# THE FINE SCALE PHYSICAL ATTRIBUTES OF COARSE WOODY DEBRIS AND EFFECTS OF SURROUNDING STAND STRUCTURE ON ITS UTILIZATION BY ANTS (HYMENOPTERA: FORMICIDAE) IN BRITISH COLUMBIA, CANADA

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**Abstract—**Coarse woody debris (CWD) is increasingly recognized in Canada for its contribution toward biodiversity. It is a particularly vital resource in subboreal forests as nesting habitat for ants (Formicidae). Wood, which has low specific heat, provides a thermally favorable environment in this cool climate. Ants contribute to the physical breakdown of wood, and colonies are a significant food source for many vertebrates. However, this resource differs significantly between harvested and non-harvested stands. This study examined the physical attributes of CWD in 8-10 year old harvested and non-harvested stands while also examining the associated ant fauna. We found no significant difference in volume or total surface area between stand types. However, in harvested stands CWD is smaller in diameter, shorter, has less bark and has less evenly distributed decay classes as compared to non-harvested stands. In addition, the lack of earliest decay class and the physical damage evident on the majority of CWD pieces in harvested stands creates concern regarding the long term availability of CWD in harvested stands. Ants exploit available CWD in harvested stands but the community structure of this fauna appears to be young in these 8-10 year post-harvest stands. Larger ant species such as *Camponotus herculeanus* and *Formica aserva* were present but not common in these stands. They seem to require larger pieces of CWD and stumps for nesting habitat than is the average for CWD in harvested stands. The desirability of these ants as prey for bears and birds makes management of their nesting habitat of interest for conservation biology. Ants were largely excluded from non-harvested stands, probably because of cool and humid conditions. Historically, the ant fauna of this landscape was probably restricted to natural gaps and disturbed areas.

## INTRODUCTION

In recent years there has been a move away from considering coarse woody debris (CWD) as unsalvaged waste (Maser and others 1979) and toward an appreciation of this resource as a significant contributor toward both forest ecological processes (Lofroth 1998, Maser and others 1994, Stevens 1997) and as habitat for many species (Keisker 2000). This change in attitude has been reflected by review publications in North America (Laudenslayer and others 2002), England (Hodge and Peterken 1998), Australia (Grove 2002, Waldendorp and others 2002), and Fennoscandia (Jonsson and Kruys 2001). In Canada, recognition of the role of CWD within forest ecosystems has grown, and it has now been included by some forestry companies as a critical filter habitat and biodiversity indicator within their Canadian Standards Association sustainable forest management certificate (Todd 2002).

Ants (Hymenoptera: Formicidae) constitute one of the most abundant and ubiquitous animal taxa in the world. In one of the few studies on comparative biomass in ecosystems, Fittkau and Klinge (1973) reported that the biomass of ants in the Amazon constituted over 25 percent of total animal biomass, and was more than twice that of all vertebrates combined. Ants are also one of the most widely distributed taxa, ranging from the tropics (Fittkau and Klinge 1973) to the northern treeline, with sporadic colonies found some distances beyond this (Francoeur 1983). Further, they are known to contribute significantly to ecosystem processes that include but are not limited to: pest management (Carlson and others 1984, Torgersen and Mason 1987, Way and Khoo 1992), soil nutrient turnover (Wagner and others 1997), seed dispersal (Gorn and others 2000, Heithaus 1981), grain consumption (Brown and others 1979), predation (McNeil and others 1978), and decomposition of organic material (Haines 1978). In addition, and of particular relevance to the forests of British Columbia, ants serve as a significant food source for birds (Bull and others 1995, Knowlton and others 1946, Torgersen and Bull 1995) and bears (Noyce and others 1997, Raine and Kansas 1990, Swenson and others 1999) thus playing an important role in the forest food web.

Ants (Hymenoptera: Formicidae) are a thermophilic taxon that in cooler climates must select nesting habitats which maximize daily heat gain (Hölldobler and Wilson 1990). In boreal and subboreal forests three common strategies are employed: (1) nesting under rocks; (2) the construction of thatched nests from forest litter, and; (3) nesting in dead wood (Hölldobler and Wilson 1990). Ideal nesting substrate should gain heat quickly, be of sufficient mass to hold that heat as ambient temperature declines, and be elevated above the soil to maximize insolation. Of these cooler climate nesting strategies, CWD best meets these criteria throughout the colony lifecycle.

North American literature directed at surveying the ant fauna of specific geographical regions illustrate the increasing

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dependence of ants upon CWD with increasing latitude. While just less than 10 percent of species use dead wood as nesting habitat in Nevada, which has an average latitude of 38° N (Wheeler and Wheeler 1986), just over 35 percent used dead wood in North Dakota (average latitude 48° N) (Wheeler and Wheeler 1963), and just under 60 percent of species collected near Prince George British Columbia were dead wood associated (latitude 53° N) (Lindgren and MacIsaac 2002). Further, the latitude effect is mirrored by cooling climate. Colorado, at the same approximate latitude as Nevada, has a much greater percentage of dead wood dependent ants than Nevada. That is, 33 percent of the ant fauna is dead wood dependent in Colorado (Gregg 1963), compared to just less than 10 percent in Nevada (Wheeler and Wheeler 1986).

Currently, forest managers have few criteria upon which to base decisions regarding CWD management. Attention has been given to easily measured parameters such as volume and total surface area, the latter often expressed as percentage ground cover. It is then assumed that maintaining volume or total surface area of CWD in harvested plots, as compared to non-harvested plots will maintain the ecological functionality of CWD. However, as will be discussed, there are significant differences in the physical attributes of CWD between harvested and non-harvested sites.

The objective of our study is to examine variations in the physical attributes of CWD between harvested and non-harvested sites in the subboreal spruce biogeoclimatic zone of British Columbia. Attributes associated with utilization by ants are highlighted along with the effect of surrounding stand structure.

## PROCEDURES

### Coarse Woody Debris in Harvested and Non-Harvested Stands

Using records obtained from Houston Forest Products (Weldwood Canada), non-harvested and 8-10 year old harvested sites were identified in pine (*Pinus contorta* var. *latifolia*) leading stands within the subboreal spruce (SBS) biogeoclimatic zone and moist cold (SBSmc) subzone (Meidinger and Pojar 1991). Pine leading stands were chosen given the commercial significance of this species in the area. Stands were identified within a 100-km radius of Houston, British Columbia (54° 23' 59" N - 126° 40' 0" W). Four non-harvested sites and four 8-10 year old post-harvest sites were identified. Within each, a 1-ha sampling plot was randomly positioned at least 50 m away from an edge (i.e., road, stream, significant elevation change, forest or cutblock edge).

Coarse woody debris was sampled within two sets of 4X100 m strip plots randomly placed within the 1-ha sampling plot. Coarse woody debris was defined as any piece of dead wood within the strip plot with a maximum diameter of 10 cm or greater, including stumps. Each piece within the plot was measured for large and small diameter at strip edge, large end diameter, length in plot, and total length. The percentage bark retained was estimated visually and it was noted if the piece was in contact with the ground or elevated (i.e., greater than half of its total length off the ground). The decay class was determined for the sapwood and heartwood following Maser and others (1979). Woody debris of decay class 2, the most common solid wood decay class found in recently harvested stands, often exhibited signs of mechanical damage and was recorded as either 2A (no damage) or 2B (damaged) following Lloyd (2002). Stumps within the harvested plots were included in the assessment and analyzed separately from the downed woody debris. Both stumps and CWD were identified to species where possible.

The physical attributes of the CWD were recorded within 12.5-m segments within the 4X100 m transect, thus creating 50-$m^2$ sub-samples. The surface area of CWD pieces was derived by taking the average of the large and small end diameters at the plot boundaries and multiplying by the length. Volume was calculated as a frustrum using the large and small end diameters at the plot boundary and length in the plot. Total area and volume within the 50-$m^2$ sub-sample was then used as the basis of the estimate of CWD volume per hectare.

### Environmental Attributes of Study Sites

Direct insolation in the harvested and non-harvested sites was approximated by determination of canopy cover. Canopy cover was assessed photographically using a Nikon Coolpix 990 digital camera fitted with a 0.63X wide angle lens. Within each plot, 5 randomly chosen points were used to photograph the canopy from a height of 1m. A 12X9 dot grid was then used to assess canopy cover on each photograph.

Temperature in the forest duff was monitored for approximately a one month period from July 7 to August 11, 2003 using iButton (Dallas Technologies) temperature dataloggers placed approximately 1 cm below the surface of the forest litter at two random points within each plot. The dataloggers recorded temperature every 30 minutes.

### Ant Utilization of Coarse Woody Debris

Ant utilization of CWD was assessed within the 4X100 m strip plots indicated above. After measuring the physical attributes of CWD, each piece of wood was opened by hatchet and assessed for ant fauna. Ants were collected for species identification in the lab and the position of the ant or colony within the CWD was recorded.

To assess the ant fauna of the site that was not directly nesting within CWD, Nordlander style pitfall traps (Nordlander 1987) were set in place along four randomly placed 80-m long transects. These traps were placed at 20-m intervals along each 80-m transect (5 traps per transect, for a total of 20). Pitfall traps were left in place for one month and samples were collected at the end each second week.

### Statistical Analysis

All data were assessed for normality using the Anderson-Darling test. Sample data failing to meet normality were then analyzed non-parametrically using the Mann-Whitney test.

## RESULTS AND DISCUSSION

### Coarse Woody Debris in Harvested and Non-Harvested Stands

The mean volume of CWD reported here (table 1) for non-harvested stands is lower than the 159 $m^3$/ha previously reported for this biogeoclimatic zone and subzone in a review by Lofroth (1998). This is not surprising given the great variability noted for this resource. However, the volume reported here is similar to volumes reported in a review of boreal forest CWD in Fennoscandia (Siitonen 2001).

Siittonen (2001) notes an order of magnitude reduction in CWD volumes following harvesting. Such a reduction has not been seen in this study where in fact, post-harvest volumes are higher than those found in non-harvested stands (table 1). This is likely due to the values placed upon woody material in Fennoscandia for fuel and chip production (Ehnström 2001). The reduction in volume in Fennoscandia has been associated with placing many CWD dependent invertebrate species at risk (Ehnström 2001). In response to this Ehnström (2001) recommends that CWD retention following harvesting be increased by approximately 50 percent. Following this recommendation, Ehnström (2001) discusses the need to manage the quality of the CWD as well as the total volume. As will be seen, observations from our study support that recommendation.

While we found no reductions in CWD volume and the related parameter, total surface area, variations in the physical attributes of the CWD between harvested and non-harvested sites are evident (table 2). Stumps differ fundamentally from downed woody debris with respect to physical attributes such as length (i.e., height in the case of stumps), and are not present within the non-harvested stands. Thus, they have been removed from the dataset presented in table 2. Coarse woody debris in which stumps have been excluded is referred to here as downed woody debris (DWD). DWD pieces in harvested plots are smaller in diameter, shorter, have lower bark retention, and differ in the distribution of decay classes when compared to non-harvested stands.

**Table 1—Average total surface area and total volume of coarse woody debris in four harvested and four non-harvested stands within the subboreal spruce moist cold biogeoclimatic zone and subzone of British Columbia (each estimate is derived from a 50-$m^2$ subplot)**

| | Average total surface area covered by CWD | Average total volume of CWD |
|---|---|---|
| | *$m^2$/ha ± SD* | *$m^3$/ha ± SD* |
| Non-harvested stands | 656 ± 622<br>n = 57 | 83.8 ± 87<br>n = 57 |
| Harvested stands (8-10 years post-harvest) | 684 ± 904<br>n = 61 | 119.9 ± 184<br>n = 61 |
| Mann-Whitney two sample test | p = .9499 | p = .1082 |

CWD = coarse woody debris.

**Table 2—Physical attributes of downed woody debris in four harvested and four non-harvested stands within the subboreal spruce moist cold (SBSmc) biogeoclimatic zone and subzone of British Columbia**

| | Mean large end diameter | Mean total length | Mean percentage bark | Mean sapwood decay class | Mean heartwood decay class |
|---|---|---|---|---|---|
| | *cm ± SD* | *m ± SD* | - - - - - - - - | - - - - - - *± SD* - - - - - - | - - - - - - - - |
| Non-harvested stands | 18.9 ± 6.8<br>n = 321 | 12.9 ± 7.5<br>n = 324 | 29 ± 39<br>n = 322 | 2.5 ± 0.8<br>n = 323 | 2.4 ± 1<br>n = 323 |
| Harvested stands (8-10 years post-harvest, DWD) | 16.5 ± 6.8<br>n = 439 | 3.7 ± 3.7<br>n = 439 | 8.6 ± 18.8<br>n = 439 | 2.4 ± 0.6<br>n = 432 | 2.4 ± 0.7<br>n = 418 |
| Mann-Whitney Test | $p < 0.0001$ | $p < 0.0001$ | $p < 0.0001$ | $p = 0.0001$ | $p = 0.2776$ |

DWD = downed woody debris.

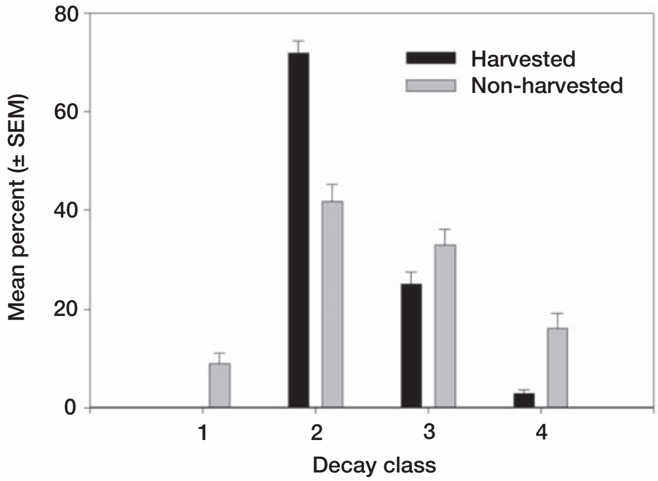


Figure 1—Percentage distribution of sapwood decay classes for coarse woody debris sampled in four non-harvested and four 8 to 10 years postharvest stands (non-harvested: n = 323; harvested: n = 701). Decay classifications follow Maser and others (1979).

It might seem surprising that a significant difference was seen in sapwood decay class between harvested and non-harvested stands given the similar average decay class (table 2). However, an examination of the distribution of decay classes between stand types (fig. 1), shows a strongly leptokurtic distribution in harvested stands, with just over 70 percent of all pieces in decay class 2, as compared to just over 40 percent in non-harvested stands. Decay class 1 was virtually absent in harvested stands, with only a single piece recorded. As a consequence this cohort will not be available for contributing toward later decay classes as stand succession progresses.

Also evident was the high degree of physical damage (i.e., crushed wood and splintering) to decay class 2 wood in harvested stands, presumably as a result of the activity of heavy machinery. In harvested plots, 63 percent of decay class 2 stumps (n=177) and 59 percent of DWD (n=301) displayed evidence of such mechanical damage. While this characteristic was almost certainly exploited by pioneering ant species (e.g., *Leptothorax canadensis* and *Myrmica alaskensis)* for access to nesting sites it could also allow more water penetration that may increase the rate of decay and, thus, the rate of removal of this resource from the stand. Exacerbating this potential increase in the rate of decay is the observation that 85 percent of pieces of CWD in the 8-10 year old post-harvest stand were in full contact with the ground, as compared to 53 percent of pieces in non-harvested stands.

## Environmental Attributes of Study Sites

Harvested stands differed from 8-10 year old non-harvested stands in attributes such as canopy cover and soil litter temperature. Mean canopy cover in non-harvested stands was 78 percent ±9.24 (SD) as compared to 3.0 percent ±8.0 (SD) in harvested stands. As expected, the mean overall temperature of soil litter in the harvested stands was significantly higher than in non-harvested stands (table 3). In addition, the temperature range in harvested stands exceeded that of non-harvested stands in both daily high and low temperatures. However, this was most pronounced for daily highs (table 3).

Naturally, the higher canopy cover of non-harvested stands moderates the daily temperature fluctuations on the ground (table 3). Ants are thermophilic and are averse to cool moist conditions (Hölldobler and Wilson 1990) prevalent in forests of the subboreal spruce (SBS) moist cold (mc) biogeoclimatic zone and subzone. Thus, the low temperatures and high humidity explain the almost complete absence of ants in mature forests in this area (see below). If we assume that the canopy cover seen today in non-harvested stands is typical of that found historically on this landscape, then the ant fauna was likely restricted to naturally created gaps and disturbances arising from factors such as windthrow, insect disturbance and fire. In harvested stands, the fauna and flora must be capable of tolerating large fluctuations in daily temperature either physiologically or behaviorally. Nesting in CWD offers one mechanism of behaviorally controlling temperature.

Coarse woody debris has a low specific heat capacity (1.23kJ/kg/C at 25 °C (Wenzl 1970) compared to water (4.2 kJ/kg/C at 25 °C) (Lide 1991)). Thus, the temperature of woody debris should rise quickly from the absorption of energy as long as the wood is not excessively wet. As a consequence coarse woody debris offers a nesting substrate that can gain heat quickly when exposed to direct sunlight (e.g., in the low canopy cover of a harvested stand) and through its bulk hold some of that heat through the night. It also provides a physical matrix that allows an ant colony to reposition itself to optimize temperature and humidity or at least avoid deleterious conditions. Finally, the CWD is elevated above early successional ground flora allowing for direct exposure to sunlight.

**Table 3—Temperature variations over a 1-month period (July 11, 2003 to August 11, 2003) in four harvested (8 to 10 years postharvest) and four non-harvested stands (all differences are statistically significant at $\alpha$ = 0.05 as determined by the Mann-Whitney two-sample test)**

| Stand type | Mean temperature | Mean daily low temperature | Mean daily high temperature |
|---|---|---|---|
| | | *(°C ± SD)* | |
| Harvested | 14.2 ± 7.3 | 6.1 ± 2.1 | 26.5 ± 5.5 |
| Non-harvested | 10.6 ± 2.7 | 7.6 ± 1.5 | 15.1 ± 2.2 |

## Ant Utilization of Coarse Woody Debris

A profound difference is evident in ant utilization of CWD between harvested and non-harvested stands. While 49 percent of CWD pieces (including stumps) (n=739) in harvested stands hosted ant colonies, only 3 percent of pieces (n=333) in non-harvested sites hosted ants. Further, within harvested stands ant utilization was higher for stumps than downed woody debris. On average 61 percent of stumps hosted ant colonies as compared to 41 percent of downed woody debris.

In total, 9 species of ants were collected from coarse woody debris in both harvested and non-harvested plots (appendix). However, of these, only 4 were collected within non-harvested stands whereas all 9 were present in the harvested stands. Of a total of 398 colonies of ants sampled from 1,072 pieces of CWD in this study only 11 separate colonies were located in non-harvested stands. Foraging activity was essentially absent in non-harvested stands. In total only 16 individual ants were collected in all pitfall traps set in non-harvested stands compared to 566 in harvested stands. However, even this larger number represents only 0.2 ants/trap/day. This low rate of ant capture in 8-10 year old post-harvested stands suggests that the community structure of the ant fauna is fairly young. Preliminary data (unpublished) from post-harvest stands just 5 years older has yielded 1.1 ants/trap/day, almost an order of magnitude increase.

The majority of species of ants were CWD dependent. Of the 11 species collected through all techniques, 9 were found nesting within CWD. Given that ant colonies were common in post-harvest CWD but little activity was occurring in the general stand, it is reasonable to suggest that CWD is acting as an important initiation point for ant colonization in harvested stands. However, it appears that many colonies had yet to mature and begin to fill available foraging space. In addition, of the two species not directly recorded in CWD in this study (*Polyergus breviceps* and *Myrmica fracticornis*), *P. breviceps* is known to use both CWD and soil for nesting (Wheeler and Wheeler 1963). In preliminary data from unpublished 15 year old post-harvest stands we have found evidence to suggest that soil nesting species do begin to establish. Mature colonies of a few soil nesting species of the *Formica fusca* group have been found in these older stands. However, it is possible that some of these nests may have originally established in CWD because pieces of rotten wood are often found in the center of such nests (Lindgren and MacIsaac 2002).

Given the low number of ants in non-harvested sites, the examination of the physical attributes of CWD associated with ant colonies has been limited to harvested plots. For each species present more than 10 times within the CWD survey, the physical attributes of the DWD and stumps hosting that species was compared to the overall physical attributes of all of the DWD and stumps in these stands (table 4).

Ant preferences for specific attributes of CWD however were not often clear. The most abundant species of ant colonizing CWD was *Leptothorax canadensis*. Given the average size of this ant (2.5-3.5 mm) and small colony sizes (few dozen) it is likely that it can use any CWD piece as nesting habitat. Lindgren and MacIsaac (2002) report finding this species in fragments of woody debris only 10 X 15 cm in size.

Although physically larger ant species (6-10 mm) such as *Camponotus herculeanus* and *Formica aserva* were not well established in 8-10 year old post-harvest plots some insight can be gleaned from our data about their nesting preferences. *C. herculeanus* did show a significant preference for larger pieces of CWD and *Formica aserva* was usually found in stumps rather than pieces of downed woody debris which generally had lower end diameters (table 3). These larger ants, and in particular their associated larvae, pupae, and female alates (queens) are a preferred food source for both black and grizzly bears (Noyce and others 1997, Swenson and others 1999) as well as birds (Torgersen and Bull 1995). We saw no evidence of bear foraging for ants in stumps or DWD in the 8-10 year old post-harvest sites but preliminary evidence from 15 year old stands shows signs of bear foraging on 20 percent (n=156) of stumps and 8 percent of DWD (n=185). The lack of bear foraging in 8-10 year old post-harvest stands further supports the suggestion that the ant community of these stands is immature.

We are currently expanding the range of stand types studied to further follow the relationship between CWD and ants. In particular we are beginning to examine later seral stages in harvested and naturally disturbed (burned) stands.

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**Table 4—A comparison of the physical attributes of all downed woody debris and stumps in 8- to 10-year-old harvested plots with the same attributes associated with utilization by six species of ants, using the Mann-Whitney two-sample test**

| | Type of CWD | Average end diameter | Average length | Percentage bark | Sapwood decay class | Heartwood decay class |
|---|---|---|---|---|---|---|
| | | *cm ± SD* | *m ± SD* | - - - - - - - - | ± SD | - - - - - - - - |
| Overall CWD in harvested stands | DWD (n = 439) | 16.5 ± 6.8 | 3.7 ± 3.7 | 8.6 ± 18.8 | 2.4 ± 0.6 | 2.4 ± 0.7 |
| | Stumps (n = 333) | 29.8 ± 13.7 | 0.33 ± 0.2 | 37.2 ± 32 | 2.3 ± 0.5 | 2.3 ± 0.6 |
| CWD occupied by ant species | | | | | | |
| *Camponotus herculeanus* | DWD (n = 7) | 26.2[a] ± 4.8 p = 0.002 | 3.0 ± 2.4 p = 0.57 | 5.0 ± 3.0 p = 0.67 | 2.4 ± 0.5 p = 0.74 | 2.7 ± 0.8 p = 0.35 |
| | Stumps (n = 5) | 36.1 ± 8.2 p = 0.2 | 0.4 ± 0.1 p = 0.22 | 37.5 ± 37.4 p = 0.8 | 2.2 ± 0.4 p = 0.69 | 2 ± 0 |
| *Formica accreta* | DWD (n=5) | 12.5 ± 1.4 p = 0.12 | 6.5 ± 3.6 p = 0.1 | 0 ± 0 | 2.5 ± 0.6 p = 0.63 | 2.7 ± 0.5 p = 0.28 |
| | Stumps (n = 6) | 27.5 ± 9.8 p = 0.53 | 0.33 ± 0.0 p = 0.52 | 43 ± 31.4 p = 0.66 | 2.1 ± 0.4 p = 0.57 | 2.3 ± 0.5 p = 0.91 |
| *Formica aserva* | DWD (n = 9) | 18.1 ± 8.0 p = 0.57 | 4.6 ± 3.2 p = 0.32 | 16.0 ± 24.6 p = 0.15 | 2.6 ± 0.7 p = 0.38 | 2.6 ± 0.7 p = 0.5 |
| | Stumps (n = 17) | 35.8 ± 11.0 p = 0.09 | 0.31 ± 0.1 p = 0.76 | 36 ± 31.2 p = 0.96 | 2.4 ± 0.5 p = 0.65 | 2.5 ± 0.5 p = 0.22 |
| *Formica neorufibarbis* | DWD (n = 19) | 22.9[a] ± 13.5 p = 0.04 | 4.9 ± 5.2 p = 0.33 | 6.4 ± 10.3 p = 0.47 | 2.7 ± 0.8 p = 0.11 | 2.9[a] ± 0.8 p = 0.02 |
| | Stumps (n = 28) | 40.3[a] ± 13.6 p = 0.001 | 0.37 ± 0.2 p = 0.42 | 35 ± 34.1 p = 0.72 | 2.3 ± 0.5 p = 0.66 | 2.3 ± 0.5 p = 0.89 |
| *Leptothorax canadensis* | DWD (n = 150) | 16.3 ± 6.4 p = 0.99 | 4.2 ± 3.7 p = 0.16 | 7.7 ± 16.7 p = 0.45 | 2.3 ± 0.5 p = 0.67 | 2.4 ± 0.6 p = 0.27 |
| | Stumps (n = 79) | 30.7 ± 13.4 p = 0.51 | 0.33 ± 0.1 p = 0.51 | 38.1 ± 32.8 p = 0.89 | 2.1[a] ± 0.4 p = 0.04 | 2.2 ± 0.9 p = 0.23 |
| *Myrmica alaskensis* | DWD (n = 24) | 14.5[a] ± 5.3 p = 0.048 | 6.2[a] ± 5.2 p = 0.04 | 2.1 ± 3.8 p = 0.22 | 2.6 ± 0.8 p = 0.48 | 2.8 ± 0.9 p = 0.12 |
| | Stumps (n = 36) | 30.3 ± 10.8 p = 0.84 | 0.35 ± 0.3 p = 0.11 | 50.5[a] ± 28.8 p = 0.01 | 2.4 ± 0.5 p = 0.23 | 2.5 ± 0.8 p = 0.52 |

DWD = downed woody debris; CWD = coarse woody debris.
[a] Denotes significance at $\alpha = 0.05$.

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## APPENDIX

Ant species collected in the subboreal spruce, moist cold (SBSmc) biogeoclimatic zone and subzone in British Columbia, Canada. Taxonomy follows Bolton (1995).

| FAMILY FORMICIDAE |
| --- |
| Subfamily Myrmicinae |
| *Leptothorax canadensis* Provancher |
| *Myrmica alaskensis* Wheeler |
| *Myrmica incompleta* Provancher |
| *Myrmica fracticornis* Forel |
| |
| Subfamily Formicinae |
| *Camponotus herculeanus* (Linnaeus) |
| *Camponotus noveboracensis* (Fitch) |
| *Formica fusca* group |
| *Formica accreta* Francoeur |
| *Formica neorufibarbis* Emery |
| *Formica rufa* group |
| *Formica obscuriventris* Mayr |
| *Formica sanguinea* group |
| *Formica aserva* Forel |
| *Polyergus breviceps* Emery |