

# Postfire Succession of Ants (Hymenoptera: Formicidae) Nesting in Dead Wood of Northern Boreal Forest

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**ABSTRACT** Dead wood decomposition begins immediately after tree death and involves a large array of invertebrates. Ecological successions are still poorly known for saproxylic organisms, particularly in boreal forests. We investigated the use of dead wood as nesting sites for ants along a 60-yr postfire chronosequence in northeastern coniferous forests. We sampled a total of 1,625 pieces of dead wood, in which 263 ant nests were found. Overall, ant abundance increased during the first 30 yr after wildfire, and then declined. *Leptothorax* cf. *canadensis* Provancher, the most abundant species in our study, was absent during the first 2 yr postfire, but increased steadily until 30 yr after fire, whereas *Myrmica alaskensis* Wheeler, second in abundance, was found at all stages of succession in the chronosequence. Six other species were less frequently found, among which *Camponotus herculeanus* (Linné), *Formica neorufibarbis* Emery, and *Formica aserva* Forel were locally abundant, but more scarcely distributed. Dead wood lying on the ground and showing numerous woodborer holes had a higher probability of being colonized by ants. The C:N ratio was lower for dead wood colonized by ants than for noncolonized dead wood, showing that the continuous occupation of dead wood by ants influences the carbon and nitrogen dynamics of dead wood after wildfire in northern boreal forests.

**KEY WORDS** ant, wildfire, succession, boreal forest, dead wood

Dead wood is an important component of forest ecosystems and can be produced through the gradual senescence of individual trees (Rouvinen and Kuuluvainen 2001) or from the mass killing of trees by large-scale disturbances such as wildfire (Payette et al. 1989). Dead wood is used by a large array of invertebrates (Grove 2002, Hammond et al. 2004, Azeria et al. 2012). Several xylophagous insects feed directly on dead or moribund trees and are thus primary colonizers (Coulson and Witter 1984). These insects play a major role in initiating cycling of nutrients stored in dead wood in forest ecosystems (Ausmus 1977, Zhong and Schowalter 1989, Siitonen 2001). They dig galleries that enhance colonization of dead wood by secondary decomposers (Bruno et al. 2003), to which group saproxylic ants belong. These are usually found in dead wood of mid- to late decay classes, where they excavate wood and thus contribute to its decomposition (Higgins 2010). Ants (Hymenoptera: Formicidae) are among the dominant arthropods of the world terrestrial ecosystems (Hölldobler and Wilson 1990). They influence soil and ecosystem processes in various ways and have been

called “ecosystem engineers” to highlight their ecological importance (Folgarait 1998). Ants modify soil physical and chemical properties, enhance plant growth, influence plant and animal distribution, and contribute to overall ecosystem health (Hölldobler and Wilson 1990, Lafleur et al. 2002). However, several ant species also nest in dead wood, which provides a warmer nesting environment than soil (Higgins 2010, Higgins and Lindgren 2012). This is particularly important at higher latitudes where low soil temperature becomes a limiting factor for nesting of thermophilic insects (Higgins 2010).

Many studies have reported important modifications in soil properties attributable to soil-dwelling ant activity (Nkem et al. 2000, Frouz et al. 2003, Dostal et al. 2005). While building their mounds, ants mix organic and mineral material, thus increasing the concentrations of nitrogen compounds ( $\text{NH}_4^+$ ,  $\text{NO}_3^-$ ) and of other nutrients (Lafleur et al. 2002, Dostal et al. 2005). Even if carbon and nutrient dynamics is a well-known phenomenon in the process of wood decay (Harmon et al. 1986, Bond-Lamberty et al. 2002, Laiho and Prescott 2004, Boulanger and Sirois 2006), the role of ants in this process is still unknown, as well as the relationship between ants and dead wood characteristics (Torgensen and Bull 1995, Lindgren and MacIsaac 2002).

In the boreal forest of America, wildfire is the main natural disturbance generating dead wood (Pedlar et al. 2002). While postfire succession of saproxylic beetles have received some attention over the past decade (Siitonen 2001, Grove 2002, Saint-Germain et al. 2004, Boulanger and Sirois 2007), few studies have addressed

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postfire succession of saproxylic ants. In fact, the few studies that have addressed postfire succession of ants have mostly focused on ground-nesting (Lafleur et al. 2006) or ground-dwelling and arboreal ants (Rodrigo and Retana 2006). Moreover, ecological succession of saproxylic ants is poorly known in the boreal forest, particularly with respect to changing habitats resulting from fire disturbances (Lafleur et al. 2006).

The present study aims to 1) characterize the temporal colonization of dead wood by ants along a postfire chronosequence in northern boreal forest; 2) determine which characteristics of dead wood favor nesting by ants; and 3) assess the influence of ants on cycling of carbon and nitrogen stored in dead wood.

## Materials and Methods

**Study Area.** The study was carried out in the lowlands of the James Bay area, within a 100-km radius of the Town of Radisson (53° 79' N, 77° 62' W; Fig. 1). The study area is located on the Precambrian geological formation of the Canadian Shield, which is characterized by a low-altitude (100–200 m) undulating plateau dissected by depressions. The surficial deposits in this landscape correspond primarily to ablation tills and glaciofluvial sands on uplands and marine clays in lowlands (Stockwell et al. 1968). This region is characterized by a subarctic climate with warm and short summers followed by long and cold winters. Annual temperature averages  $-3.6^{\circ}\text{C}$ , with a mean maximum of  $13^{\circ}\text{C}$  in July and a mean minimum of  $-23^{\circ}\text{C}$  in January. Annual precipitation averages 684 mm, of which 246 mm fall as snow (Environnement Canada 2003). Forest dynamics are primarily influenced by a 100-yr fire cycle (Payette et al. 1989, Parisien and Sirois 2003). Black spruce (*Picea mariana* [Mill.] BSP) is the most common tree species in the region, along with jack pine (*Pinus banksiana* Lamb.) in fire-prone sites such as those studied here. The understory vegetation is mainly composed of ericaceous shrubs and the forest floor is covered either by lichens of the genus *Cladonia* or by pleurocarpous mosses.

Sampling sites were located within 10 black spruce stands that respectively burned in 2002, 2001, 1998, 1996, 1989, 1988, 1973 (two stands, a and b), and 1941 (two stands, a and b). We also established two control sites in adjacent black spruce stands that had not burned for at least 200 yr. All sites were sampled in June 2003. Burns were located using maps from the Société de protection des forêts contre le feu (SOP-FEU) and verified with fire scars found on the sites. All sites were located on well-drained soils on which mature black spruce stands were growing prior to fire. The study area was not affected by salvage logging, as it was located outside of the commercial harvesting area.

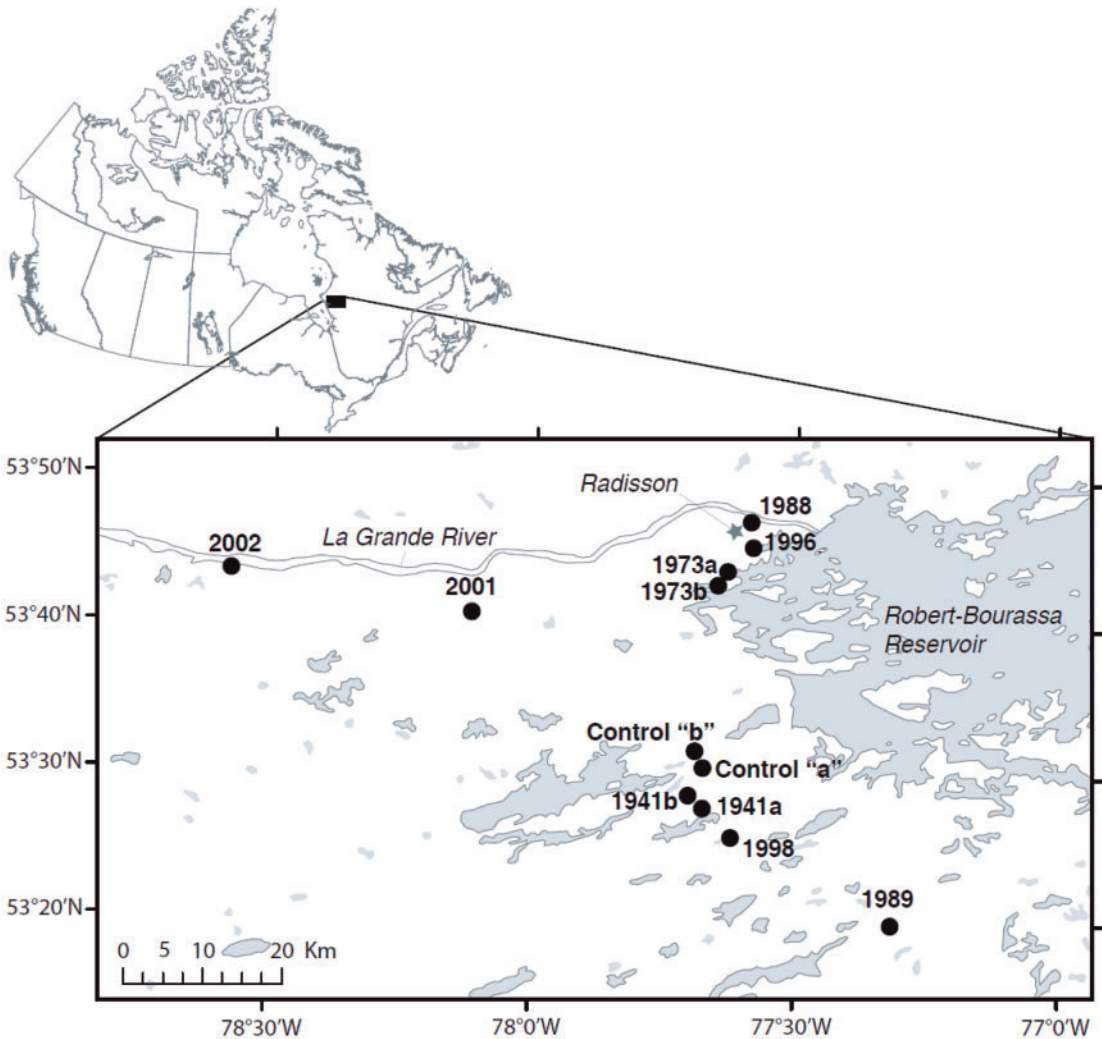
**Sampling and Analysis.** Four square 100-m<sup>2</sup> sample plots were set up 50 m apart from each other within each sampling site. All dead wood pieces (logs, snags, and stumps)  $\geq 5$  cm diameter were counted in each plot and were carefully examined to detect ant nests. Because many ant species are polydomous (Bourke

and Franks 1995, Debout et al. 2007), we defined an ant nest as a group of worker ants taking care of a brood, with or without the presence of a queen. For each piece of dead wood housing one or more nests, we recorded values for the following attributes: number of woodborer holes, position (snag or log lying on the ground), stump diameter (cm), length or height of the dead wood piece (cm), bark cover (%), maximal length of twigs (cm), contact with the ground (%), moss and lichen cover (%), and decay class according to the criteria shown in Table 1. In order to identify attributes favoring ant colonization, we also sampled, for comparison purposes, 5–10 noncolonized pieces of dead wood in each plot and described them with the same attributes. All noncolonized pieces were described in plots with less than five pieces of dead wood.

To compare biological traits of ant species nesting in dead wood, we estimated the volume ( $V_{\text{cylinder}} = \pi r^2 h$ ) of each nest by measuring the length and thickness of the cavity occupied within each piece of dead wood (Foitzik and Heinze 1998). In addition, we noted if ants were using the space between the piece of dead wood and the ground, the space between the bark and the wood, or the wood itself. In the latter case, we also noted if ants were mostly using the periphery or the center of the debris. We used a vacuum to collect a minimum of 20 specimens from each nest, which were kept in 95% ethanol until species identification. Vouchers are kept at the Université du Québec à Rimouski (Rimouski, QC, Canada).

In order to estimate the role of ants in wood decomposition, we collected two wood samples of the same decay class (one from a colonized and one from a noncolonized piece of dead wood) in each plot of the control sites, as well as from plots of the 1989, 1988, 1973, and 1941 burns. These sites were selected because they contained at least one ant nest per plot. Wood disk samples (5 cm thick) were collected using a bow saw, placed in sealed plastic bags to avoid desiccation, and stored at  $-20^{\circ}\text{C}$ . Finely ground subsamples (3 g) were analyzed to determine carbon and nitrogen contents by high temperature combustion and thermoconductometric detection (2400 CHN Elemental Analyzer, PerkinElmer Corp., Norwalk, CT). Each piece of dead wood colonized by ants was sampled at two locations: inside and outside the nest. None of the nitrogen measurements were lower than the detection sensitivity of the analyzer (1.0  $\mu\text{g}$ /subsample).

**Statistical Analysis.** Because colonization by ants is of binary nature (colonized versus noncolonized), we used a binary logistic regression (Quinn and Keough 2002) to determine which dead wood attributes influence ant colonization at the plot level. To examine multicollinearity between variables, we built a correlation matrix between all variables, and only those with a coefficient ( $R$ ) lower than 0.60 were included in the logistic regression. These variables were time since fire, mean length of dead wood, snag and log densities in each of the three decay classes, mean % bark cover, mean % contact with the ground, mean % mosses and lichens cover, and mean number of woodborer holes per piece of dead wood. The likelihood of the model



**Fig. 1.** Study area and distribution of the 12 black spruce stands sampled in northern boreal Quebec (Canada). Numbers refer to the year of each burn; control “a” and “b” sites are stands that have not burned over the last 200 yr.

**Table 1.** Dead wood decay classification (modified from Stevens 1997)

Criteria	Decay classes		
	Weak	Moderate	Advanced
Bark	Intact, firmly attached	If present, not firmly attached	Absent
Twigs	Present	Absent	Absent
Texture	Intact, solid wood	Breaks into large pieces	Small pieces to powdery
Shape	Round	Round	Round to oval
Wood color	Original color	Original to faded color	Light brown to dark brown
Contact with the ground <sup>a</sup>	Bole supported by branches but may sag slightly	Bole sagging near the ground	Bole entirely on the ground

<sup>a</sup>For logs lying on the ground only.

was estimated using Hosmer and Lemeshow’s ( $\hat{C}$ ) goodness-of-fit test (Hosmer and Lemeshow 1989), as well as the proportion of well-classified dependent variables (dead wood colonized versus noncolonized by ants). The Hosmer–Lemeshow test was used to determine if predicted values were significantly different

from the observed values. The logistic regression was done using SPSS 9.0.

Relationships between ant species assemblages and dead wood attributes at the plot level were examined using a redundancy analysis (RDA), which constrains the ordination in a space defined by the linear

combination of environmental attributes included in the model (Jongman et al. 1995, Legendre and Legendre 1998). This analysis was carried out using CANOCO version 4.5 (ter Braak and Šmilauer 2002). Species included in the RDA were present in at least 10% of the plots, and species' nests per plot data were Hellinger-transformed to account for the low occurrence of certain species (Legendre and Gallagher 2001). Only dead wood attributes that had a significant ( $P < 0.05$ ) effect on ant nest distribution were retained in the RDA. The strength of each attribute in explaining species distribution was assessed by running a series of partial RDAs (each attribute analyzed separately) tested by 999 Monte Carlo permutations. The variance inflation factor (VIF) was examined in the complete RDA to make sure that variables showing multicollinearity were not included in the model (ter Braak and Šmilauer 2002). One by one, variables having a VIF higher than five were discarded, beginning with the highest VIF. Thus, variables included in the RDA were mean length and diameter of dead wood pieces, snag, log, and stump densities in each of the three decay classes (weak, moderate, and advanced decay), mean % bark cover, mean % contact with the ground, mean % mosses and lichens cover, and mean density of woodborer holes. Complete RDA model and axis significance were assessed using the Monte Carlo's test of permutations (999 unconstrained permutations).

We used the Wilcoxon  $T$  test (Zar 1999) to compare carbon:nitrogen (hereinafter C:N) ratio and nitrogen content between noncolonized and colonized dead wood, as well as between areas within the nest and outside the nest of colonized dead wood pieces. These tests were done using SPSS 9.0.

## Results

A total of 1,625 pieces of dead wood were examined, among which 211 were colonized by 263 ant nests belonging to eight species. Thus, more than one nest can be found in one single piece of dead wood. *Leptothorax* cf. *canadensis* Provancher (previously known as *L. muscorum*) and *Myrmica alaskensis* Wheeler were by far the most abundant species, accounting for 65.4 and 21.7%, respectively, of the nests observed. *L. cf. canadensis* was absent during the first 2 yr after fire, but increased steadily until 30 yr after fire, whereas *M. alaskensis* was found at all successional stages along the chronosequence (Fig. 2). Some species of the Formicinae subfamily, such as *Formica neorufibarbis* Emery and *Camponotus herculeanus* (Linné), arrive late in the postfire succession, being mostly found in dead wood of stands that burned 60 yr ago (1941 burns) and in control sites. The occurrence of the other species (*Formica aserua* Forel (= *subnuda*), *Formica podzolica* Francoeur, *Myrmica fracticornis* Emery, and *Tapinoma sessile* (Say)) was more sporadic. As a general pattern, the abundance of nests and of colonized pieces of dead wood by ants increased during the first 30 yr after fire, while the abundance of dead wood pieces slightly decreased (Fig. 3a). However, burns of 62 yr showed a strong reduction in the abundance of dead wood and

ant nests. Nevertheless, ant utilization of the available pieces of dead wood dropped only by about 15% in these 62-yr postfire stands (Fig. 3b). Although the availability of dead wood rises in old-growth forests, the abundance of ant nests remained similar to that found in the 62-yr burns and thus, ant utilization of the available pieces of dead wood dropped by 50% compared with the 62-yr postfire stands (Fig. 3a, b).

The logistic regression model correctly predicted the colonization of dead wood by ants in 85.23% of the cases at the plot level (Table 2;  $\hat{C}_{dl=s} = 4.712$ ;  $P = 0.788$ ). Average contact of dead wood pieces with the ground was a determining factor for ant colonization. Moreover, the probability of ant colonization increased with the number of woodborer holes, but decreased with increasing cover of mosses and lichens.

The RDA ordination explained 87.2% (Fig. 4a, Axis 1: 60.9%; Axis 2: 26.3%) of the relationship between ants and dead wood attributes at the plot level. The Monte Carlo test of permutations indicated that the first two axes were significant ( $P < 0.05$ ), as well as the complete RDA model ( $F = 1.975$ ;  $P = 0.012$ ). The negative side of the first axis was mainly associated with the density of dead wood of weak and moderate decay classes and with the number of woodborer holes. The most abundant ant species in our study, *L. cf. canadensis*, was also strongly associated with the negative side of this axis. The positive side of the first axis was mostly associated with average contact of dead wood with the ground. The second axis was essentially explained by the average length of dead wood on the positive side, while the density of snags and that of weakly decayed logs were associated with the negative side. A gradient in dead wood decomposition is perceived from the bottom left to the top right of the RDA ordination (Fig. 4a), going from standing and weakly decayed to highly decayed, large diameter logs lying on the ground. Indeed, plots burned 5 to 30 yr ago, in which *L. cf. canadensis* was mainly found, were located on the bottom left of the ordination, while the other plots were mostly found at the opposite end of the ordination (Fig. 4b). Plots from the first 2 yr postfire were weakly colonized by ants and found along old burns and control sites. Further analysis showed that dead wood colonized by ants in plots of these first 2 yr postfire were mainly large logs lying on the ground with <10% bark cover, without twigs, and showing moderate to advanced decay.

Ant nest volume varied largely among species (Fig. 5), with *C. herculeanus* occupying the largest volume, with an average of  $7,417 \pm 10,356 \text{ cm}^3$  ( $n = 8$ ), and *L. cf. canadensis* having the smallest volume ( $195 \pm 343 \text{ cm}^3$ ;  $n = 172$ ). As a general pattern, ants preferred to occupy the inner part of dead wood (sapwood, heartwood, or both; Fig. 6). However, *F. aserua* and *F. podzolica* preferred using the space at the interface between the ground and dead wood as well as the sapwood underneath the bark.

Generally, the C:N ratio tended to be lower in colonized than in noncolonized dead wood (Fig. 7a), mainly because of the higher levels of nitrogen in colonized pieces of dead wood (Fig. 8a). The difference in C:N

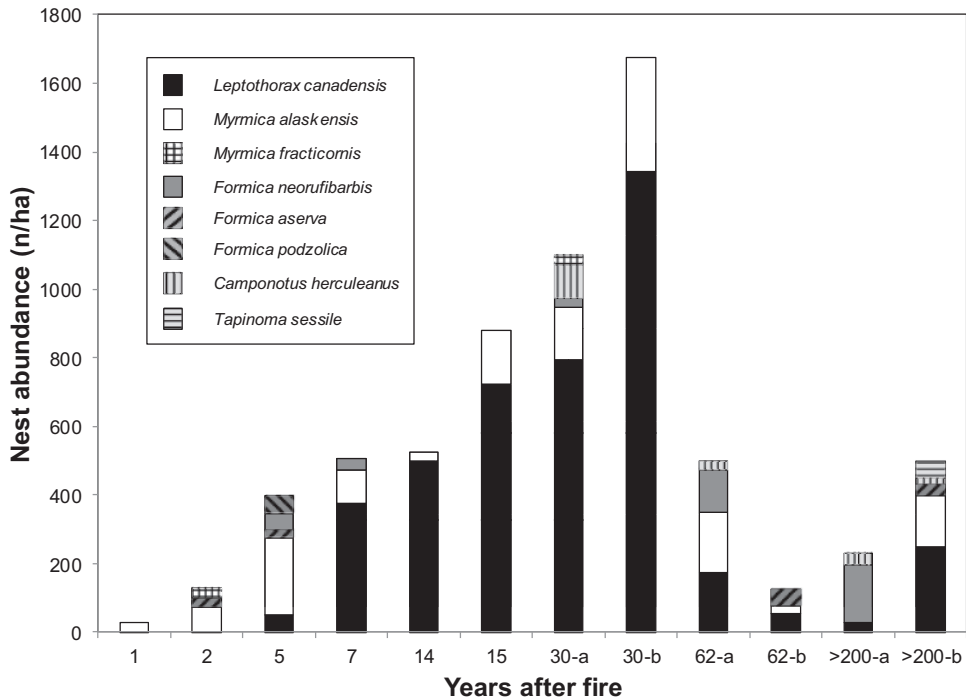


Fig. 2. Ant nest abundance for each species collected in June 2003 in the 10 burned and two control sites (>200 yr).

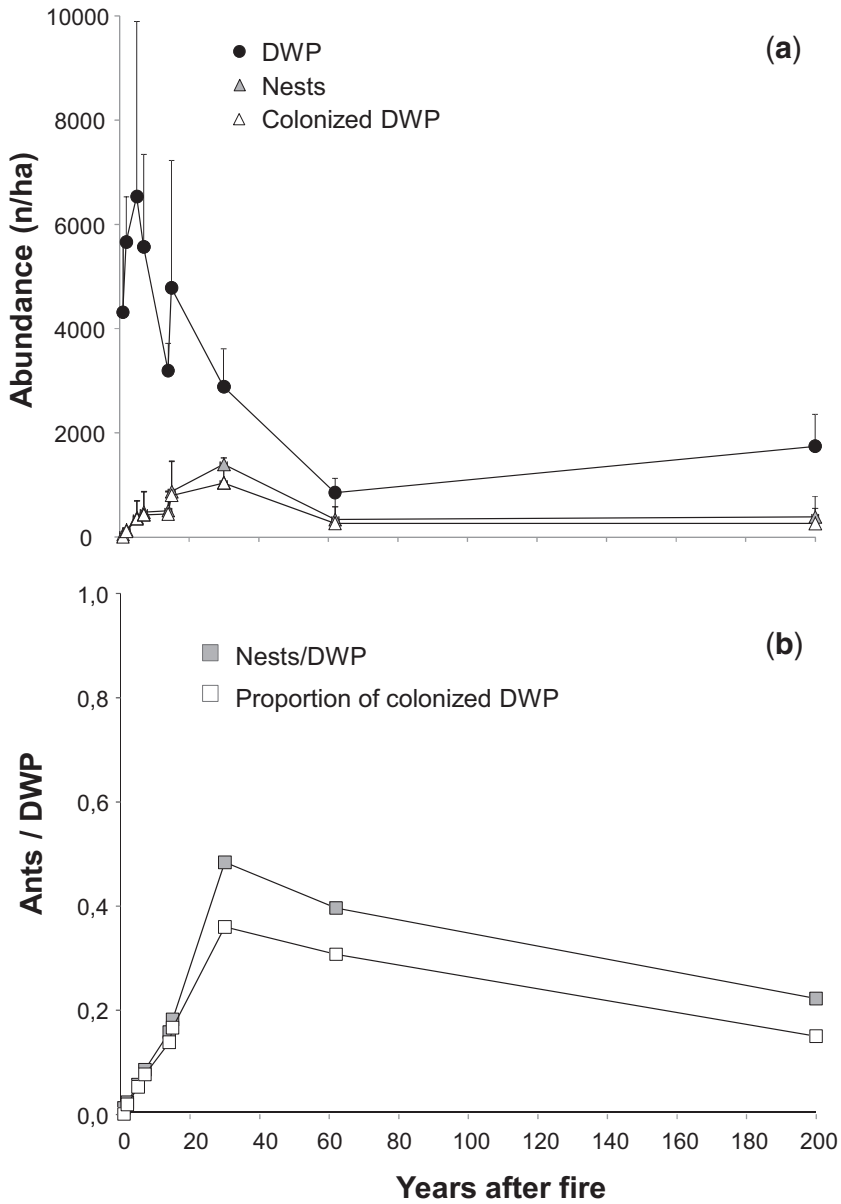
ratio was significant for dead wood found in four burns (1989, 1988, 1973a, and 1941b). This ratio was also lower within the nest than in the wood surrounding the nest (Fig. 7b); this was also due to the higher amounts of nitrogen within the nests (Fig. 8b).

### Discussion

Our study shows that dead wood is widely used for nesting by ants along a postfire chronosequence in northern boreal forest. The ant fauna recorded in our study is truly typical of the northern boreal forest (Francoeur 1983, 2001). Among the eight species recorded, three prefer nesting into dead wood: *L. canadensis*, *F. neorufibarbis*, and *C. herculeanus* (Béique and Francoeur 1966, 1968). Dead wood provides a warmer nesting environment than soil (Higgins 2010), which is important in areas where low soil temperature becomes a limiting factor for nesting of thermophilic insects (Higgins 2010).

Few nests were found in the first 2 yr postfire; only *M. alaskensis* was found in the first year, and it dominated plots during the second year postfire along with *M. fracticornis* and *F. aserva*, whose nests were also found, but in much lower abundance. In these young burns, colonies were mainly found in large logs lying on the ground and showing moderate to advanced decay, indicating that these trees had already been killed by previous fire or from another cause. The colonies found in these young burns were formed by dozens of workers (hundreds in the case of *F. aserva*), and contained nymphs, males, and gynes. The probability

that these colonies originate from postfire colonization is thus very low, and it strongly suggests that these ant species can survive to wildfire. According to Oster and Wilson (1978), a colony needs several years to reach hundreds of workers, as *F. aserva* founds its nests by parasitizing other ant species of the *F. fusca* group. Thus, *F. aserva* may have survived through parasitizing *F. podzolica* which live primarily into the soil (Francoeur 1983) and which was also present in the 4-yr old burn. In fact, *F. aserva* is known to nest in both the soil and dead wood (Francoeur 1983). It has been suggested that ants inhabiting the soil would be less vulnerable to direct destruction by fire (Punttila et al. 1991, Francoeur 2001). Lafleur et al. (2006) reported that 68% of *M. alaskensis* nests were found in mineral soil uncovered by duff layer. They also reported high abundance of *Myrmica* nests (including *alaskensis* and *fracticornis*) in a 1-yr-old burned lichen spruce boreal forest, and suggested that it might be caused by high survival to fire. In our study, *M. alaskensis* preferred dead wood pieces in close contact with the ground; indeed, nearly a third of its nests were built at the interface between dead wood and the ground. This species is also known to be found in microhabitats maintaining a certain level of moisture (Francoeur 1983). The royal chamber is usually found along tree roots on which aphids feed and where ergates build long subterranean galleries (Francoeur 1997). Hence, species inhabiting logs on the ground prior to fire could benefit from similar conditions as those surviving underground, and thus survive fire. The proximity of unburned forest can also facilitate recolonization of

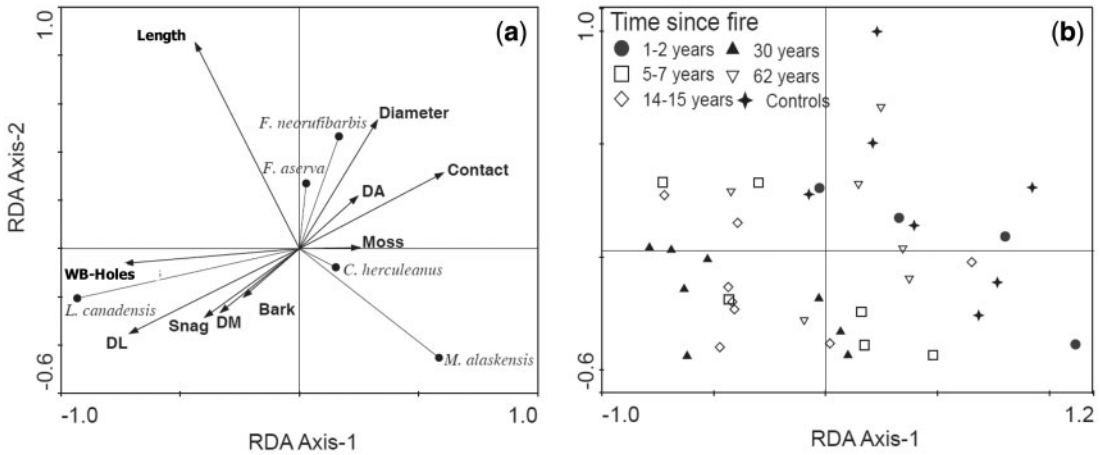


**Fig. 3.** (a) Mean abundance ( $\pm$  SE) of dead wood pieces (DWP), ant nests, and colonized dead wood pieces found in June 2003 and (b) proportion of colonized DWP or nests and DWP in the 10 burned and two control sites.

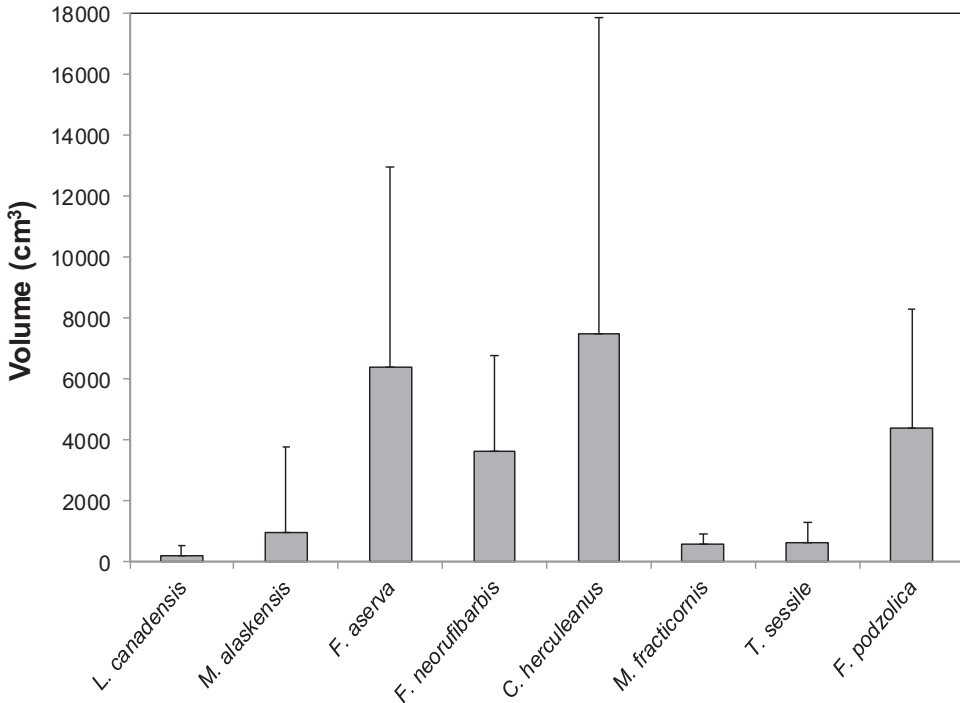
**Table 2. Results of a logistic regression model using 10 habitat attributes for predicting dead wood colonization by ants**

Predictor variables	$\beta$ (SE)	Wald	P	Odds ratio	CI (95%)
Length	0.007 (0.003)	4.568	<b>0.033</b>	1.007	1.001–1.013
Time since fire	-0.002 (0.005)	0.238	0.625	0.998	0.989–1.007
Dead wood abundance	-0.014 (0.202)	0.005	0.946	0.986	0.663–1.467
Weak class of decay	-0.177 (0.168)	1.113	0.292	0.838	0.603–1.164
Moderate class of decay	0.389 (0.246)	2.509	0.113	1.475	0.912–2.387
Advanced class of decay	-0.010 (0.254)	0.154	0.695	0.905	0.550–1.490
Bark cover	-2.000 (1.186)	2.845	0.092	0.135	0.013–1.383
Ground contact	3.555 (1.467)	5.873	<b>0.015</b>	34.972	1.934–619.708
Moss/lichen cover	-7.153 (3.367)	4.514	<b>0.034</b>	0.001	<0.001–0.575
Longhorn beetle holes	0.466 (0.177)	6.928	<b>0.009</b>	1.594	1.127–2.256

$\beta$ , estimated parameter; SE, standard error; CI, confidence interval (95%).



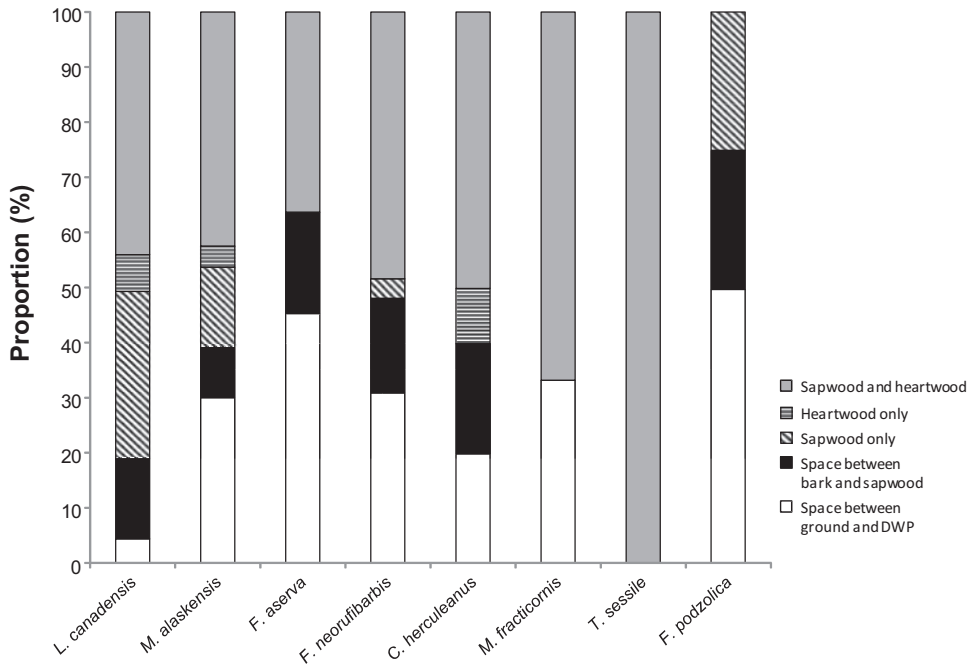
**Fig. 4.** Redundancy analysis showing relationships between dead wood attributes and (a) ant species and (b) sampling sites. Dead wood characteristics are—Length, mean length; Diameter, mean diameter; Snag, snag abundance; DL, low decomposition class; DM, moderate decomposition class; DA, advanced decomposition class; Bark, mean % bark cover; Contact, mean % ground contact; Moss, mean % moss and lichen cover; WB-Holes, mean number of woodborer holes.



**Fig. 5.** Average ( $\pm$  SE) nest sizes of the different ant species inhabiting postfire black spruce pieces of dead wood sampled in the northern boreal forest.

burned stands by ants. Colonies that survive fire, whether they were established underground or in dead wood, would then have an advantage for colonizing the new dead wood resulting from wildfire. This could be a clear advantage for species (e.g., almost all species of *Myrmica*; Passera and Aron 2005) that use a habitat saturation strategy based on polygynous colonies that expand through budding (Bourke and Franks 1995). Some species use a habitat saturation strategy when

facing environmental constraints, e.g., a limitation in favorable nesting sites or a harsh climate, which drives young queens to stay in their birth nest (Passera and Aron 2005). Later on, these queens colonize nesting sites adjacent to their birth nest, thus monopolizing all favorable nesting sites in the surroundings. Colonies of *M. alaskensis*, the only species found at all stages of succession along the chronosequence, could thus be favored over other species of *Myrmica* by filling the



**Fig. 6.** Nest localization in postfire dead wood pieces of black spruce for each ant species.

available niches quite rapidly (Vepsäläinen and Pisarski 1982). Fire seems to destroy the colonies of other species, whether by its direct effect or by removing the main sources of food, such as aphids feeding on aerial parts of the plants (Punttila et al. 1994a).

As a general pattern, the amount of colonized dead wood pieces increases during the first 30 yr after fire, before decreasing in 62-yr-old stands, in which the amount of suitable dead wood decreases markedly combined with an increase in forest canopy closure. Ant utilization of the available pieces of dead wood also increases up to 30 yr after fire but dropped only slightly (by about 15%) in 62-yr postfire stands, suggesting that enough radiant energy still readily reaches the ground in 62-yr postfire stands. This is in agreement with a previous study carried out in a subarctic habitat of the Laurentian Reserve, a 45–50-yr-old natural black spruce and lichen forest, where Béique and Francoeur (1966) reported nine ant species. Ground temperature is a limiting factor for the growth and development of colonies of most ant species (Brian and Brian 1951, Punttila et al. 1994b), with nordic species generally preferring dry, warm, and open habitats (Vepsäläinen et al. 2000). However, the low tree density of northern black spruce forest maintain suitable thermal conditions to maintain several ant species even in >200 yr stands.

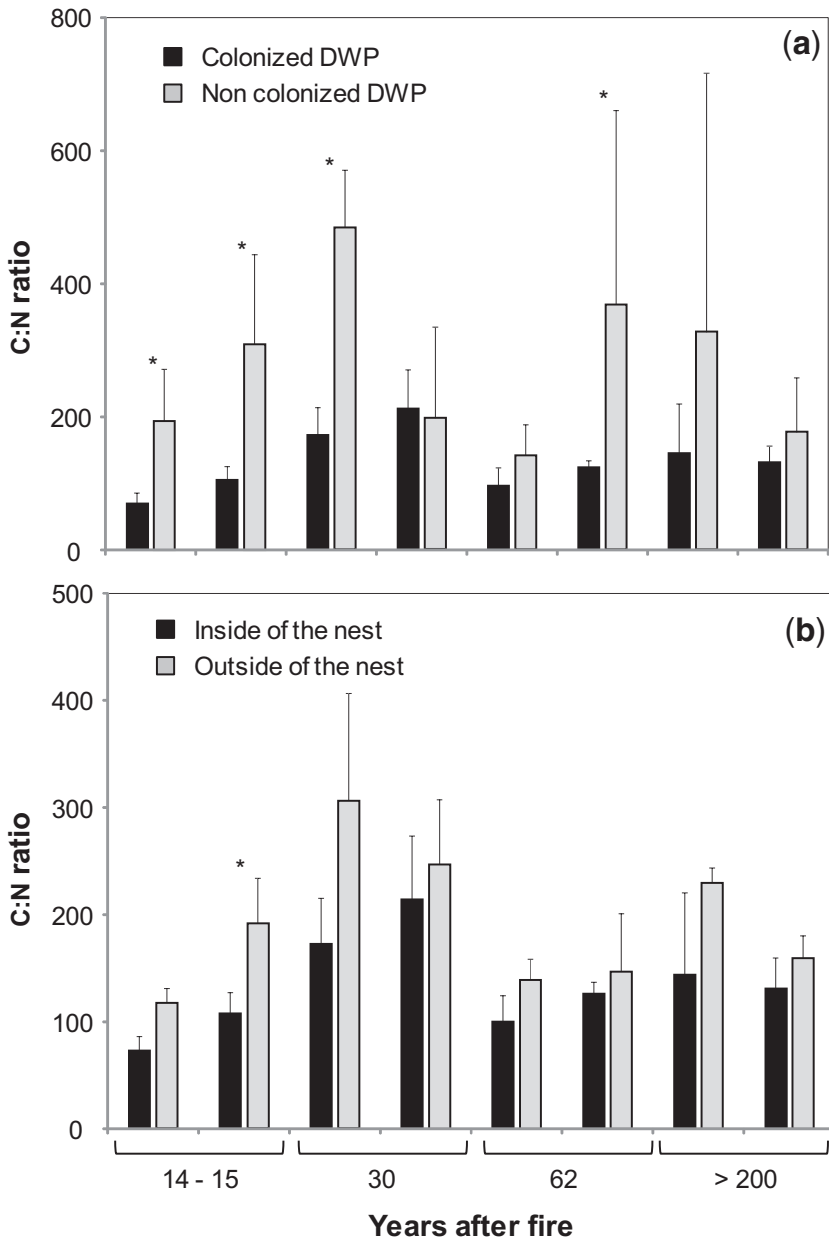
Our study demonstrates that dead wood pieces have a much higher probability of being colonized by ants if they are in contact with the ground. We also noticed that all colonized snags had ant nests at their base and in their root system. Stumps are warmer and thus make better habitats for ant nesting in the north than either logs or soil (Higgins and Lindgren 2012). Ground proximity of dead wood may also be important,

as it makes it possible for ergates to forage either in the decaying wood or in the nearby soil. Logs lying on the ground also provide a wider variability of microclimates compared with those that are not in close contact with the ground. Dead wood touching the ground provides humid and cool areas, while sun-exposed areas are much warmer. Such heterogeneity in microclimatic conditions might help ergates optimize brood rearing (Hölldobler and Wilson 1990). Furthermore, the colonization of dead wood is positively influenced by the presence of woodborer holes. In the studied region, the white spotted sawyer, *Monochamus scutellatus scutellatus* (Say), dominates postfire woodborer communities (Boulanger and Sirois 2007, Boulanger et al. 2013). The larvae of this xylophagous insect bore galleries deep into the wood, and these galleries are abandoned once larval development is completed, 1 or 2 yr later. It has been suggested that such galleries could be used as nesting sites by ant species (Foitzik and Heinze 1998, Passera and Aron 2005). Our study is the first to show that dead wood drilled by woodborers have a higher probability of being colonized by ants, mostly by the small *L. cf. canadensis*, as suggested by the redundancy analysis.

The most abundant species of the study, *L. cf. canadensis*, peaked in density in 30-yr-old burns. Usually, this species occupies small wood volumes in weakly decayed debris (Higgins 2010). Its high abundance in such pieces of dead wood could have a significant impact on wood decomposition after fire. Other *Leptothorax* ants have been reported to widen the cavity of their nests (Foitzik and Heinze 1998).

Our results indicate that *F. neorufibarbis* and *C. herculeanus* arrive late in the postfire succession, being

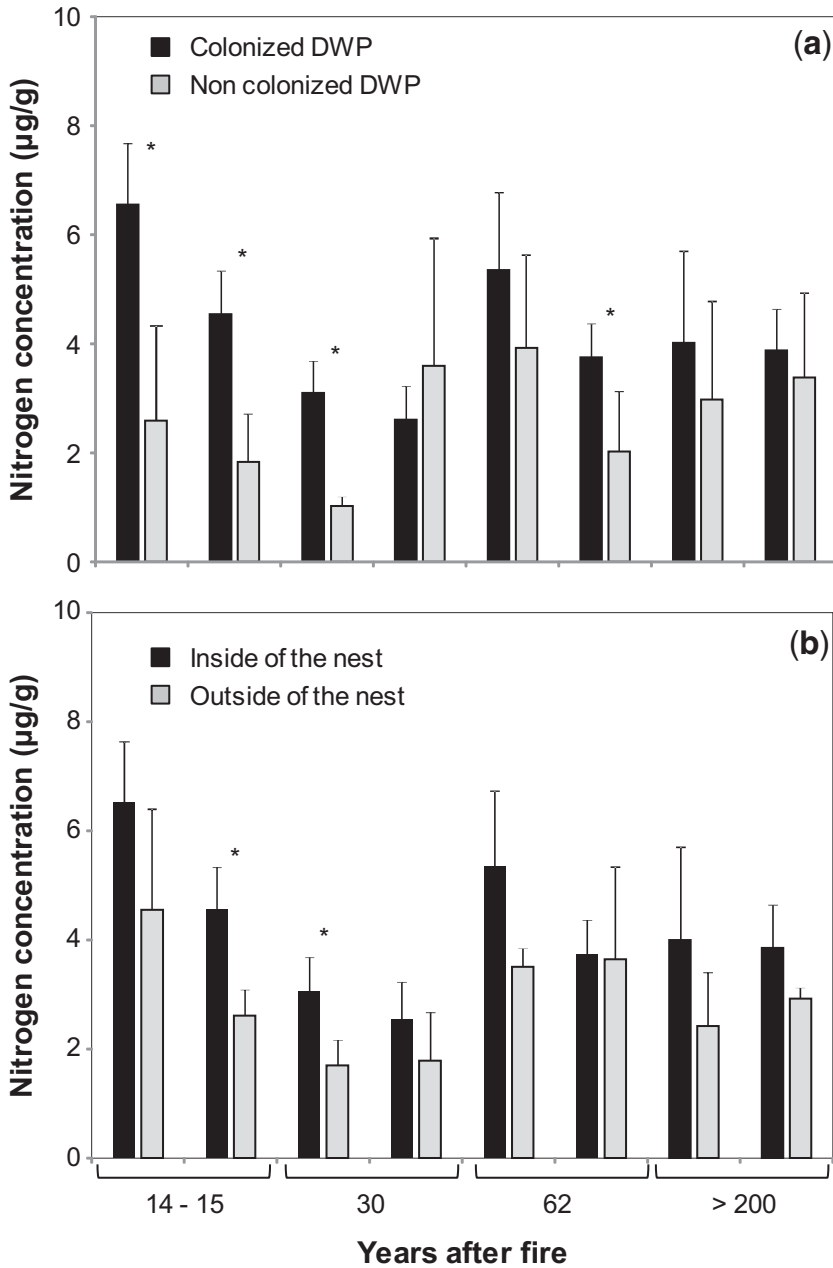




**Fig. 7.** Comparison of the C:N ratio between postfire dead wood pieces of black spruce (a) colonized or not by ants, and (b) inside versus outside the nests in northern boreal Quebec (Canada). Asterisks (\*) indicate significant differences ( $P < 0.05$ ; Wilcoxon  $T$  test).

mostly found in dead wood of stands that burned 60 yr ago (1941 burns) and in control sites. This differs from postharvest succession in Lodgepole pine subboreal forests of British Columbia, Canada, in which these two species were found up to 25-yr postharvest but were absent from nonharvested forests (Higgins and Lindgren 2015). Fire strongly disturbs ecosystems and essentially produces an ant-free territory into which pioneering species immigrate (Puntilla and Haila 1994). *F. neorufibarbis* and *C. herculeanus* form

colonies of thousands of individuals (Sanders 1970, Francoeur 1983) and usually nest in large-diameter debris. As the fall rate of large snags is lower than for small ones, large-diameter debris may become available only after several decades after wildfire, particularly in northern boreal forests where trees are small, the mean diameter at stump height being only 13.5 cm (Boullanger et al. 2010). Moreover, when they die, and particularly when they fall, large trees generate gaps in the forest matrix that increase sun exposure and thus



**Fig. 8.** Nitrogen concentration comparison between postfire dead wood pieces of black spruce (a) colonized or not by ants, and (b) inside versus outside the nests in northern boreal Quebec (Canada). Asterisks (\*) indicate significant differences ( $P < 0.05$ ; Wilcoxon  $T$  test).

provide suitable environmental conditions for ant nesting. When these ants colonize dead wood, they use up to 60% of the sapwood and heartwood areas. By boring numerous galleries into dead wood, *C. herculeanus* is known to have a major impact on dead wood decomposition (Sanders 1964). The ecological role of the other two *Formica* species (*aserva* and *podzolica*) in dead wood decomposition remains to be determined.

Our results suggest that the colonization of dead wood by ants has an impact on carbon and nitrogen dynamics. Indeed, the C:N ratio is consistently lower in colonized compared with noncolonized dead wood pieces. The same trend is also observed when comparing the C:N ratio inside the nest to the ratio measured outside the nest for a particular piece. While such changes in C:N ratio may result from wood degradation by saprophytic fungi, the lower C:N ratio inside versus

outside the nests and in colonized versus noncolonized dead wood suggests that some nitrogen import occurs inside ant nests. It is likely that this nitrogen comes from metabolic waste accumulated in rooms inside the nest that are used as dumps by ergates. Although it is the first insight into the role of ants in wood decay and nutrient cycling of dead wood in the northern boreal forest, the interaction of ants and saprophytic fungi in this process remains to be demonstrated.

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