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| Keyword: | Cerambycidae, vertical distribution, boreal forest, bark thickness, fire severity |

# Vertical distribution of three longhorned beetle species (Coleoptera: Cerambycidae) in burned trees of the boreal forest

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**Abstract:** This study aimed to characterize the vertical distribution of longhorned beetle larvae in burned trees of the eastern Canadian boreal forest. Black spruce and jack pine trees burned at three severity levels were cut, and 30-cm boles were collected from the ground up to a height of 9.45 m. Boles were debarked and dissected to collect insect larvae. Results show that the three most abundant longhorned beetle species were vertically segregated among burned jack pine and black spruce trees, but the section having the highest timber value was heavily infested by woodborer larvae. Larval density distribution of *Monochamus scutellatus scutellatus* and of *Acmaeops proteus proteus* could be linked with bark thickness, which also depends on fire severity. Lightly burned stands of black spruce were the most heavily infested and should be salvaged only if they are easily accessible and can thus be rapidly harvested and processed at the mill. More severely burned stands should be salvaged later as they will be less affected by woodborers, as should jack pine which is lightly infested compared with black spruce. The ecological role of stumps should be further investigated since they could still have an ecological value after salvage logging as *Arhopalus foveicollis* uses them specifically.

*Keywords*: Cerambycidae, vertical distribution, boreal forest, bark thickness, fire severity.

**Résumé:** Cette étude visait à caractériser la répartition verticale des larves de longicornes dans des arbres brûlés de la forêt boréale de l'est du Canada. Des épinettes noires et des pins gris brûlés à trois degrés de sévérité ont été coupés et des bûches de 30 cm ont été récoltées, à partir du sol jusqu'à une hauteur de 9.45 m. Les bûches ont été écorcées et disséquées pour récolter les larves d'insectes. Les résultats révèlent que les trois espèces les plus abondantes de longicornes montraient une ségrégation verticale sur le pin gris et l'épinette noire brûlés, mais que la section ayant la plus grande valeur commerciale était fortement infestée par des larves de longicorne. La densité larvaire de *Monochamus scutellatus scutellatus* et celle d'*Acmaeops proteus proteus* pourraient être liées à l'épaisseur de l'écorce, qui dépend elle aussi de la sévérité du feu. Les peuplements d'épinette noire légèrement brûlés étaient les plus infestés et devraient être récupérés seulement s'ils sont faciles d'accès et peuvent ainsi être rapidement récupérés et traités à l'usine. Les peuplements plus gravement brûlés devraient être récupérés plus tard, car ils sont moins affectés par les longicornes, de même que le pin gris qui est moins infesté que l'épinette noire. Le rôle écologique des souches devrait être étudié davantage car elles pourraient conserver une valeur écologique même après la coupe de récupération puisque *Arhopalus foveicollis* les utilisent spécifiquement.

*Mots-clés*: Cerambycidae, répartition verticale, forêt boréale, épaisseur de l'écorce, sévérité du feu.

# Introduction

Wildfire is considered a dominant natural disturbance in the Canadian boreal forest (Nappi et al. 2011). Between 2000 and 2010, an average of 1,784,590 ha of forest has burned annually in Canada (CIFFC 2011). Fire frequency and burned area have both increased over the last three decades (Soja et al. 2007). Post-fire ecosystems are characterized by large amounts of freshly killed trees that are considered high-quality deadwood, by higher air and soil temperatures, and by a reduction in competition between organisms, all of which favour several xylophagous insects (Wikars 1997).

Longhorned beetles (Coleoptera: Cerambycidae) are known for rapidly colonizing stands and attacking trees after fire (Boulanger et al. 2013). Some species, such as *Monochamus scutellatus scutellatus* (Say) (whitespotted sawyer), *Acmaeops proteus proteus* (Kirby) and *Arhopalus foveicollis* (Haldeman) are found in huge numbers during weeks following fire in the boreal forest of eastern Canada (Bélanger 2013). For example, in 2009, nearly 99% of the >15,000 longhorned beetle adults captured in a 665 ha burn near Chibougamau, Quebec, consisted of these three species (Berthiaume et al. 2010). The whitespotted sawyer is known to be one of the most damaging xylophagous insects after wildfire in the eastern Canadian boreal forest (Raske 1972). Its larvae develop successfully in a wide range of coniferous trees, including pines (*Pinus* spp.), spruces (*Picea* spp.), balsam fir (*Abies balsamea* (L.) Mill.) and, occasionally, tamarack (*Larix laricina* (Du Roi) K. Koch) (Wilson 1975). Larvae of the first two instars feed on the inner bark and do not reduce wood value (Rose 1957). However, third- and fourth-instar larvae of the whitespotted sawyer penetrate the sapwood and bore galleries reaching about 7.5 cm in depth (Bélanger et al. 2013). *Acmaeops p. proteus* is a small species breeding in various dead coniferous trees (Gardiner 1954). All larval instars of this species feed on the inner bark and pupation occurs in the soil (Gardiner 1957*b*). As its entire larval development occurs outside the sapwood, this species does not reduce wood value for the timber industry. Little is known about the habits and life cycle of *A. foveicollis,* but its larvae were reported to dwell in the base of dead pines and spruces (Knull 1946). Furthermore, larvae were also collected in burned trees 8 and 11 years after fire (Nappi et al. 2010), suggesting their long persistence in burns. Other species of the genus *Arhopalus* are recognized as important pests in New Zealand, where they attack freshly cut or burned pine trees (Suckling et al. 2001). In that country, Hosking and Bain (1977) reported the presence of *Arhopalus tristis* (then identified as *A. ferus*) in stumps and also on the main stem of standing burned trees, where they can completely destroy subcortical tissues in less than 6 months and then enter the sapwood. Nevertheless, it prefers feeding on the inner bark, where nitrogen and soluble carbohydrates are much more abundant than in sapwood (Hosking and Hutcheson 1979). This species completes its life cycle in 1 or 2 years in New Zealand, where the climate is mild, but it takes 3 to 4 years to do so in Europe (Wang and Leschen 2003).

Salvage logging of burned trees is increasing in most Canadian provinces as well as in many countries around the world in order to reduce the economic losses resulting from forest fires (Schmiegelow et al. 2006; Lindenmayer et al. 2008; Saint-Germain and Greene 2009). However, attacks by xylophagous insects, mainly longhorned beetles, rapidly reduce wood value; thus, trees must be salvaged and processed rapidly to limit lumber damage. For example, damage caused by *Monochamus* sp. can downgrade logs and reduce their economic wood value by as much as 30 to 35% after harvesting, in wood piled along forest roads (Wilson 1962). Furthermore, longhorned beetle galleries facilitate wood colonization by fungi, which can increase economic losses as much as the galleries themselves (Raske 1972). Therefore, salvage logging profitability is limited by the degradation of lumber quality resulting from attacks by these insects. To improve management of burned forests, we need to understand how these beetles use this resource. Recent studies have tried to understand the spatial distribution of longhorned beetles within burns shortly after fire (Saint-Germain et al. 2004; Boulanger et al. 2013). These studies also appraised the importance of attributes at the tree level, but nothing exists on the vertical distribution of longhorned beetles along the stem of burned trees. Vertical segregation along the tree bole has been reported for Scolytinae, with larger species being found at the base of trees, where the bark is thicker, and smaller species attacking branches in the canopy, where the bark is thinner (Price 1984). Since post-fire habitats are known to harbour large concentrations of some species of longhorned beetles (Boucher et al. 2012), we can hypothesize that competition may occur and influence the vertical larval distribution of these species.



Numerous studies carried out on other insects have shown spatial segregation of some guilds of arthropods using the same habitat or prey (O'Neill 1967; Fitzgerald 1973; Price 1984). Using trunk-window traps, Berthiaume et al. (2010) characterized the spatial distribution of adult *M. s. scutellatus*, *A. p. proteus* and *A. foveicollis* on black spruce (*Picea mariana* Mill.) and jack pine (*Pinus banksiana* Lamb.) across a burn severity gradient. They suggested that a spatial segregation was apparent between *M. s. scutellatus* and *A. foveicollis*, the first being mostly associated with black spruce, without particular link with fire severity, while the latter was associated with severely burned jack pine.

The aim of our study was to characterize the vertical larval distribution of the three most abundant longhorned beetle species (*M. s. scutellatus*, *A. p. proteus* and *A. foveicollis*) after fire in the northern boreal forest. Consequently, we used bole dissection at the laboratory. Specifically, larval density was measured at different heights along the stem of black spruce and jack pine and across three degrees of burn severity.

## Materials and methods

### Study area

Field sampling was conducted in the Chibougamau area, in northern Quebec. The territory belongs to the western spruce moss subdomain. During spring 2010, three burns that occurred in 2009 were selected based on their proximity and forest composition: burn #1 covered 73 ha (49°56'N; 75°25'W), burn #2 covered 665 ha (50°06'N; 75°07'W) and burn #3 covered 9,948 ha (50°32'N; 75°49'W). Burn #2 was the same burn in which Berthiaume et al. (2010) caught >15,000 longhorned beetles in 2009. Salvage logging was carried out only in burn #3, but operations were stopped rapidly because of severe woodborer damage. Stands from these three burns were dominated by black spruce, with jack pine and balsam fir as companion species.



### Vertical distribution

In order to characterize the vertical distribution of longhorned beetles, we estimated their larval density along the stem of black spruce and jack pine across three burn severity classes (high, moderate or low severity), based on the classification used by the Ministère des forêts, de la faune et des parcs du Québec (MFFPQ 2013). The bark of highly burned trees was charred on its entire length and twigs and needles were absent because they had been entirely consumed by fire. The bark of moderately burned trees was charred at the base, but twigs were still present. Immediately after fire, the needles of those trees were still present but scorched by heat. Finally, the bark of lightly burned trees was charred at the base, at least on one side, not higher than breast height, and the trees were still alive immediately after fire, with only a few needles scorched by heat. Most of those trees died in the following months and, as a result, all trees cut in spring 2010 were dead.

In each burn, plots dominated by each tree species at a given burn severity (total of six plots per burn) were selected using the ecoforest and fire severity maps produced by the Ministère des forêts, de la faune et des parcs du Québec. In late May 2010, plots were validated, and those that did not fit these criteria (tree composition and fire severity) were simply discarded and replaced by other randomly selected plots. In each plot, four trees with a diameter at breast height (DBH) ranging between 15 and 20 cm were selected and felled (for a total of 72 trees for the entire sampling plan). For each tree, seven 30-cm bole sections were collected at different heights, starting from the ground: 0-0.30 m, 0.60-0.90 m, 1.30-1.60 m, 3.15-3.45 m, 5.15-5.45 m, 7.15-7.45 m and 9.15-9.45 m. Overall, 504 bole sections were collected, identified (burn #, tree species, burn severity class, tree number and height) and brought back to the Laurentian Forestry Centre of Natural Resources Canada in Quebec City. Bole sections were kept at 4°C to prevent insect emergence until further investigation. For each bole section collected, bark thickness was measured at four equidistant points along the log circumference using an electronic digital calliper (Mastercraft) and the diameter was measured with a tape. Since the bark protects the phloem/cambium interface from fire, bark thickness was used as a proxy for food quality for the three longhorned beetles studied. Bole sections were then debarked, and larvae were collected and preserved in 70% ethyl alcohol until identification. Only larvae of *M. s. scutellatus*, *A. p. proteus* and *A. foveicollis* were identified and counted. We used our collections obtained from rearing performed in previous studies to confirm identifications of *A. p. proteus* and *M. s. scutellatus* larvae. However, in jack pine, some larvae of *Monochamus mutator* Leconte may have been mixed with those of *M. s. scutellatus.* Current knowledge does not allow to distinguish larvae of these two species (Craighead 1923; Gardiner 1957*a*) and *M. mutator* is specific to pines (Akbulut and Stamps 2013; Boucher et al. 2013). However, among the >15,000 longhorned beetles caught in Burn #2 in 2009 (see Berthiaume et al. 2010), only four adult specimens belonged to *M. mutator* compared with 7763 for *M. s. scutellatus*. Also, based on the trap captures reported by Berthiaume et al. (2010), we assumed that most Aseminae larvae, which were identified at the subfamily level using Craighead (1923), belonged to *A. foveicollis* (3651 adults caught). Only 13 other Aseminae were caught (7 *Asemum striatum* (Linneaeus) and 6 *Tetropium cinnamopterum* Kirby) and, according to Boucher et al. (2013), these two species are not associated with burned forests, contrary to *A. foveicollis*. Larvae of *A. foveicollis* were not described in Craighead (1923), but they largely differed from the two other cerambycid species found in our study by being very small (2-3 mm).

We also counted *Monochamus* entrance holes on each bole section. All woodborer galleries were excavated using chisels in order to extract the buried larvae when less than five entrance holes were found on a bole section. A minimum of five galleries were excavated when <20 entrance holes were found on a bole section; when >20 entrance holes were found, 25% of the galleries were excavated. Thereafter, the ratio of occupied holes (larvae found/excavated holes) was used to estimate the number of buried larvae. Because only *Monochamus* larvae were found inside the galleries (only a few *A. foveicollis* larvae had begun digging into the sapwood, and these galleries were small and shallow), this estimate was added to the total number of larvae of this taxa found on each bole section to calculate its larval density.

We estimated the water content of each tree sampled using a 3.5-cm disk collected at breast height (1.3 m). Disks were weighed and then oven dried at 65°C until their dried weight stabilized, which required a minimum of 48 h. Water content was calculated as: water content = [fresh weight – dry weight] / fresh weight x 100 (Akbulut and Linit 1999).

**Statistical analyses**

We used three factor generalized linear mixed models (GLMM) to determine how tree species, burn severity and height in the tree influenced larval density (number of larvae/bole surface area) of each of the three longhorned beetle species. Bark thickness was also compared using three-factor GLMM with bole diameter as a covariable. In all GLMM, fixed effects were tree species, burn severity and height in the tree while random effects were burns and trees. Water content was compared with a two-factor GLMM with tree species and burn severity as fixed effects and burns and trees as random effects. Water content means were compared using Tukey's contrasts. In all GLMM, assumptions of normality and variance homogeneity were checked with model residuals and were respected, except for bark thickness which was log transformed.



To determine if bark thickness influenced larval density of each longhorned beetle species in the bole sections, linear regressions were used for each tree species and burn severity separately. To determine if water content influenced larval density of the three longhorned beetle species, we also used linear regressions with bark thickness as a covariable for each tree species. Bark thickness and longhorned beetle larval density at breast height (1.3 m) were used in these analyses because water content was estimated only from wood disks collected at this height, except for *A. foveicollis* for which larval density and bark thickness were taken from the stump and water content was estimated from the disk collected at breast height on the same tree. The relationship between water content and bark thickness was tested using simple linear regression on measures done on boles and disks collected at DBH on each tree.

To test if there was any interaction in bole sections between *M. s. scutellatus* and *A. p. proteus*, we extracted the residuals of their previous respective models and used a linear regression to test if they were related (Saint-Germain et al. 2004). The same approach was used to determine if there was any interaction between *A. foveicollis* and *M. s. scutellatus* or *A. p. proteus* in the stumps.

All GLMM analyses were done using the “lme” function in the “nlme” package of the R software (R.2.15.0), while linear regressions were done using the “lm” function in the “stats” package.



# Results

## Longhorned beetle larval distribution in trees

A total of 9,549 larvae were collected in boles, and 8,315 of them were Cerambycidae larvae. From this number, *M. s. scutellatus* (1,153 larvae), *A. p. proteus* (5,019 larvae) and *A. foveicollis* (2,031 larvae) represented 98.7% of the collected Cerambycidae larvae. Larval density of *M. s. scutellatus* was significantly influenced by height in interaction with both tree species ($F_{1, 423} = 9.42$, $p = 0.0023$; Table 1) and burn severity ($F_{2, 423} = 46.97$, $p < 0.0001$; Table 1). Furthermore, tree species in interaction with burn severity also influenced larval density in *M. s. scutellatus* ($F_{2, 64} = 5.24$, $p = 0.0077$; Table 1). For both tree species, larval density decreased as a function of height in trees moderately or highly burned, while it tended to increase in trees with low burn severity (Fig. 1). Larval density also tended to decrease faster as a function of height in moderately or highly burned jack pine than in black spruce; it even fell to less than 1 larva/$m^2$ at 5 m and higher on highly burned jack pine. Moreover, lightly burned jack pine tended to harbour much higher larval density further up along the bole compared with trees burned at moderate or high severity, which was not as apparent in black spruce.

A significant interaction between tree species, burn severity and height ($F_{2, 423} = 5.70$, $p = 0.0036$; Table 1) was observed for larval density of *A. p. proteus*. Larval density of this species was lower in jack pine than in black spruce, and it decreased with tree height for all burn severities in jack pine, though slightly less at a low burn severity, whereas it remained almost the same in black spruce (Fig. 2).

*Arhopalus foveicollis* larvae were only found in the stumps (0-0.30 m); thus, height was removed from the analysis. Tree species in interaction with burn severity significantly influenced *A. foveicollis* larval density ($F_{2, 64} = 3.20$, $p = 0.0473$; Table 1), which was much higher in jack pine than in black spruce. Jack pine stumps burned at low severity maintained higher larval density than those moderately or severely burned, whereas it remained low and constant for each burn severity in black spruce (Fig. 3).

No significant relationship was found between residuals of larval density of *M. s. scutellatus* and *A. p. proteus* ($t = 0.345$, $df = 500$, $p = 0.7302$). Likewise, there were no significant relationships between residuals of larval density of *A. foveicollis* and those of *M. s. scutellatus* ($t = 0.700$, $df = 71$, $p = 0.4865$) and *A. p. proteus* in the stumps ($t = -0.412$, $df = 71$, $p = 0.6812$).

**Bark thickness and water content**

Bole section diameter, which was used as a covariable in the model that aimed to determine the effects of tree species, burn severity and height on bark thickness, had a significant effect ($F_{1, 407} = 78.25$, $p < 0.0001$; Table 1). A significant interaction was also detected between tree species, burn severity and height ($F_{2, 407} = 4.01$, $p = 0.0188$; Table 1) on bark thickness. Bark was thicker in black spruce than in jack pine, and it decreased with bole height in both tree species, but not at the same rate. In jack pine, bark thickness decreased up to 5.15 m and remained rather stable higher on the stem (nearly 1.5 mm thick); in black spruce, it decreased up to 3.15 m, remained stable and then slightly dropped again at 9.15 m (almost always >1.5 mm thick; Fig. 4). Furthermore, bark was thicker on trees with low burn severity, but the difference with the other burn severities was greater in jack pine than in black spruce. Bark thickness was similar at moderate and high burn severity in black spruce while it was slightly different up to 3.15-m in jack pine, where the bark was thicker at moderate burn severity. We also found significant effects of burn severity on tree water content ($F_{2, 62} = 17.11$, $p < 0.0001$; Table 1), which was higher at low than at moderate or high burn severity (Fig. 5).

The relationship between larval density and bark thickness differed for the three longhorned beetle species depending on tree species and burn severity, but it was always positive when significant (Table 2). However, because *A. foveicollis* larvae were only found in stumps, it provided few data to test the relationship for each burn severity in each tree species. Thus, the relationship was only tested for the two tree species. Bark thickness of black spruce had no effect on *A. p. proteus* and *A. foveicollis*, but the higher larval density of these two species was significantly related with bark thickness in jack pine; this was also true at all burn severities for *A. p. proteus* (Table 2). *Monochamus s. scutellatus* larvae were more abundant in boles with thicker bark in both tree species, but only for trees that burned at moderate or high severity (Table 2). Bark thickness of lightly burned trees in both tree species had no significant effect on the larval density of *M. s. scutellatus* (Table 2).

Water content of trees had no significant effect on larval density of any of the three longhorned beetle species (Table 3). Bark thickness, which was used as a covariable in the models, significantly affected larval density of *M. s. scutellatus* in black spruce ($t = 5.014$, $p < 0.001$), but not in jack pine (Table 3). Water content was significantly related to bark thickness in both tree species, but more strongly so in jack pine than in black spruce (Fig. 6).

## Discussion

To our knowledge, this is the first study to appraise the vertical distribution of longhorned beetle larvae in burned trees of the boreal forest. While *M. s. scutellatus* and *A. p. proteus* larvae were found at every height, with varying densities, *A. foveicollis* larvae were spatially restricted to tree stumps. Our results also show that the three longhorned beetles were segregated among burned jack pine and black spruce trees. *Monochamus s. scutellatus* and *A. p. proteus* larvae were 2-3 times more abundant in black spruce than in jack pine, the reverse being true for *A. foveicollis* larvae, which were 10 times more abundant in jack pine than in black spruce.

Larval density of *M. s. scutellatus* remained similar or even increased with height (mostly in jack pine) in trees burned at low severity, but it decreased rapidly with height in trees burned at moderate or high severity. This distribution could be linked with bark thickness as *M. s. scutellatus* larval density was correlated with bark thickness in both tree species, but only for trees burned at moderate or high severity. This is in agreement with the study of Boulanger et al. (2013) who observed that bark thickness had no effect on whitespotted sawyer occurrence at low burn severity while it had a positive effect in severely burned trees, as seen with height in both tree species in our study. In fact, bark thickness was reduced on trees burned at moderate or high severity. Bark thickness measured at 9 m along the bole of trees burned at low severity was similar to that measured at 3 m on trees burned at moderate or high severity. As *M. s. scutellatus* larval density decreased rapidly with increasing height in trees burned at moderate or high severity compared with those burned at low severity, 3 m appears to be the height at which bark thickness may become a limiting factor for *M. s. scutellatus* oviposition and/or larval survival when burn severity reaches moderate severity. On burned jack pine trees, which had a thinner bark than black spruce, almost no *M. s. scutellatus* larvae were observed at ≥5 m on trees burned at moderate or high severity. Bark thickness varied very lightly as expressed by standard errors around the mean, suggesting that 1 mm might be a threshold to allow *Monochamus* oviposition and/or larval survival on jack pine. Zhang *et al*. (1993) observed that emergence hole density of *Monochamus sutor* L. was highest at a height of 2-4 m, and then decreased with height on burned dahurian larch (*Larix dahurica* Turcz. ex Trautv.) and Scots pine (*Pinus sylvestris* var. *mongolica* Litv.) as the bark became thinner. Foit (2010) identified bark thickness as the most important factor for explaining community composition of saproxylic beetles in Scots pine in the Czech Republic. Bark thickness in itself might not be a key factor, but rather an indicator of food quality for longhorned beetles. Likewise, water content followed the same trend, being higher in trees burned at low severity than in those burned at moderate or high severity. In fact, water content is related to bark thickness for both tree species and thus bark thickness appears to be a good proxy for it, as well as, probably, the overall food quality for xylophagous insects.

Larval density of *A. p. proteus* remained similar at various heights on black spruce for all burn severities, but it decreased on jack pine for all burn severities, and more rapidly so on jack pine trees burned at moderate or high severity. This distribution could also be linked with bark thickness as larval density of *A. p. proteus* was correlated with bark thickness of jack pine for all burn severities. However, *A. p. proteus* larvae seem less sensitive to this variable than *M. s. scutellatus* larvae since no effect of burn severity was observed in black spruce. If bark thickness is an indicator of food quality, it suggests that the development requirements of *A. p. proteus* larvae could be lower than those of the much larger whitespotted sawyer. This could explain the vertical segregation observed between these species on moderate and highly burned black spruces. Such vertical distribution, where smaller species are found in higher parts of the trees while larger ones are in lower parts, has been reported for Scolytinae and could be related to bark thickness (Price 1984). On burned jack pine, which has a thinner bark, 3 m appears to be the height at which bark thickness becomes a limiting factor for *A. p. proteus* oviposition or survival when moderate burn severity is reached. Larval density continues to decrease, but at a much slower rate, on jack pines burned at low severity. However, no threshold for bark thickness was reached to stop *A. p. proteus* oviposition or survival as seen for *M. s. scutellatus*, strengthening the idea of lower development requirements for smaller species. As for the whitespotted sawyer, Boulanger et al. (2013) also reported that bark thickness was one of the most important variables affecting neonate abundance of *A. p. proteus* on severely burned black spruces. Our study corroborated the effect of bark thickness but only in jack pine, no effect being observed in black spruce. However, our study involved counting larvae found after debarking boles collected at different heights, while Boulanger et al. (2013) counted insects emerged from encaged boles collected only at breast height. Thus, black spruces burned at high severity might have been colonized (i.e egg laying and larval development in our study) to the same level as trees less severely burned, but lower food quality may have reduced larval survival in trees severely burned (as in the Boulanger et al. 2013 study).

Larvae of *A. foveicollis* were exclusively found at the stump level and mainly on jack pine. This differs from Nappi et al. (2010) who found no difference in larval density between jack pine and black spruce 8 years after fire. Regarding within-tree distribution, a study in which black spruce stumps/roots and boles from snags were placed in rearing conditions found that *A. foveicollis* adults emerged only from stumps/roots (Jeffrey et al. pers. comm). Together with Nappi et al. (2010), who collected their boles 0-1 m above the ground, these two Quebec boreal studies support our findings that *A. foveicollis* was exclusively found at the stump level. Knull (1946) also reported larvae of this species at the base of dead pines and spruces. While several *Arhopalus* species are known to dwell in stumps and roots (Lindhe et al. 2010), it is the first time, to our knowledge, that a species from this genus is restricted to this part of a tree. In the Czech Republic, *A. rusticus* was mainly found in the first section (from 0 to about 1 m high) of recently killed Scots Pine, but the insect was also found in the other three bole sections that follow (Foit 2010). Nappi et al. (2010) suggested that *A. foveicollis* may have a long life cycle as they found larvae in burned trees 8 and 11 year after fire. Species with long life cycles should benefit from living in a stable habitat. In a recent study carried out along a 15-year postfire chronosequence, water content was much less variable in black spruce stumps than in snags at breast height, which dried faster (Jeffrey 2013). Moreover, lightly burned jack pines had higher larval density than those burned at moderate or high severity. This suggests that *A. foveicollis* females may prefer colonizing habitats of higher quality as those will provide better conditions for a longer time. However, these differences in larval density may have resulted from higher larval mortality in severely burned trees. Further investigation is needed to confirm these hypotheses. Monitoring temporal changes in water content and in wood nutritional quality and determining how it influences Cerambycid development and survival would improve our understanding of woodborer dynamics after wildfire and would result in improved forest management.

Results of this study show that no part of black spruce or jack pine stems were free from *M. s. scutellatus* larvae 1 year after fire, limiting the economic benefits of any vertical salvage logging. In fact, the section having the highest timber value (i.e., the first few meters) is heavily infested by woodborer larvae. In order to promote sustainable management in burned forests, salvage logging should maximize the profitability of logging operations while maintaining biodiversity and ecological functions in the ecosystem (Nappi et al. 2004). Thus, lightly burned stands of black spruce, which are the most heavily infested, should be salvaged only if they are easily accessible and can thus be rapidly harvested and processed at the mill. Stands that are less accessible would not be profitable and should be left for their ecological value for biodiversity. More severely burned stands should be salvaged later as they will be less affected by woodborers, as should jack pine which is lightly infested compared with black spruce. Finally, the ecological role of stumps after salvage logging should be further investigated since they could still have an ecological value if they host *Arhopalus foveicollis*, a species that uses this part of the tree specifically, and which is also a prey of the black-backed woodpecker, *Picoides arcticus* (Ibarzabal, pers. obs.).

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**Table 1.** Effects of tree species, burn severity and height on the larval density of *Monochamus scutellatus scutellatus*, *Acmaeops proteus proteus* and *Arhopalus foveicollis*, and on bark thickness and water content of burned trees using generalized linear mixed models (GLMM) ($\alpha = 0.05$).

| | Variable | NumDF | DenDF | F | *p* |
|---|---|---|---|---|---|
| ***Monochamus s. scutellatus*** | Tree species (TS) | 1 | 64 | 99.32 | **<0.0001** |
| | Burn severity (BS) | 2 | 64 | 15.57 | **<0.0001** |
| | Height (H) | 1 | 423 | 19.84 | **<0.0001** |
| | TS*BS | 2 | 64 | 5.24 | **0.0077** |
| | TS*H | 1 | 423 | 9.42 | **0.0023** |
| | BS*H | 2 | 423 | 46.97 | **<0.0001** |
| | TS*BS*H | 2 | 423 | 0.81 | 0.4476 |
| ***Acmaeops p. proteus*** | Tree species | 1 | 64 | 59.78 | **<0.0001** |
| | Burn severity | 2 | 64 | 0.01 | 0.9863 |
| | Height | 1 | 423 | 40.82 | **<0.0001** |
| | TS*BS | 2 | 64 | 6.11 | **0.0037** |
| | TS*H | 1 | 423 | 33.36 | **<0.0001** |
| | BS*H | 2 | 423 | 2.57 | 0.0780 |
| | TS*BS*H | 2 | 423 | 5.70 | **0.0036** |
| ***Arhopalus foveicollis*** | Tree species | 1 | 64 | 39.05 | **<0.0001** |
| | Burn severity | 2 | 64 | 0.25 | 0.7777 |
| | TS*BS | 2 | 64 | 3.20 | **0.0473** |
| **Bark thickness** | Tree species | 1 | 64 | 91.21 | **<0.0001** |
| | Burn severity | 2 | 64 | 19.30 | **<0.0001** |
| | Height | 1 | 407 | 893.54 | **<0.0001** |
| | Diameter (Covar.) | 1 | 407 | 78.25 | **<0.0001** |
| | TS*BS | 2 | 64 | 2.60 | 0.0823 |
| | TS*H | 1 | 407 | 92.53 | **<0.0001** |
| | BS*H | 2 | 407 | 4.07 | **0.0177** |
| | TS*BS*H | 2 | 407 | 4.01 | **0.0188** |
| **Water content** | Tree species | 1 | 62 | 2.77 | 0.1013 |
| | Burn severity | 2 | 62 | 17.11 | **<0.0001** |
| | TS*BS | 2 | 62 | 1.57 | 0.2160 |

**Table 2.** Summary of linear regression aiming to predict the larval density of *Monochamus scutellatus scutellatus*, *Acmaeops proteus proteus* and *Arhopalus foveicollis* as a function of bark thickness for each tree species burned at various severities (α = 0.05).

| | Tree species | Burn severity | *t* | $r^2$ | *p* |
|---|---|---|---|---|---|
| ***Monochamus s. scutellatus*** | Black spruce | Low | 0.796 | 0.008 | 0.428 |
| | | Moderate | 5.371 | 0.265 | **<0.001** |
| | | High | 3.780 | 0.160 | **<0.001** |
| | Jack pine | Low | -1.853 | 0.041 | 0.068 |
| | | Moderate | 5.025 | 0.247 | **<0.001** |
| | | High | 6.039 | 0.308 | **<0.001** |
| ***Acmaeops p. proteus*** | Black spruce | Low | -0.065 | <0.001 | 0.949 |
| | | Moderate | 0.077 | <0.001 | 0.939 |
| | | High | -0.917 | 0.011 | 0.362 |
| | Jack pine | Low | 2.064 | 0.051 | **0.042** |
| | | Moderate | 4.330 | 0.196 | **<0.001** |
| | | High | 6.403 | 0.333 | **<0.001** |
| ***Arhopalus foveicollis*** | Black spruce | All | 1.168 | 0.041 | 0.251 |
| | Jack pine | All | 2.207 | 0.129 | **0.034** |

**Table 3.** Summary of linear regression aiming to predict the larval density of *Monochamus scutellatus scutellatus*, *Acmaeops proteus proteus* and *Arhopalus foveicollis* as a function of water content, with bark thickness as a covariable, in black spruce and jack pine bole sections collected at breast height (1.3 m) (α = 0.05).

| | Tree species | Variable | t | *p* |
|---|---|---|---|---|
| ***Monochamus s. scutellatus*** | Black spruce | Water content | 0.526 | 0.603 |
| | | Bark thickness | 5.014 | **<0.001** |
| | Jack pine | Water content | 0.356 | 0.724 |
| | | Bark thickness | 0.578 | 0.568 |
| ***Acmaeops p. proteus*** | Black spruce | Water content | 0.885 | 0.383 |
| | | Bark thickness | -0.317 | 0.754 |
| | Jack pine | Water content | -0.425 | 0.674 |
| | | Bark thickness | 0.927 | 0.361 |
| ***Arhopalus foveicollis*** | Black spruce | Water content | -0.015 | 0.988 |
| | | Bark thickness | 0.913 | 0.369 |
| | Jack pine | Water content | 0.385 | 0.703 |
| | | Bark thickness | 1.826 | 0.077 |

## Figure captions

**Fig. 1.** Average number of larvae/$m^2$ (mean ± SE) of *Monochamus scutellatus scutellatus* as a function of height on the tree and burn severity in A) black spruce and B) jack pine.

**Fig. 2.** Average number of larvae/$m^2$ (mean ± SE) of *Acmaeops proteus proteus* as a function of height on the tree and burn severity in A) black spruce and B) jack pine.

**Fig. 3.** Average number of larvae/$m^2$ (mean ± SE) of *Arhopalus foveicollis* as a function of burn severity on black spruce and jack pine

**Fig. 4.** Average bark thickness (mean ± SE) as a function of height on the tree and burn severity on A) black spruce and B) jack pine.

**Fig. 5.** Average water content (mean ± SE) as a function of burn severity. Letters indicate significant differences obtained by multiple comparisons of means with Tukey's contrasts.

**Fig. 6**. Relationship between water content and bark thickness in burned black spruce (A) and burned jack pine (B).

Figure 1

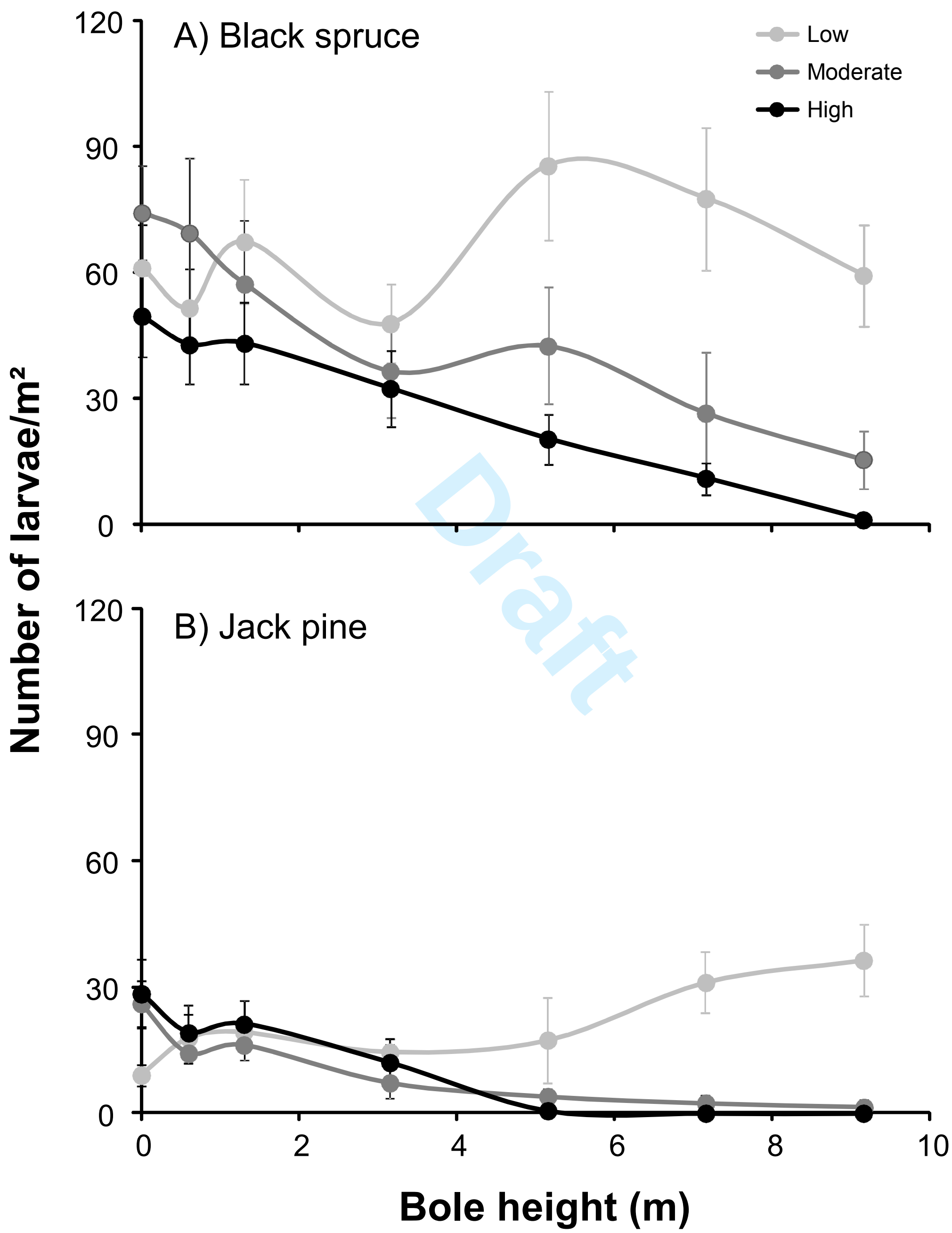

A) Black spruce
B) Jack pine
Low
Moderate
High
Number of larvae/m²
Bole height (m)
0
30
60
90
120
0
2
4
6
8
10
Draft

Figure 2

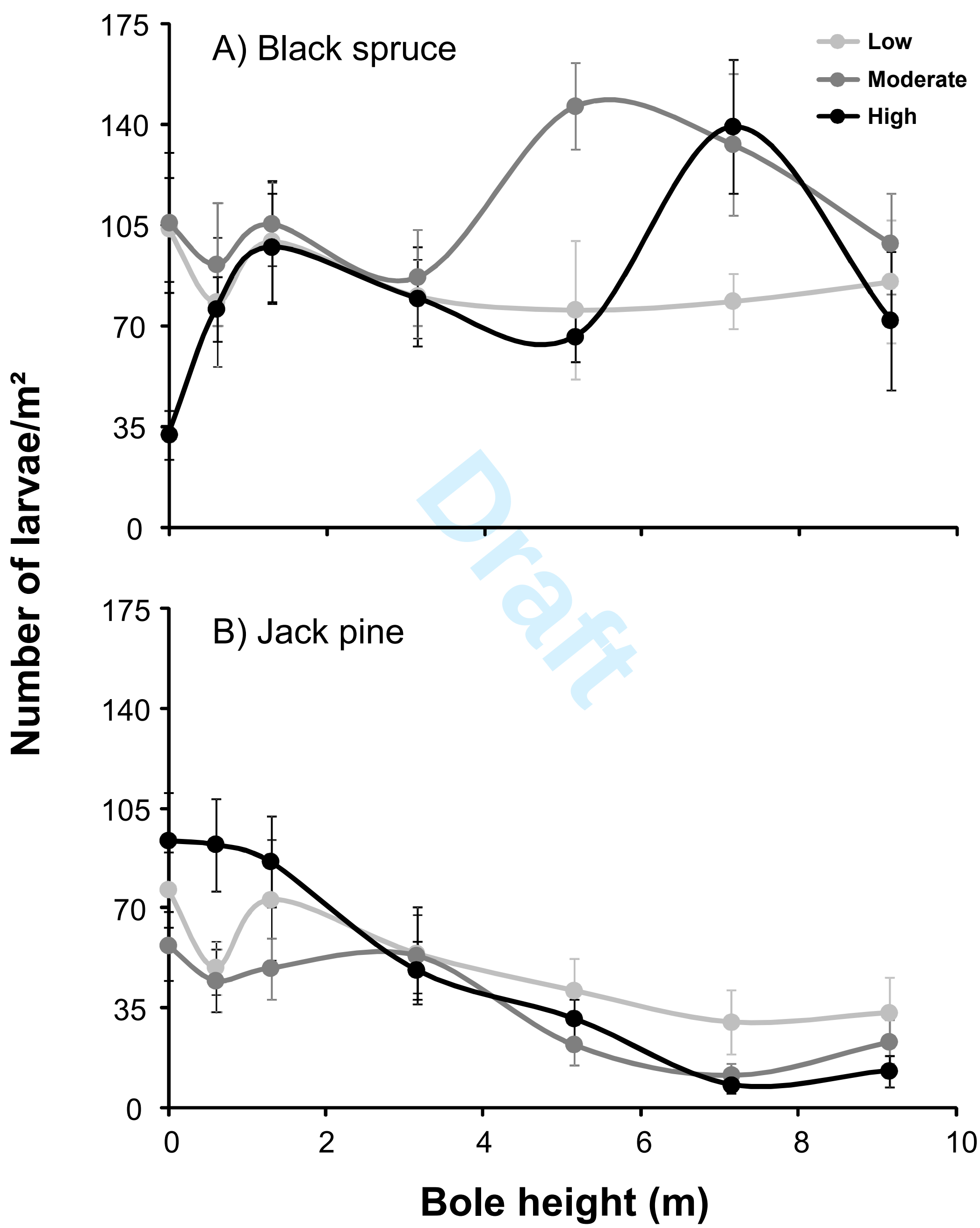

A) Black spruce
B) Jack pine
Low
Moderate
High
175
140
105
70
35
0
0
2
4
6
8
10
Number of larvae/m²
Bole height (m)

Figure 3

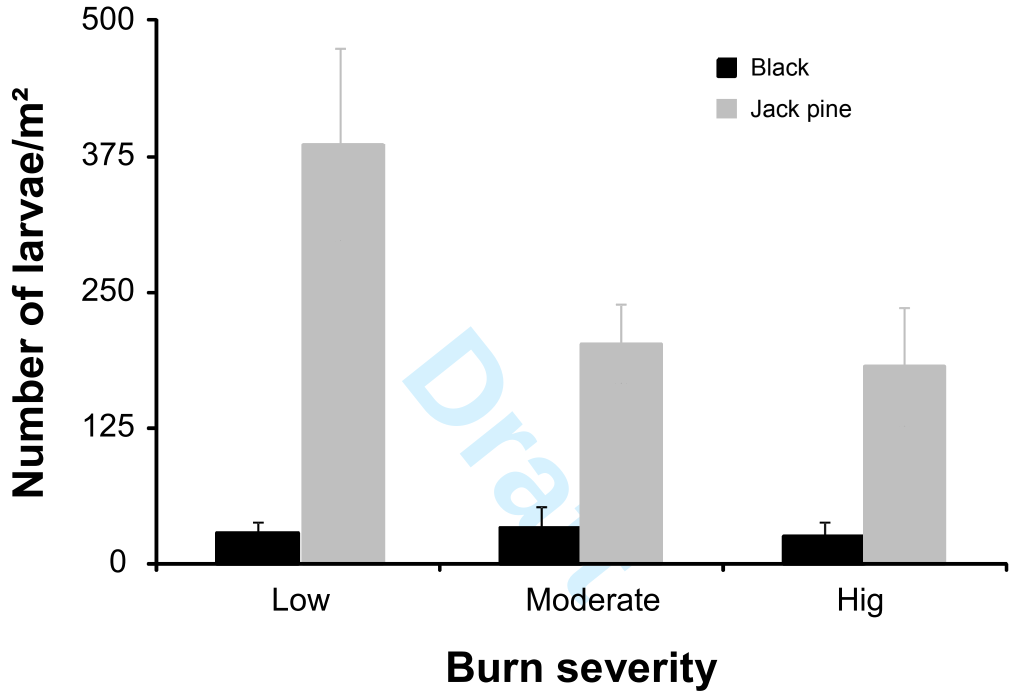

500
375
250
125
0
Number of larvae/m²
Black
Jack pine
Low
Moderate
Hig
Burn severity
Draft

Figure 4

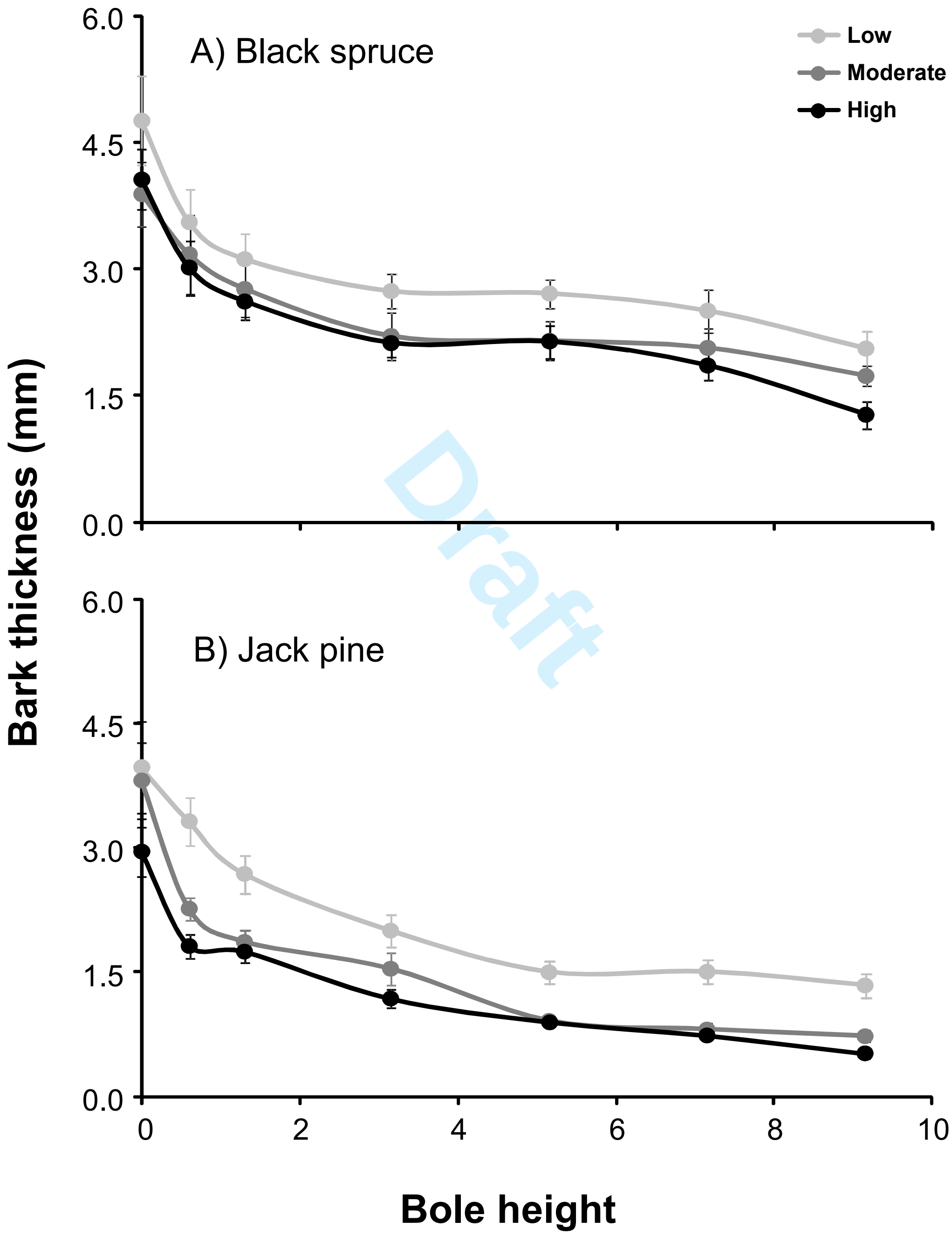

A) Black spruce
B) Jack pine
Low
Moderate
High
Bark thickness (mm)
Bole height
6.0
4.5
3.0
1.5
0.0
0
2
4
6
8
10

Figure 5

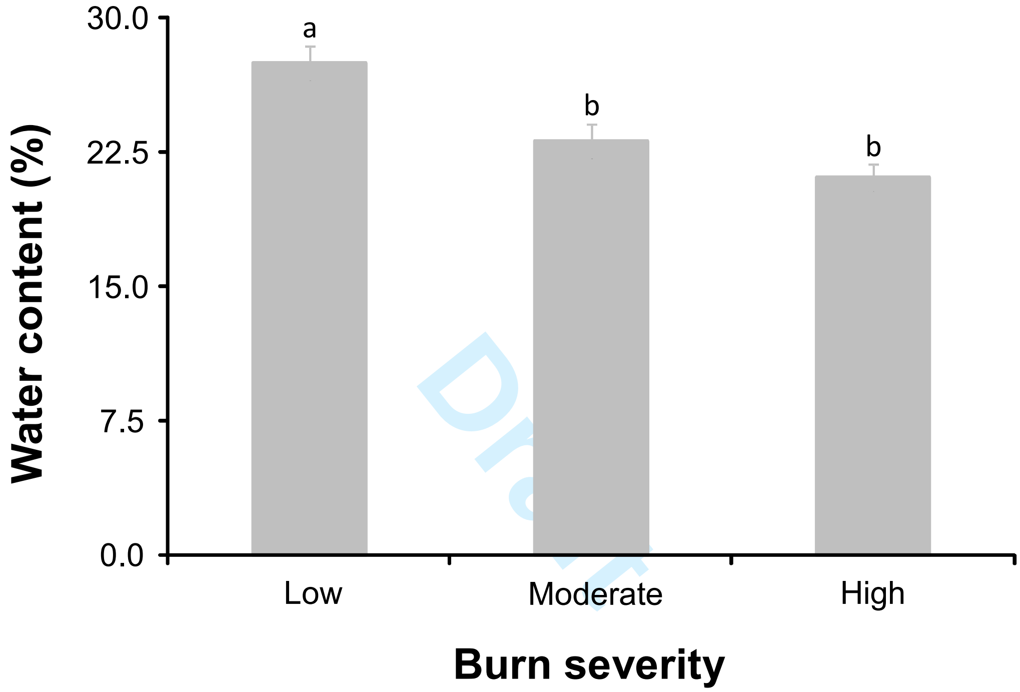
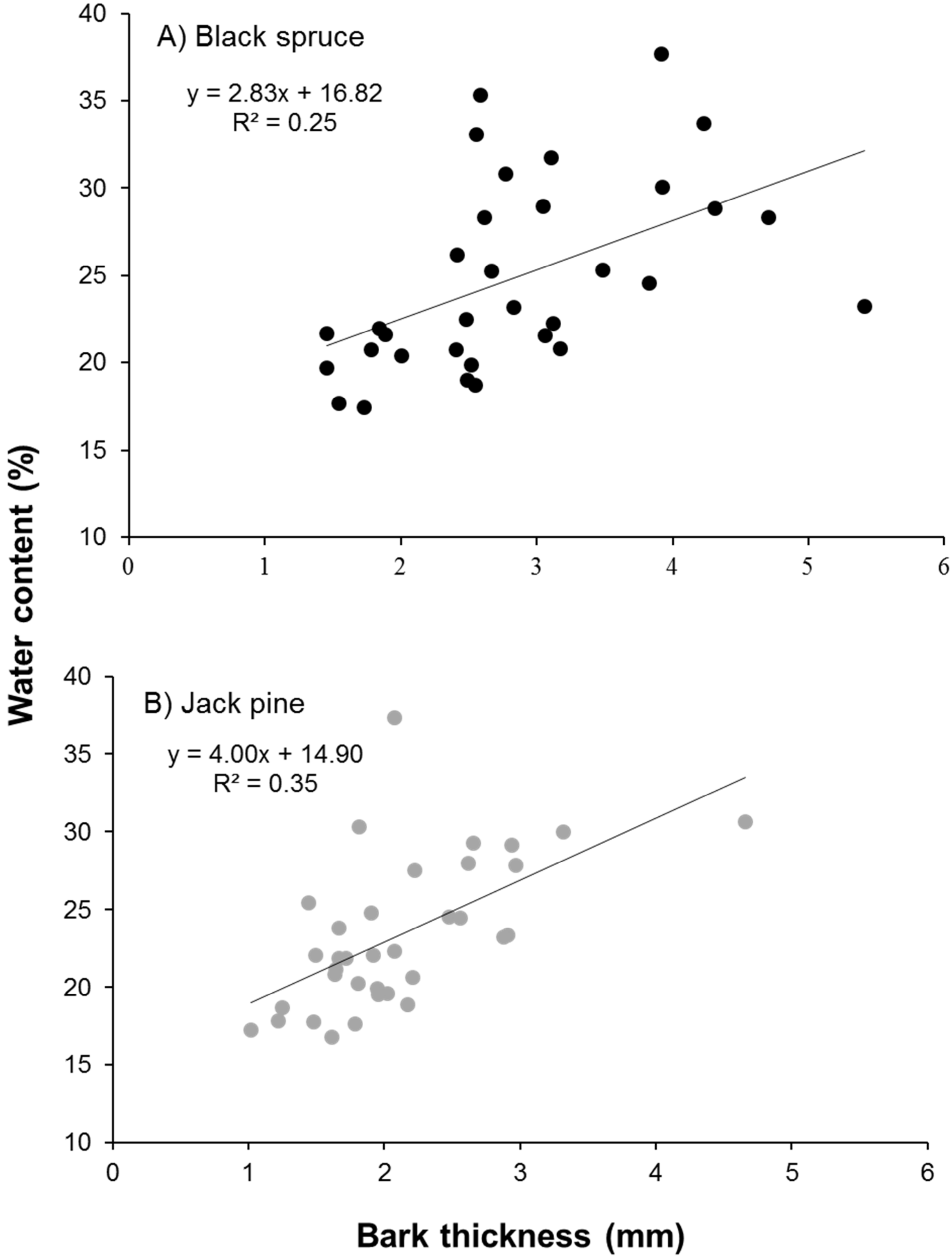

30.0
22.5
15.0
7.5
0.0
a
b
b
Water content (%)
Low
Moderate
High
Burn severity

Figure 6


A) Black spruce
y = 2.83x + 16.82
R² = 0.25
B) Jack pine
y = 4.00x + 14.90
R² = 0.35
Water content (%)
Bark thickness (mm)
40
35
30
25
20
15
10
0
1
2
3
4
5
6