reinforces the status of the black-backed woodpecker as an indicator species in eastern boreal forests, not only for confirming the presence of old-growth forests but also for evaluating the ecological value of these forests as habitat.

Discriminating old-growth forest types: a necessary step to ensure their sustainable management and biodiversity conservation

Our results highlight that the use of this old-growth typology, coupled with observations of foraging marks of an indicator species, improved the assessment of the ecological roles of the different types of old-growth forest types. Admittedly, our methodology based on the presence of foraging marks on the first meters of trunks (0–3 m) is different from an exhaustive census. Other marks can be found on branches or at the top of the tree, implying that our results do not represent the true abundance of foraging marks in the studied stands, but rather the presence or absence of foraging marks. Similarly, old-growth forests are dynamic ecosystems and marks may gradually disappear due to snag breakage and degradation. The old foraging marks identified in this study are certainly older than one year, but it was impossible to estimate their true age, which can be variable from one mark to another. Nevertheless, we consider that our standardized approach (identification of marks on the first 3 m of the trunk) limits omission errors by making the inventory less dependent on the individual tree and stand characteristics (e.g., marks hidden by a dense canopy, stand history). Similarly, and although it lacks temporal precision, we consider this approach to be a good complement to radio-tracking methods for a longer-term view of the use of forest stands by woodpeckers. We are also confident that the black-backed woodpecker was responsible for the vast majority, if not all, of the feeding marks observed in this study, given (1) the studied stands were situated within the individual home range, and (2) other woodpecker species that may have been present either forage on broadleaved trees (i.e., hairy woodpecker) or are foraging by other methods characterized by very different foraging marks (i.e., American three-toed woodpecker).

Overall, our study demonstrates that not all old-growth forest types are equivalent, and their differences in terms of structural attributes offer different foraging substrates for the black-backed woodpecker; the quality of foraging habitat is therefore highly variable. A large tract of old-growth forest is, therefore, not homogeneous but rather consists of an agglomeration of multiple forest types. Thus, our approach for determining old-growth forest types provides a clearer picture of the mosaic of forest types within large areas of old-growth forest. It also helps to evaluate the extent to which our study was representative of the diversity in old-growth forest types found in the study region.

Although our study focused on classifying old-growth forests found within black-backed woodpecker home ranges, we identified only three of the 11 old-growth types identified by Martin et al. (2018); the stands were mostly exclusive forest types, dominated by black spruce, and found at a limited number of stands. Thus, complementary studies are necessary to evaluate how biodiversity and indicator species abundance vary between old-growth types over a larger area within the black spruce−moss bioclimatic domain, as well as within other ecological domains of the boreal biome. Moreover, one of the identified clusters (cluster 3) represented a novel old-growth type that Martin et al. (2018) acknowledged as being likely missing from their typology. New research could therefore also help expand this typology, improving our knowledge of old-growth forest diversity across boreal landscapes.

Conclusion and Management Implications

This study highlights that the presence of our indicator, that is, woodpecker foraging marks, in large tracts of old-growth forest, is not homogeneous but varies depending on the particular old-growth forest type in which they are found. This variability relates mainly to differences in snag characteristics (density, size, and decay stage), which are closely related to tree senescence and mortality dynamics (Siitonen 2001, Aakala et al. 2007, Aakala 2011). Our results underscore that the diversity of old-growth forest types implies a significant variability in terms of resources and habitats (Rheault et al. 2009, Fenton and Bergeron 2011, Boudreault et al. 2013). Although our results indicate a plasticity of woodpecker stand selection for foraging, the loss or degradation of specific old-growth forest types may negatively affect their populations (sensu Tremblay et al. 2014). Therefore, maintaining the biodiversity related to old-growth forests involves maintaining the diversity in forest types beyond simply protecting the amount and configuration of forest stands (Schmiegelow and Mönkkönen 2002, Kneeshaw et al. 2018, Kuuluvainen and Gauthier 2018).

Dense and productive old-growth forests dominated by black spruce provide better substrates for woodpecker foraging than paludified stands and forests where trees from the pioneer cohort remain abundant, that is, younger old-growth forest stand types. Nonetheless, Martin et al. (2020*a*) observed that in this region significantly more logging occurs in the denser and older black spruce-dominated stands than within the younger and/or more open stands. Similarly, the high rate of logging and the short forest rotation (<100 yr) as applied to the boreal forests of Québec significantly limit the recruitment of new old-growth stands (Bergeron et al. 2002). Therefore, the old-growth forest types most favorable for our biodiversity indicator are declining in managed territories, and our results urge conservation of productive old-growth forests given that they are increasingly scarce in managed landscapes despite playing critical ecological roles in offering specific habitats to heighten biodiversity.

Acknowledgments

This work was supported by the Consortium de Recherche sur la Forêt Boréale (Université du Québec à Chicoutimi; UQAC). We thank AbitibiBowater Inc. (now Resolute Forest Products) for their logistical support, and S. Boily, C. Buidin, P. Desmeules, M. Huot, L. Morin, and Y. Rochepault for their help in the field. This study respected the protocols 0564 and 0668 of the authorized animal care regulations of UQAC. M. Martin and J. A. Tremblay contributed equally to the work related to this manuscript, and they share first authorship.

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