How important is dead wood for woodpeckers foraging in eastern North American boreal forests?

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ABSTRACT

Dead and decaying trees may be a limited resource for woodpeckers in managed forests, especially for species that rely on dead wood for nesting and foraging. Whereas recent nest web studies greatly increased our understanding of nest tree use by woodpeckers, knowledge on woodpeckers foraging requirements is much less developed. We quantified and compared tree selection patterns and foraging behavior of six bark-foraging woodpeckers – downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), American three-toed woodpecker (*Picoides dorsalis*), black-backed woodpecker (*Picoides arcticus*), yellow-bellied sapsucker (*Sphyropicus varius*) and pileated woodpecker (*Dryocopus pileatus*) – that co-occur in eastern boreal forests of North America. A total of 271 observation bouts and more than 600 foraging trees were recorded at three study sites characterized as mixedwood, conifer, and burn. Our results show that dead wood represents an important foraging substrate for most bark-foraging woodpeckers in Canadian eastern boreal forests. However, significant differences in individual species were found with regard to substrate use patterns, foraging behavior and associated prey. Woodpeckers were categorized according to their selection for specific stages of tree degradation, with the yellow-bellied sapsucker and the pileated woodpecker representing opposite ends of this gradient. The black-backed woodpecker showed the highest use of dead wood and was very specific in its tree selection by using mostly recently dead trees. We emphasize that providing foraging substrates for most woodpecker species not only requires maintaining dead wood but also paying heed to the underlying dynamics of dead wood (e.g. recruitment and degradation) in managed boreal forest landscapes.

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1. Introduction

Dead wood is a key component of biodiversity in forest ecosystems worldwide. Decaying and dead trees provide habitat resources for thousands of species such as wood-inhabiting fungi, saproxylic invertebrates and cavity-nesting vertebrates (Raphael and White, 1984; Grove, 2002; Cockle et al., 2011; Stokland et al., 2012). Saproxylic species – defined as "species that depend, during some part of their life cycle, upon wounded or decaying woody material from living, weakened or dead trees" (Stokland et al., 2012) – show strong affinities to specific tree hosts, decay stages, tree sizes and microhabitat conditions and are sensitive to the abundance of their preferred dead wood substrates in both managed and unmanaged forests (Siitonen, 2001; Stokland et al., 2012).

In the boreal forest, forestry practices still include the extensive use of low tree retention clearcuts and short harvest rotations, which result in a significant decrease in the abundance and diversity of dead wood as well as its associated biodiversity (Siitonen, 2001; Grove, 2002; Jonsson and Siitonen, 2012). In European boreal forests, intensive forest management has led to the decline or to the local extirpation of several saproxylic species (Angelstam and Mikusiński, 1994; Berg et al., 1994; Siitonen, 2012). In North American boreal forests, maintaining dead wood in managed forests is often identified as a critical issue given the extent of even-aged management and the increase of salvage logging after natural disturbances (Hannon and Drapeau, 2005). In different regions of the North American boreal forest, ecosystem-based management strategies are now aimed at providing an adequate representation of cover types and stand age structure at landscape scales (Bergeron et al., 2002; Gauthier et al., 2009), with harvesting practices such as variable retention harvest or partial cutting that maintain variable amounts of dead trees as well as significant green-tree retention in harvested blocks (Sullivan et al., 2001; Serrouya and D'Eon, 2004; Fenton et al., 2009). Although these

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new approaches likely contribute to the conservation of biodiversity, their efficiency to maintain saproxylic species still needs to be assessed (but see Cooke and Hannon, 2012). Specifically, decisions regarding management targets and prescriptions (e.g. amount of old-growth forests at landscape scales, levels and types of retention of live and dead trees in harvested blocks) will likely influence the persistence of saproxylic species populations in managed landscapes. Knowledge on these species habitat requirements as well as their dependence to dead wood may help identify the species most sensitive to the effects of forest management (focal species *sensu* Lambeck, 1997) and may be used to improve conservation planning of saproxylic species assemblage in managed landscapes.

Woodpeckers play an important ecological role in forest ecosystems by providing cavities to a broad range of vertebrate and invertebrate species ("nest-web"; Martin and Eadie, 1999; Wesolowski, 2011). These keystone species may be particularly important in conifer-dominated boreal forests where natural cavities are much less abundant (e.g. Aitken and Martin, 2007; Cockle et al., 2011). Dead wood is often identified as a critical habitat attribute for woodpeckers nesting, given that many species are known to prefer snags or living trees with decaying heartwood for their nest cavities (e.g. Raphael and White, 1984; Blanc and Martin, 2012). Yet, dead wood may also be a critical component of woodpeckers' food web. Indeed, snags are critical habitats for saproxylic insects (Saint-Germain et al. 2004, 2007), which are important prey of many woodpecker species (Murphy and Lehnhausen, 1998; Imbeau and Desrochers, 2002; Nappi et al., 2003). Given the number of trees required for foraging, woodpecker populations could be much more limited by the availability of suitable foraging substrates than by potential nest trees, and may thus in turn be more sensitive to the reduction of decaying and dead trees in managed landscapes (Imbeau et al., 2001). A decrease in the abundance of woodpeckers may thus have a cascading effect on the abundance of cavity-nesting species and on the nest-web community structure. Knowledge on woodpecker foraging requirements, in addition to nesting habitat features, may thus be crucial for setting dead wood conservation targets that could maintain the complex ecological network associated with dead wood (i.e. saproxylic food and nest webs).

Use and partitioning of foraging resources among sympatric woodpecker species has received much attention in North America and Europe (e.g. Hogstad, 1971; Bull et al., 1986; Török, 1990). Although use of decaying and dead trees has often been reported, few studies have documented the selection *per se* (disproportionate use of resources as compared to their availability; Johnson, 1980) of dead wood by foraging woodpeckers and their differential tree selection patterns. In the North American boreal forest, the few studies on foraging ecology of woodpeckers have mostly focused on single species in one habitat type and were restricted to coniferous landscapes (e.g. Imbeau and Desrochers, 2002; Tremblay et al., 2010; Nappi and Drapeau, 2011). Foraging requirements and the relative importance of dead wood as a foraging substrate have yet to be quantified for most boreal woodpeckers.

We studied the foraging ecology of the six bark-foraging woodpecker species that co-occur in the eastern North American boreal forest: downy woodpecker (*Picoides pubescens*), hairy woodpecker (*Picoides villosus*), American three-toed woodpecker (*Picoides dorsalis*), black-backed woodpecker (*Picoides arcticus*), yellow-bellied sapsucker (*Sphyropicus varius*) and pileated woodpecker (*Dryocopus pileatus*). Foraging ecology was examined by analyzing foraging tree selection, foraging behavior and woodpeckers' prey. Our study was conducted in different forest cover types – mixedwood, conifer and burned conifer stands – representative of the natural forest landscape in eastern Canada. More specifically, our study addresses the following questions: (1) what is the relative importance of dead wood as a foraging substrate for woodpeckers in the boreal forest? and (2) how do these species differ in foraging tree selection and foraging behavior?

2. Methods

2.1. Study sites

The study area is part of the northern Clay Belt of Quebec and Ontario, a large physiographic region dominated by clay deposits. Forest composition shows a latitudinal transition from mixedwood forests in the south (*Abies balsamea–Betula papyrifera* bioclimatic domain) to conifer-dominated forests in the north (*Picea mariana*-moss bioclimatic domain; Saucier et al., 1998). Fire and insect outbreaks are the main natural disturbances in these forest landscapes. We selected one study site in the southern mixedwood and two sites in the northern coniferous forest. Whereas these three sites are part of the same physiographic region, they are spatially dispersed one from another because we were interested in studying woodpeckers' foraging in unmanaged forests that represented the range of natural forest conditions (composition and structure) in this region.

The mixedwood site ("MXW") is located at the Lake Duparquet Research and Teaching Forest (LDRTF; 48°30′ N, 79°22′ W; Fig. 1). The LDRTF is a 8045-ha forest landscape composed of mainland, islands and peninsulas. The mainland fire regime is characterized by stand-replacement fires: thirteen fires within LDRTF over the last three centuries have created a complex natural forest mosaic (Harvey, 1999). Stand composition varies according to time since fire, from early seral stands dominated by deciduous (trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*)), to mixed stands (with white spruce (*Picea glauca*)), to coniferous stands (balsam fir (*Abies balsamea*), eastern white cedar (*Thuya occidentalis*)) (Bergeron, 2000). Black spruce (*Picea mariana*) and jack pine (*Pinus banksiana*) occur in localized areas as well. Three spruce budworm (*Choristoneura fumiferana*) outbreaks occurred in the last century, the most recent between 1970 and 1987, an event that was especially severe in balsam fir-dominated stands (Bergeron et al., 1995). Our study took place in the eastern part of the LDRTF mainland, a conservation area that has been lightly affected by anthropogenic disturbances.

The conifer-dominated study site ("CON") is located at the Muskuuchii Hills Projected Biodiversity Reserve (50°12′ N, 78°43′ W; Fig. 1). The biodiversity reserve covers 80,100 ha, of which half consists of peat bogs on organic deposits that support black spruce stands of varying densities. The other half is composed of terraces and hills characterized by well-drained till, sand and fine sediment deposits (Gouvernement du Québec, 2008). Our study took place in a portion of the landscape dominated by mature stands (>120 years) on mesic sites. From 1998 to 2000, experimental partial cuts were conducted in a case-control manner that resulted in a mosaic of intact and partial cut stands. Black spruce and jack pine dominate forest composition. Other species include balsam fir, trembling aspen and paper birch.

The third study site is a 8-year-old coniferous burn landscape ("BURN"), located 200 km east of the "CON" site (50°30′ N, 75°43′ W; Fig. 1). Vegetation is dominated by black spruce and jack pine with scattered white birch and trembling aspen. Burn severity was highly variable, with close to 50% of the area consisting of unburned and low-severity burned stands (details in Nappi et al., 2010).

Woodpecker foraging observations were collected in predefined large sampling blocks at the MXW and CON sites (Fig. 1). At the MXW site, sampling blocks were distributed in four 60-year classes (60–120, 120–180, 180–240 and >240 years), based on fire history mapping (Dansereau and Bergeron, 1993). We selected three sampling blocks in forests of each age class (total of 12 blocks). Each
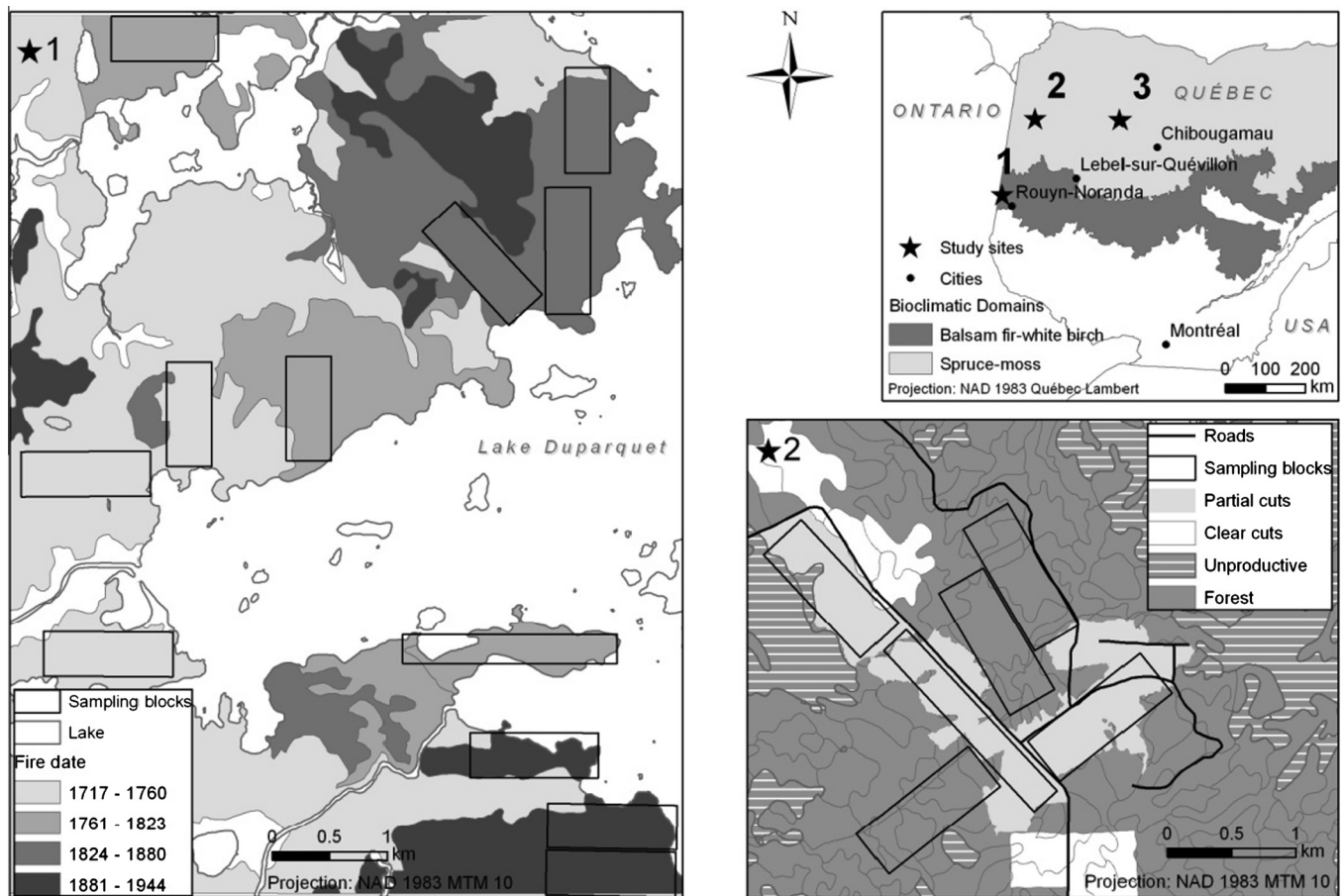
Fig. 1. Location of study sites (1 – Mixedwood site; 2 – Conifer site; 3 – Burn site) in the boreal forest of Quebec, Canada. Enlargements show location of sampling blocks at the mixedwood and conifer sites within which foraging observations were made.

sampling block consisted of one or two linear transects, generally 1 km long, with a 100-m buffer on each side within which woodpecker foraging observations were made. Blocks ranged from 24 to 40 ha in size (total of 448 ha). At the CON site, six sampling blocks ranging from 20 to 48 ha (total of 268 ha) were selected. Three of these were in unharvested mature stands whereas the other three were located in partially harvested mature stands. The blocks were designed to represent large but homogeneous areas in terms of stand age, structure and composition. At the BURN site, no sampling blocks were used and foraging activities of black-backed woodpeckers were recorded opportunistically to provide additional information on the foraging ecology of this species in burned forest habitats.

2.2. Foraging observations

Observations of foraging woodpeckers were made from mid-May to early July (breeding season of these species in our study area) in 2003 and 2004. For MXW and CON sites, observers walked systematically along the predefined linear transects. When a bird was heard or seen within 100 m of the transect line, it was followed until it flew out of sight or up to a maximum of 10 min (hereafter an "observation bout"). An observation bout had to involve at least one foraging technique (see below) and could include a single or multiple trees. Because birds were not banded, a sampling procedure was used in order to reduce the possibility of resampling the same individuals. After data was collected on a given individual, we continued walking the line transects until we found an individual of a different gender or species. Two consecutive observation bouts of the same species and gender had to

be separated by at least an hour. For each species, a similar proportion of males and females were sampled. We also distributed our sampling efforts among sampling blocks so that observations of foraging birds were made at the highest number of different locations as possible. At the BURN site, although no sampling blocks were used to record foraging observations, similar sampling procedures were taken to cover different areas of the burned landscape. Observations were distributed among point count sampling stations used for another research project (Nappi et al., 2010).

During each observation bout, we recorded foraging activities continuously using a recording system. Information was later transcribed using instantaneous sampling (i.e. fixed-interval time point; Martin and Bateson, 1993). Observation bouts were divided into 5-s periods at the end of which we noted the corresponding predefined foraging activity. We recorded the following four variables related to foraging behavior: foraging height, tree section, substrate condition and foraging technique. Foraging height was recorded in four classes: lower, middle and upper third of the tree, and coarse woody debris (downed logs and stumps <1 m height). Tree section corresponded to the specific part of the tree used: trunk, branch, junction of trunk-branch and foliage. Substrate condition referred to wood condition where the bird was foraging and was noted as live or dead. We distinguished between five foraging techniques following an adaptation of classifications used by other authors (Hogstad, 1976; Murphy and Lehnhausen, 1998; Imbeau and Desrochers, 2002): gleaning (picking insects from the surface and within bark fissures); pecking (striking the wood superficially); scaling (flaking off the bark); excavating (digging holes to access deep wood-dwelling arthropods); sap licking (digging sap holes and sucking sap from ringed trees).

Each tree with recorded foraging activities was marked and was characterized (tree species, diameter at breast height (dbh), tree position (standing or fallen) and tree degradation) at the end of the observation bout. Tree degradation was classified based on visual appearance in five categories according to a modified version of Maser et al. (1979): Deg1 ("live healthy", >20% green foliage); Deg2 ("live decaying", <20% green foliage); Deg3 ("recently dead", hard wood, firm bark cover, dead foliage or small twigs); Deg4 ("moderately degraded", soft wood, some bark missing, no dead foliage or small twigs, main branches remaining, usually intact top); Deg5 ("highly degraded", decayed wood, little bark remaining, very few branches, often broken top). Observation bouts were difficult to record for the pileated woodpecker so we searched for the typically large and deep foraging excavations of the pileated woodpecker (Lemaître and Villard, 2005) and characterized trees with recent foraging excavations (<1 year, based on fresh wood chips).

To compare characteristics of trees used for foraging with available trees, we collected vegetation data in sampling blocks (for the MXW and CON sites only). At each block, sampling plots 200 m apart were distributed along the linear transects (MXW = 112; CON = 34). Each sampling plot was 0.06 ha (60 × 10 m), a minimum size for estimating the density of the entire range of tree degradation stages (e.g. including rare degradation classes). We sampled all standing trees >5 cm of dbh and noted species, dbh and degradation stage of each tree.

2.3. Wood-dwelling arthropods

To investigate the link between tree selection, foraging behavior and prey type, we collected arthropods through wood dissection in a subset of trees that were used for foraging by the four *Picoides* species. Wood dissection is a useful technique for inspecting potential woodpecker prey as it gives an instant and exact portrait of the arthropod assemblage, including deep wood-dwelling insects, present in selected trees (Saint-Germain et al., 2007; Nappi et al., 2010). For each woodpecker species, we selected the trees most intensively used in 2004 (based on observed foraging time). A total of 47 foraging trees were cut down and dissected to collect and identify wood-dwelling arthropods (10 for downy and 10 for hairy woodpeckers at the MXW site; 10 for black-backed and 10 for American three-toed woodpeckers at the CON site; 10 for the black-backed woodpecker at the BURN site).

Tree cutting and dissection were conducted during the last two weeks of June 2004 to obtain a representative sample of the prey species present in the wood when foraging observations were made. From each tree, two 1-m bole segments were taken, the first at the base of the tree (0–1 m) and the second at 4 m (conifers) or at half of the tree height (deciduous trees). These wood samples were taken to the laboratory for wood dissection and all arthropods were identified to family, genus or species depending on available identification criteria (see methods in Saint-Germain et al., 2007). All specimens were classified by their length (> or <1 cm) and by the portion of the bole in which they were found ("bark-associates": within or under the bark; "wood-associates": within sapwood or heartwood).

2.4. Statistical analyses

Foraging tree selection analyses were based on observations made at the MXW and CON sites. For each woodpecker species, foraging tree selection was assessed by comparing trees used for foraging with available trees in neighboring 0.6 ha sampling plots. We restricted our analyses to standing trees since these comprised the vast majority of substrates used and these could be directly compared to available standing tree data. Foraging tree selection was

assessed using random-effect discrete-choice logit models (Cooper and Millspaugh, 1999; Güthlin et al., 2011; Kneib et al., 2011). This approach models the probability of a tree being used for foraging by identifying important characteristics of tree selection with regard to tree species, tree diameter and tree degradation stage. Tree availability may also be defined separately for each individual or location, so that trees identified as available were likely accessible to the animal. In our analyses, foraging trees were compared to available trees characterized at the closest sampling plot. We also used the vegetation sampling plot as our "observational unit" for the analyses: all observations close to (or within) a sampling plot for the same species were assumed to involve the same individual. This decision was applied to the yellow-bellied sapsucker and to the downy, black-backed and American three-toed woodpeckers and was based on location of nests (*P. Drapeau, unpublished data*) which suggested that observations made close to different vegetation sampling plots were from different individuals. For hairy and pileated woodpeckers, we used the sampling block (instead of the sampling plot) as the observational unit, given the much larger home-ranges of these species in our study area. In our analyses, the observational unit is considered as a random effect allowing for each unit specific deviations in selection preferences from the general model. Random effects are assumed to follow a normal distribution. Analyses were performed with the R package (Viton, 2014).

Differences in the foraging ecology of woodpeckers were investigated using discriminant analysis. Foraging behaviors recorded during observation bouts were compiled for each variable as a percentage of time per observation bout (Pechacek, 2006). For instance, if a given bird was observed excavating a total of 6 time points during a 60-s observation bout, the percentage of time spent excavating would have been 50% (6 of 12 time points). We also included tree use variables in the analysis (tree species (deciduous or coniferous) and dbh). Tree species was compiled as percentage of time per observation bout whereas dbh corresponded to the mean dbh of all trees used during each observation bout. Some variables were excluded from the analysis because of high multicollinearity (e.g. dead vs live substrates). Each observation bout was weighted so that all observation bouts of the same species and gender at a given sampling plot contributed to only one degree of freedom in the analysis. The pileated woodpecker was not included in the analysis because we had no foraging observations. Also, a preliminary analysis involving the yellow-bellied sapsucker showed a very distinct foraging behavior of this species that obscured the comparison of the other woodpecker species. Therefore, we restricted our analysis to the four *Picoides* species. Discriminant analysis was performed using SPSS 15.0. Mean proportions of foraging time for variables presented in tables and figures are based on weighted means (weighting by sampling station).

Wood-dwelling arthropods were compared among trees used by the different *Picoides* species. Individuals were pooled by tree (sum of two bole segments) and density was calculated as the number of individuals per square meter of bark sampled. Densities for each wood-dwelling arthropod group (e.g. size, wood association or family) with at least 20 individuals were compared between trees used by co-occurring species at each site (downy and hairy woodpeckers at the MXW site; black-backed and American three-toed woodpeckers at the CON site) or by the black-backed woodpecker at the CON and BURN sites using Mann–Whitney non-parametric tests.

3. Results

Foraging activities of woodpeckers were recorded during 271 observation bouts (Table 1), for a total of 9592 foraging

observations (5-s time points). For all species combined, standing trees (n = 627) represented 82% of all substrates used for foraging (Table 1, last column). Standing trees represented the majority of foraging substrates, except for the black-backed woodpecker which used logs and stumps in higher proportion.

3.1. Selection of foraging trees

Discrete-choice models revealed clear and distinct patterns of tree selection among species (Table 2). Tree degradation was an important selection criterion for most species (Table 2, Fig. 2a). The yellow-bellied sapsucker avoided snags and showed a preference for live decaying trees. Downy woodpeckers used trees in different degradation stages and only avoided highly degraded snags. The American three-toed woodpecker showed no significant preference for either tree degradation class. The black-backed woodpecker showed a high preference toward live decaying and recently dead trees. Recently dead trees alone represented 70% of all foraging trees of the black-backed woodpecker (Fig. 2a). The hairy woodpecker avoided live healthy trees and selected other degradation stages, from live decaying trees to highly degraded snags. The pileated woodpecker showed a preference for highly degraded snags; these represented 56% of all foraging trees of this species.

The yellow-bellied sapsucker, the downy woodpecker and the hairy woodpecker showed a clear preference for deciduous trees (paper birch and/or trembling aspen) (Table 2, Fig. 2b). Pileated woodpeckers used both deciduous (mostly dead trembling aspen) and conifer trees (mostly live eastern white cedar and dead balsam fir). American three-toed woodpeckers selected conifers (mainly

black spruce) whereas black-backed woodpeckers used conifers in the same proportion than their availability. Three species – the black-backed, the hairy and the pileated woodpeckers – selected larger trees (Table 2, Fig. 2c). Mean dbh of foraging trees were respectively 18.5, 26.7 and 26.9 cm for these species.

Tree selection was further investigated for the hairy woodpecker at the MXW and CON sites separately. We found similar patterns in tree selection with regard to degradation, tree species or dbh (the only difference being the lack of preference for Deg4 at the CON site).

3.2. Differences in foraging behavior

Picoides species showed a clear partitioning of their foraging behavior based on both substrate use and foraging technique (Fig. 3, Table 3). The first two discriminant functions accounted for 94% of the explained variance. The first discriminant function mainly partitioned *Picoides* based on their relative use of conifers and the scaling foraging technique. The second discriminant function was mainly associated with the relative use of dead wood and excavation technique.

The downy woodpecker showed the less variation in foraging behavior in comparison with other *Picoides* species (Fig. 3). This species foraged mainly on deciduous trees, made extensive use of branches and used pecking and gleaning as its main foraging techniques (Figs. 3 and 4, Table 3). The hairy woodpecker occupied an intermediate position on the discriminant function scatter plot but overlapped broadly with the downy woodpecker. The main differences between these two species were the higher use of dead wood and the broader range of foraging techniques used by the hairy

Table 1
Number of observation bouts and foraging trees recorded for six woodpecker species at the mixedwood (MXW), conifer (CON) and burn (BURN) sites.

Species	Observation bouts				Foraging trees				
	MXW	CON	BURN	Total	MXW	CON	BURN	Total	% of all substrates
Yellow-bellied sapsucker (YBSA)	74	5		79	202	13		215	100
Downy woodpecker (DOWO)	64			64	159			159	99
Hairy woodpecker (HAWO)	33	12		45	84	19		103	82
American three-toed woodpecker (ATWO)		34		34		49		49	68
Black-backed woodpecker (BBWO)		37	12	49		43	15	58	35
Pileated Woodpecker (PIWO)[a]					41	2		43	100
Total	171	88	12	271	486	126	15	627	82

[a] Based on recent foraging excavations (see methods).

Table 2
Woodpecker species preferences for different degradation stages, tree species and tree diameter (dbh). Reference degradation class corresponds to live healthy trees (DEG1). Tree species refers to preference (positive estimate) or avoidance (negative estimate) of deciduous trees. The number of sampling plots or blocks used as "observational units" in the discrete-choice model analyses are indicated (n). Odd ratios provide information on the relative preference for a woodpecker species to forage on a specific class of tree degradation or tree species whereas in the case of a continuous variable such as tree diameter, odd ratios indicate the relative increase in the probability of a tree to be used with one unit increment in dbh.

Variable	Yellow-bellied sapsucker (n = 35)		Downy woodpecker (n = 36)		Hairy woodpecker (n = 11)		American three-toed woodpecker (n = 12)		Black-backed woodpecker (n = 9)		Pileated woodpecker (n = 12)	
	β	Odd ratio	β	Odd ratio	β	Odd ratio	β	Odd ratio	β	Odd ratio	β	Odd ratio
Degradation												
Live decaying (DEG2)	0.916[***]	2.499	0.551	1.735	3.000[***]	20.070	0.898	2.454	3.966[***]	52.792	1.037	2.821
Recently dead (DEG3)	−1.608[**]	0.200	−0.902	0.406	2.981[***]	19.716	0.727	2.068	2.717[***]	15.140	0.317	1.373
Moderately degraded (DEG4)	−2.060[***]	0.127	−0.719	0.487	2.485[***]	12.000	−17.057	<0.001	2.254[**]	9.526	1.251	3.493
Highly degraded (DEG5)	−3.715[***]	0.024	−1.730[***]	0.177	0.834[*]	2.302	−1.302	0.272	0.877	2.403	3.302[***]	27.166
Tree species (deciduous)	1.015[***]	2.759	4.224[***]	68.285	2.164[***]	8.707	−1.974[**]	0.139	−1.725	0.178	−0.220	0.803
Tree diameter	0.067	1.069	0.063	1.065	0.085[***]	1.089	0.046	1.047	0.322[***]	1.380	0.135[***]	1.144

Significance level.
[*] P < 0.05.
[**] P < 0.01.
[***] P < 0.001.
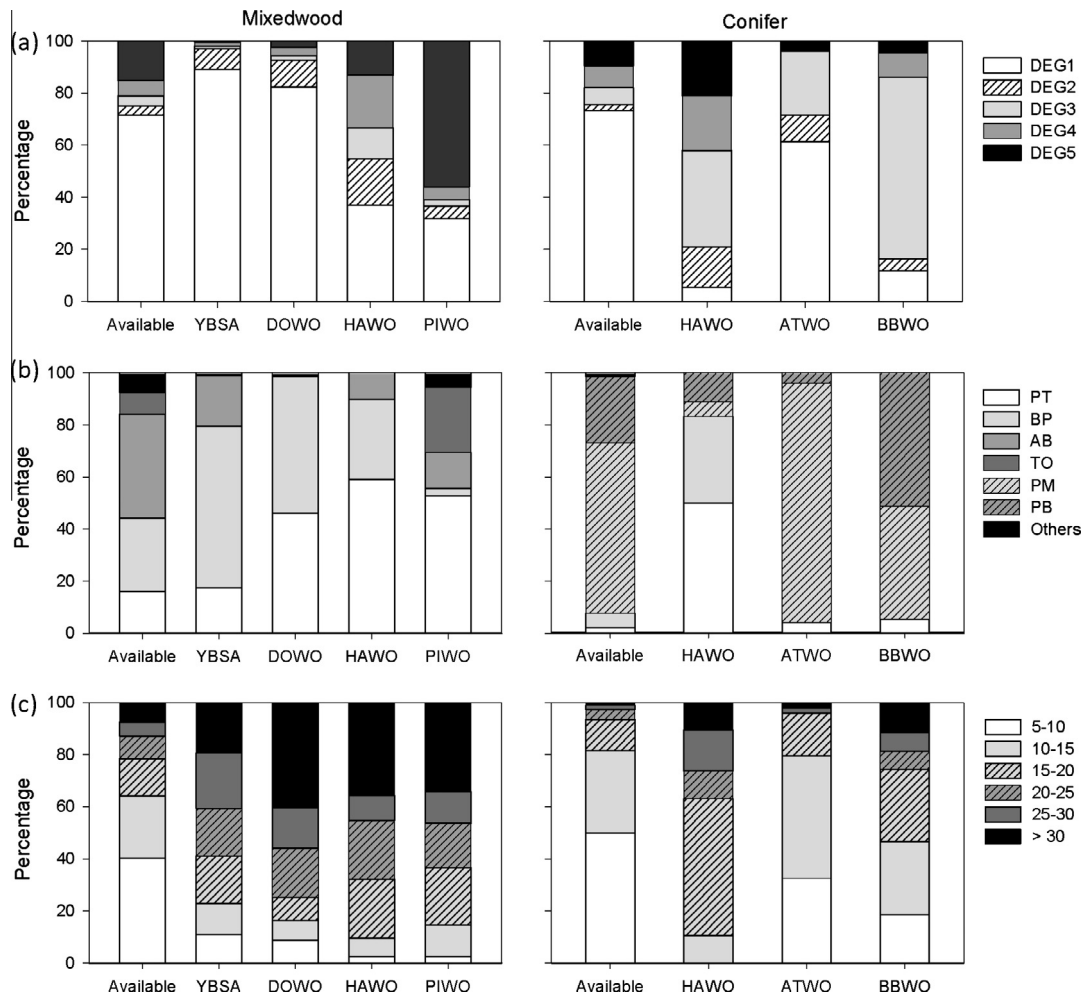
Fig. 2. Proportion of available trees and trees used by foraging woodpeckers based on (a) degradation stage, (b) tree species and (c) diameter at breast height (dbh) class (see Table 1 for woodpecker species codes). Degradation classes: Deg1 = live healthy, Deg2 = live decaying, Deg3 = recently dead, Deg4 = moderately degraded, Deg5 = highly degraded. Tree species: PT = *Populus tremuloides*, BP = *Betula papyrifera*, AB = *Abies balsamea*, TO = *Thuya occidentalis*, PM = *Picea mariana*, PB = *Pinus banksiana*. Results are presented for species with more than 15 foraging trees at the mixedwood or conifer site. "Availability" is based on the overall availability of tree substrates based on all vegetation sampling plots.
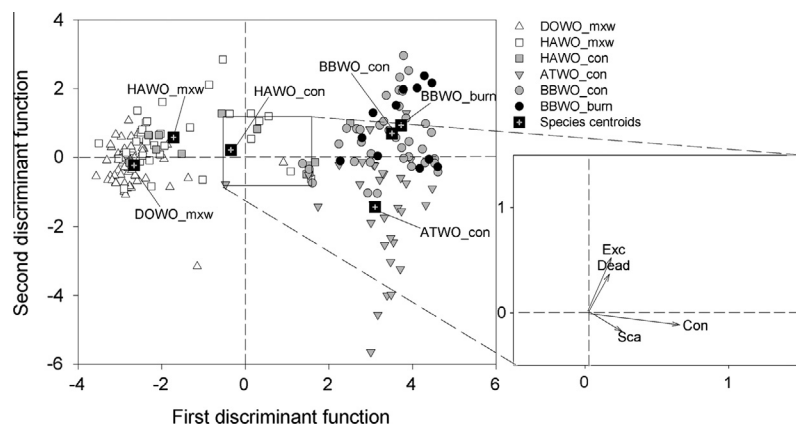
Fig. 3. Partitioning of *Picoides* woodpeckers' foraging behavior on a discriminant analysis diagram. Group centroids are the mean discriminant scores for each group of species and sites (MXW = Mixedwood site; CON = Conifer site; BURN = burn site). See Table 1 for species codes and Table 3 for foraging variables. The two variables most highly correlated with each discriminant function are shown.

woodpecker at both the mixedwood and conifer sites (Figs. 3 and 4).

The American three-toed woodpecker was mainly associated with the use of conifers and scaling (Figs. 3 and 4). It was the only

woodpecker to use all bark-foraging techniques as well as the only *Picoides* species to use sap-licking frequently. The black-backed woodpecker was the species most associated with dead wood, including coarse woody debris, and was the species that used most

Table 3
List of explanatory variables included in the discriminant analysis to compare foraging behavior of *Picoides* woodpeckers. Some variables were excluded from the analysis because of high multicollinearity (e.g. dead vs live substrates). Values indicate correlations of these variables with discriminant functions (structure matrix).

| Variable	Code	Discriminant function	
		First	Second
Tree species			
Conifer	Con	0.77	−0.12
Tree diameter	DBH	−0.23	0.32
Foraging height			
Upper third	Upp	−0.21	−0.03
Middle third	Mid	−0.02	−0.23
Coarse woody debris	CWD	0.22	0.23
Tree section			
Branches	Bra	−0.27	−0.01
Substrate condition			
Dead wood	Dead	0.20	0.45
Foraging technique			
Scaling	Sca	0.31	−0.23
Excavating	Exc	0.20	0.60
Pecking	Pec	−0.25	0.00
Gleaning	Gle	−0.18	−0.05

frequently the excavating foraging technique (Figs. 3 and 4, Table 3). A great overlap in the foraging behavior of this species was observed at the burned and unburned sites (Fig. 3).

The yellow-bellied sapsucker showed little overlap in foraging with *Picoides* species, as it was the only species to use sap-licking as its main foraging technique (not included in the discriminant analysis; Fig. 4).

Although they differed in several aspects of their foraging behavior, all four *Picoides* species used dead wood substrates for a substantial portion of their foraging time (Fig. 5). At the MXW and CON sites, mean percentage of time spent foraging on dead wood varied from 33% for the downy woodpecker to 89% for the black-backed woodpecker. Black-backed woodpeckers foraged exclusively on dead wood at the BURN site. Dead wood included snags but also dead portions of live trees such as dead branches. For instance, when foraging on branches of live trees, downy and hairy woodpeckers spent respectively 44% and 56% of their time on dead branches.

3.3. Wood-dwelling arthropods in foraging trees

The foraging trees used for wood dissection were representative of the woodpeckers' species-specific tree selection patterns described above (Table 4). Foraging trees of downy woodpeckers corresponded to live deciduous trees (trembling aspen and paper
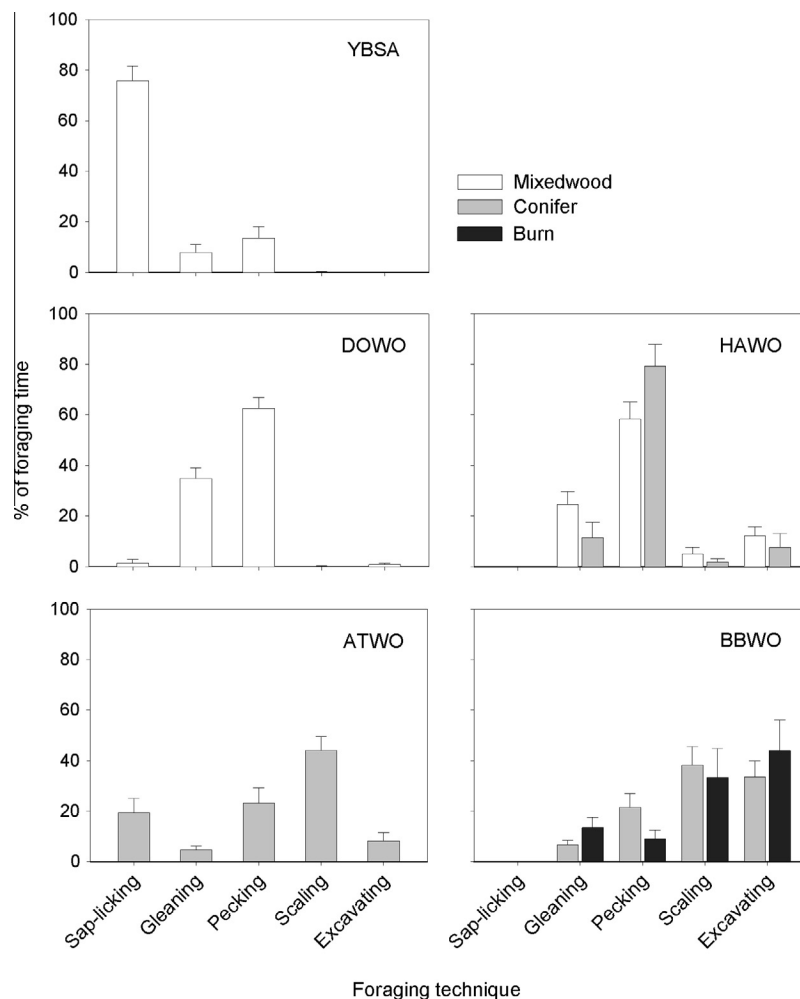
Fig. 4. Mean proportion of foraging time spent using different foraging techniques by five woodpecker species at the mixedwood, conifer and burn sites (weighed means + 1 SE). See Table 1 for species code.
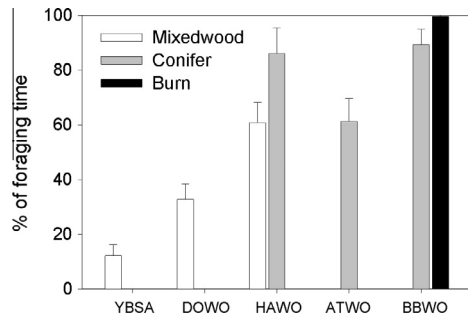
Fig. 5. Mean proportion of foraging time spent on dead wood substrates (snags, coarse woody debris or dead portions of live trees) by five woodpecker species at the mixedwood, conifer and burn sites (weighed means + 1 SE). See Table 1 for species code.

Table 4
Characteristics of trees used by foraging woodpeckers and sampled to examine wood-dwelling arthropod composition and abundance at the mixedwood (MXW), conifer (CON) and burn (BURN) sites.

Tree characteristics	DOWO (MXW)	HAWO (MXW)	ATWO (CON)	BBWO (CON)	BBWO (BURN)
Tree species[a]					
Populus tremuloides	5	5			
Betula papyrifera	5	5			
Picea mariana			10	10	6
Pinus banksiana					1
Diameter at breast height[b]	24.8 (13.3–31.8)	15.1 (12.5–31.3)	9.5 (6.2–14.3)	17.8 (13.2–22.0)	15.1 (10.7–20.7)
Degradation class[b]	1 (1–1)	3 (1–5)	3 (2–4)	3 (3–4)	4 (4–4)

[a] Number of trees for each tree species.
[b] Median (Min–Max).

birch) whereas those of hairy woodpeckers were deciduous trees of different degradation stages. Foraging trees of both American three-toed and black-backed woodpeckers consisted mainly of recently dead spruce trees, although conifer trees used by black-backed woodpeckers at the BURN site were slightly more degraded than those used at the CON site. Foraging trees of the American three-toed were smaller in diameter than those of black-backed woodpeckers.

We collected 773 arthropods from the bole segments, of which 32% and 24% were Cerambycidae and Scolytinae (sub-family of Curculionidae) respectively. At the MXW site, foraging trees of hairy woodpeckers contained significantly higher densities of large wood-dwelling arthropods (from various taxons) than trees used by downy woodpeckers (Fig. 6). At the CON site, foraging trees of black-backed woodpeckers supported higher densities of wood-associated arthropods (e.g. *Monochamus* species from the Cerambycidae family) than trees used by American three-toed woodpeckers. In contrast, Scolytinae (mostly bark-associates) were exclusively found in trees selected by American three-toed woodpeckers. Foraging trees of black-backed woodpeckers at the CON and BURN sites supported similar densities of Cerambycidae, large and wood-associated arthropods. However, foraging trees of black-backed woodpeckers at the CON site contained higher densities of small and bark-associated arthropods from Cerambycidae and other taxons.

4. Discussion

4.1. Importance of dead wood for foraging

This study is the first to quantify and compare the foraging requirements of all bark-foraging woodpeckers that co-occur in the eastern North-American boreal forest. By looking simultaneously at tree selection, foraging behavior and potential prey, this study provides a comprehensive portrait of the foraging ecology of these woodpeckers in natural-dominated boreal landscapes.
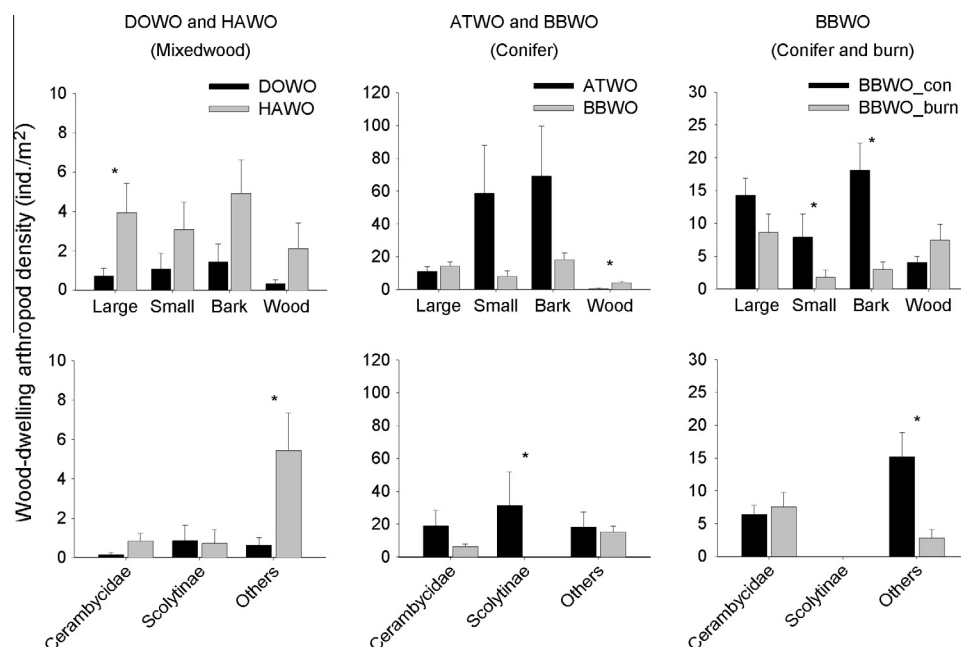
Fig. 6. Wood-dwelling arthropod densities in trees used for foraging by co-occurring species at each site (downy and hairy woodpeckers at the mixedwood site; black-backed and American three-toed woodpeckers at the conifer site) and by the black-backed woodpecker at the conifer and burn sites. Categories of wood-dwelling arthropods are: large (>1 cm in length), small (<1 cm in length), bark (found in or under bark), wood (found within sapwood or heartwood). Stars indicate significant differences between species or sites (P < 0.05).

Based on both tree selection and foraging behavior analyses, our results clearly demonstrate that dead wood (i.e. live decaying trees and snags in various stages of decay) represent an important foraging substrate for boreal woodpeckers as a group. The hairy, the black-backed and the pileated woodpeckers showed strong selection for live decaying trees and/or snags. In complement with tree selection analyses, foraging observations revealed that most woodpeckers used dead wood substrates for a substantial portion of their foraging time. Indeed, in addition to their time spent on standing snags, we observed that several species increased their foraging time on dead wood by using logs and stumps (American three-toed, black-backed and hairy woodpeckers) or by using dead portions of live deciduous trees such as dead branches or other defects (downy and hairy woodpeckers, yellow-bellied sapsucker). Among the species analyzed, the black-backed woodpecker showed the highest association with dead wood. Our results also revealed clear patterns of foraging tree preferences (degradation stage, tree species or tree diameter) among boreal woodpeckers, which were linked to species-specific differences in foraging behavior and related prey.

4.2. Associations with degradation stages

We found that woodpecker species could be categorized according to their preference for specific tree degradation stages, a pattern that was linked to their foraging behavior. The yellow-bellied sapsucker and the pileated woodpecker occupied opposite ends of the tree degradation gradient. The yellow-bellied sapsucker, well-known for its sap-licking foraging behavior and the importance of sap in its summer diet (Tate, 1973; Eberhardt, 2000), was the species most strongly associated with live trees. However, this species showed a preference for decaying over live healthy trees, a pattern that has also been reported by Eberhardt (2000).

At the opposite end of this degradation gradient was the pileated woodpecker, a species that selected mostly highly degraded snags. This woodpecker's diet is composed primarily of forest-dwelling ants, in particular carpenter ants (Camponotus species), but may also include bark and wood-boring beetles and other arthropods (Bull et al., 1992). Given our observations for the pileated woodpecker were based on this species' typical large foraging excavations, our results are restricted to its use of carpenter ants. Large snags, logs and stumps with a certain amount of decay are known as important nesting sites for carpenter ants (Torgersen and Bull, 1995) and selection of snags by pileated woodpeckers has been documented in different studies (Bull and Holthausen, 1993; Lemaître and Villard, 2005; Newell et al., 2009). However, to our knowledge, our study is the first to show a preference for more degraded snags, suggesting a higher abundance of carpenter ants in such substrates. These snags were mainly trembling aspens but also included balsam fir snags created after the most recent spruce budworm outbreak.

Although all Picoides species made extensive use of dead wood, our results highlight significant differences in each species patterns of substrate use, foraging behavior and associated wood-dwelling arthropods. The downy woodpecker selected deciduous trees and avoided highly degraded snags. This species was often seen pecking on dead branches of live trees or snags to feed on sub-cortical prey. In his detailed account of the feeding behavior of downy woodpeckers on paper birch, Kilham (1970) noted trees with broken branches and other defects to be the most attractive to downy woodpeckers. The relatively high use of dead wood by the downy woodpecker in our study (more than 30% of its foraging time) is consistent with this pattern. It suggests that partial mortality in live deciduous trees, in addition to snags in early stages of degradation, may play an important role in providing foraging substrates for this species.

In contrast to the downy woodpecker, the hairy woodpecker showed a clear preference for live decaying trees to highly degraded deciduous snags and was seen foraging more often on dead wood (more than 60% of its foraging time). The majority of hairy woodpecker foraging trees were dead (50% and 80% at mixedwood and conifer sites respectively), a pattern similar to what has been reported for this species elsewhere (Raphael and White, 1984; Weikel and Hayes, 1999). The hairy woodpecker was also the species that made the highest use of moderately degraded trees. In our study area, Saint-Germain et al. (2007) showed wood-feeding insects to be more abundant in middle to late than in earlier stages of decay in aspens. In our study, the more degraded deciduous trees used by hairy woodpeckers supported large wood-dwelling arthropods from many different guilds including wood-feeders, fungivores and sub-cortical insect predators. This prey diversity may explain the wider foraging strategy used by this species for capturing wood-dwelling arthropods, in comparison with the downy woodpecker.

Black-backed and American three-toed woodpeckers were only observed in northern coniferous forests where they specialized on conifers for foraging. The black-backed woodpecker foraged almost exclusively on dead wood (89% of foraging time at the conifer site). It showed a strong selection for live decaying and recently dead conifers and used scaling and excavation frequently to feed on wood-boring beetles. This selection pattern may be explained by the higher abundance of wood-feeding Coleoptera associated with conifers in the early stages of decay (Saint-Germain et al., 2007). Preferred foraging trees of the black-backed woodpecker differed from those of the American three-toed woodpecker by the higher abundance of wood-boring arthropods. We also noted a similar foraging behavior of black-backed woodpeckers at unburned and burned conifer sites, suggesting a consistent foraging niche across different habitat types in the boreal forest.

The American three-toed woodpecker made extensive use of both live and dead conifers in different stages of degradation. The use of decaying and recently dead trees and the associated use of scaling and pecking as predominant foraging techniques may be explained by its feeding specialization on bark beetles (Murphy and Lehnhausen, 1998; Imbeau and Desrochers, 2002). Indeed, we found that foraging trees of American three-toed woodpeckers contained more Scolytinae beetles (mostly bark-associates) than black-backed woodpecker foraging trees. Our results also emphasize the use of live healthy spruces for sap-licking, a foraging behavior that has been generally reported to be marginal for the American and European (Picoides tridactylus) three-toed woodpeckers. For instance, sap-licking represented less than 3% of foraging time in studies conducted in North America (Villard, 1994; Imbeau and Desrochers, 2002) and Europe (Pechacek, 2006). In contrast, we found that about 20% of foraging time was devoted to sap-licking (i.e. sap licking and related drilling behaviors), suggesting that this foraging behavior may be much more important during the breeding season than previously reported.

Picoides woodpeckers generally experience significant increases following recent natural disturbances and associated insect outbreaks in conifer forests (Murphy and Lehnhausen, 1998; Fayt et al., 2005; Covert-Bratland et al., 2006; Nappi and Drapeau, 2009; Rota et al., 2014b). Foraging specializations found in our study emphasize that the abundance of these woodpeckers (in particular the black-backed woodpecker) is tightly linked to the abundance of saproxylic insects and thus to the presence of dying and recently dead conifers in both disturbed (Murphy and Lehnhausen, 1998; Nappi and Drapeau, 2009; Rota et al., 2014b) and undisturbed coniferous forests (Imbeau and Desrochers, 2002; Tremblay et al., 2009, 2010; this study). Moreover, differences in the foraging ecology of these species may explain the response patterns observed following different disturbance agents.

Foraging specialization on wood-boring beetles by the black-backed woodpecker is consistent with its propensity to occupy burned coniferous forests, where these insects are generally abundant (Saint-Germain et al., 2004; Hannon and Drapeau, 2005). Conversely, the more pronounced response of the American three-toed woodpecker in forests disturbed by bark beetle outbreaks is consistent with its foraging specialization (Fayt et al., 2005). Natural disturbances that create large amount of snags and logs have also been shown to provide suitable habitats for the pileated woodpecker for several decades after disturbance (Bull et al., 2007). Indeed, in our study area, the most recent spruce budworm outbreak that occurred 20–30 years ago provided a significant amount of well-decayed snags that were highly used by foraging pileated woodpeckers.

4.3. Tree diameter

Although all woodpecker species showed a tendency to use larger diameter trees, this pattern was significant only for the black-backed, the hairy and the pileated woodpeckers. These three species often excavate to extract large wood-boring beetles or, in the case of the pileated woodpecker, carpenter ants. Larger trees typically contain higher densities of wood-boring insect larvae. This pattern may be attributed to the requirements of late-instar larvae that excavate deep galleries into sapwood and heartwood, to the thicker bark that increases protection against desiccation, and to the thicker phloem which is of higher nutritional quality for first-instar larvae (Gardiner, 1957; Rose, 1957; Saint-Germain et al., 2004). Selection of larger trees and logs by pileated woodpeckers has been well documented throughout its range and has been linked to the nesting preference of carpenter ants, its main prey (Torgersen and Bull, 1995; Lemaître and Villard, 2005; Newell et al., 2009).

4.4. Conservation and management implications

We found that most bark-foraging woodpeckers in eastern North American boreal forests show strong associations with live decaying and/or snags for foraging. Among the six species examined, the black-backed woodpecker showed the strongest association with dead wood and was very specific in its tree selection with regard to degradation stage. This finding suggests a high dependence of this species on recently dead wood and likewise a high vulnerability to the reduction of this tree degradation stage in managed boreal forests. For woodpeckers as a guild, their high use of dead wood for foraging suggests that they may be much more limited by the availability of foraging trees than nest trees. Limitation of foraging substrates for woodpeckers may have a cascading effect on the structure of the nest web in these forests, especially in conifer stands, because of their key ecological roles in providing nest cavities to secondary-cavity users. This study thus reiterates the importance of planning the conservation of dead wood for a wide range of tree age, species and decay classes to ensure a steady supply of suitable foraging trees (Drapeau et al., 2009b) in addition to cavity-bearing tree requirements (Edworthy and Martin, 2013) in managed boreal forest landscapes.

Providing trees of high forage value for woodpeckers in managed boreal forests may require different strategies for species associated with deciduous trees (e.g. downy or hairy woodpecker) compared to those associated with conifers (e.g. American three-toed or black-backed woodpeckers). For deciduous trees, suitable dead wood substrates may be provided by both the partial mortality present in live decaying trees (e.g. dead branches) and snags of different degradation stages. In contrast, the temporal window of foraging opportunities appears to be much shorter in conifers, which generally support high densities of saproxylic insects mainly in their declining and recently dead stages (Saint-Germain et al.,

2007). Hence, in conifer landscapes, maintaining foraging habitat in managed forests implies ensuring a continuous recruitment of recent conifer snags.

In the boreal ecosystem, old-growth and post-disturbance forests are the two most important sources of dead wood in natural forest landscapes. Late seral stands are shaped by small-scale mortality processes that may provide a constant recruitment of recent snags for woodpeckers (Imbeau and Desrochers, 2002; Tremblay et al., 2009). Yet, at the landscape scale, natural stand-replacement disturbances such as fire and insect outbreaks may represent important sources of dead wood that provide high quality habitats for woodpeckers (Saab et al., 2005). For the black-backed woodpecker for instance, high concentrations of recently dead trees such as the ones created following stand-replacement wildfires clearly represent optimal habitats for the species (Nappi and Drapeau, 2009; Rota et al., 2014a). Although these foraging habitats are ephemeral (because all snags are created more or less simultaneously), the recurrence of these events at regional scales provide a continuous source of foraging habitats for woodpeckers. In North American boreal forests where old-growth forests are decreasing because of short harvest rotations and post-disturbance forests are increasingly salvage-logged, both habitats are thus of conservation concern for the persistence of woodpecker populations (Nappi et al., 2004; Schmiegelow et al., 2006; Drapeau et al., 2009a).

Harvesting practices such as variable retention or partial cutting may provide woodpecker foraging habitat depending on the abundance and quality of dead wood that is left as well as the level of green-tree retention that is maintained for future dead wood recruitment. At our conifer site, partial cutting provided short-term suitable foraging substrates for black-backed and American three-toed woodpeckers, as was evidenced by the numerous foraging observations within partial cut stands. These partial cuts, while maintaining live trees, also resulted in mortality of standing trees and in high amounts of downed logs. Given our study took place 3–6 years after partial cutting, downed logs and snags were still in early stages of degradation and supported high abundance of wood-dwelling insects. By creating a combination of sun-exposed habitat and a high abundance of recently dead trees and downed logs, partial cutting may also resembled post-disturbance forests. Indeed, many of the saproxylic insects found during wood dissection (e.g. *Monochamus* spp., *Acmaeops proteus*) are well-known for their high abundance following fire (Saint-Germain et al., 2004; Boulanger and Sirois, 2007).

Woodpeckers are often identified as species of interest in forest management because of their role as "keystone" species in nest-webs (Martin and Eadie, 1999) and because they are generally good indicators of forest bird diversity (Mikusiński et al., 2001; Roberge and Angelstam, 2006; Drever et al., 2008). Our study emphasizes the strong association of woodpeckers with dead wood for foraging, which makes them good indicators of the abundance of this habitat resource in managed forests. Because use of foraging trees is mainly linked to prey abundance, woodpeckers may also represent good indicators of the presence of saproxylic insect species in managed boreal forests (see also Martikainen et al., 1998). Moreover, because of their association with specific degradation stages and snag recruitment, woodpeckers as a group could be used as indicators of snag dynamics and therefore be considered as "process-limited" species (*sensu* Lambeck, 1997). Maintaining the woodpecker guild in managed forests would thus benefit the conservation of a diversity of saproxylic plant and animal species associated with distinct stages of wood degradation.

Acknowledgments

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