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Response of saproxylic insect communities to logging history, tree species, stage of decay, and wood posture in the central Nearctic boreal forest

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Abstract Saproxylic insect assemblages are essential functional components of forest ecosystems that can be affected by forest management. We used a split-plot ANOVA design to analyze differences in selected saproxylic insects (all arthropod orders and dipteran and parasitic hymenopteran families) emerging from dead wood of sites with different logging histories (horse-logged, mechanically-logged and unlogged), tree species (*Populus* and *Picea*), stage of decay (early- and late-decay stages) and posture (standing and downed logs) in the boreal forest of central Canada. No clear effects of logging history were seen for the studied taxa; however, interaction between logging history and other dead wood features was apparent. Cecidomyiidae consistently emerged more from *Populus* than from *Picea* dead wood. Most of the studied saproxylic families were more abundant in late-decay than in early-decay wood. Dipterans of the Cecidomyiidae, Ceratopogonidae, Empididae, Mycetophilidae and Sciariidae families, and hymenopterans of the Diapriidae and

Ichneumonidae families were significantly more abundant in downed than in standing dead wood. In contrast, Mymaridae was most abundant in standing dead wood. Our study provides evidence that some insects at high taxonomic levels respond differently to dead wood quality, and this could inform future management strategies in the boreal forest for the conservation of saproxylic fauna and their ecological functions.

Keywords Boreal forest · Dead wood quality · Forest harvesting · High-level taxa · Saproxylic insects

Introduction

Dead wood provides unique habitat for a range of specialized organisms (Harmon et al. 1986; Jonsson and Krus 2001). The highly diverse saproxylic fauna, dependent solely on dead wood, is likely one of the most threatened functional groups in managed forests due to its distinct niche specialization (Siitonen 2001; Grove 2002). Forest management that reduces the amount and diversity of woody debris can have significant negative impacts on saproxylic insect communities as evidenced in both Palearctic (e.g. Martikainen et al. 1999; Väisänen et al. 1993) and Nearctic boreal forests (e.g. Spence et al. 1996; Hammond et al. 2004). For example, there is evidence that industrial forestry and forest degradation has resulted in the decline of saproxylic diversity and local extinction for some species in northern Europe (e.g., Siitonen 2001; Seibold et al. 2015) and North America (e.g. Boucher et al. 2012). Stump harvesting for bioenergy can detrimentally affect saproxylic insect diversity (Ols et al. 2013). Sustainable forest management must be based on sound understanding of the dynamics of dead wood availability,

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and on the implications of variation in dead wood quality and quantity for biodiversity. Forest management at the landscape scale and the maintenance of dead wood at the local scale, are required to sustain saproxylic assemblages and their ecological functions (e.g. Mason and Zapponi 2015; Kraut et al. 2016).

A fundamental difference between European and North American boreal forests, is that industrial harvesting in the North American boreal forest has been extensive only within the last century. In central Canada, the mature boreal forests were cut by either horse-logging (before 1963 in northeastern Ontario) or, subsequently, mechanized-logging. Although both harvesting methods resulted in substantial removal of wood through clear-cutting, horse-logging had less impact on the forest floor and was followed by more rapid regeneration (Carleton and MacLellan 1994). The net effect of mechanized logging has been to increase the abundance of tolerant hardwoods in post-logged forests, especially on upland sites (Carleton and MacLellan 1994; Jackson et al. 2000). Currently, both intensive and extensive forest management is being conducted in the Canadian boreal forest.

Forestry practices can affect both the quality and quantity of dead wood (e.g., Sturtevant et al. 1997; Sippola et al. 1998) and can have specific implications for saproxylic fauna diversity (Freedman et al. 1996; Siitonen 2001). The change in tree species composition due to harvesting is a factor impacting saproxylic insects. Scandinavian and North American studies in the boreal forest have shown that saproxylic insect assemblages differ between major tree genera such as spruce (*Picea* spp.) and poplar (*Populus* spp.) (Jonsell et al. 1998; Siitonen 2001; Hammond et al. 2001; Jacobs et al. 2007; Saint-Germain et al. 2007; Janssen et al. 2011).

The saproxylic assemblage is expected to change through ecological succession in the process of wood decomposition. The decay process usually differs between conifer and deciduous species (e.g. Yatskov et al. 2003; Vanderwel et al. 2006b; Saint-Germain et al. 2007), and the early stages of decay are ephemeral relative to the overall decay process (Vanderwel et al. 2006b). Decay timelines also consistently vary with log size (Vanderwel et al. 2006b; Edman et al. 2007), ambient temperature (Chambers et al. 2000), and fungal or insect colonization (Edman et al. 2007). Changes in physical and chemical qualities of dead wood over time have significant implications for insects (Grove 2002). In the early stages of decay, insect colonizers are often specific to the tree genus (Hammond et al. 2001; Langor et al. 2006). Nonetheless, differences between coniferous and deciduous colonizers also occur in the later stages of decay (Ås 1993). Early colonizers are predominantly coleopterans (e.g., Pawlowsky 1961; Heliövaara and Väisänen 1984), which start

the breakdown of wood by feeding directly on freshly dead material (Dajoz 2000); they also bring along their associated predators and parasitoids (Hammond et al. 2001; Vanderwel et al. 2006a). Some insects also assist further wood breakdown indirectly by dispersing wood-decaying fungal spores (Muller et al. 2002). The frass and galleries left behind by xylophages allow for further colonization by fungi and bacteria (Carpenter et al. 1988), which in turn attracts fungivores (e.g., Jonsell et al. 1998) and their associated insects, thus further advancing wood decay. Little is known about later colonizers, but insects associated with heavily decayed wood are predominantly of higher trophic levels such as fungivores, predators, and parasitoids (Vanderwel et al. 2006a). Few studies on saproxylic insects have explored differences in assemblages according to the stage of wood decay. This might be partly because the best understood saproxylic insects are xylophagus coleopterans, a group essentially absent from later stages of wood decay (Simandl 1993; Irmiler et al. 1996; Vanderwel et al. 2006a). Dipterans and parasitic hymenopterans are often very abundant in heavily decayed wood (Vanderwel et al. 2006a), yet it is difficult to study these diverse groups much beyond the family level due to taxonomic limitations (e.g. Selby 2006; Stenbacka et al. 2010).

Harvesting affects the amount of dead wood that remains on a site, both standing (snags) and downed (logs), and the saproxylic insect communities show compositional differences between these two postures (Jonsell and Westlien 2003; Hilszczański et al. 2005; Ulyshen et al. 2011). Snags and logs are important components of forest ecosystems, providing carbon storage, structural complexity, and wildlife habitat, and their loss affects saproxylic insects at the landscape scale (Økland 1996; Gibb et al. 2006). Logging reduces ecological complexity greatly (Debeljak 2006), especially with respect to snags, which are removed disproportionately more than logs. The effects of reduced habitat complexity due to logging can be seen when comparing insect communities found in these two postures of dead wood. The decay process, which drives saproxylic faunal diversity, has different characteristics in snags and logs because microclimate factors, such as moisture and temperature, differ between them; typically, snags are dryer and warmer than logs because they are exposed to more direct sunlight than are logs (Martikainen et al. 2000; Ehnström 2001). Furthermore, saproxylic assemblages in snags are vertically stratified due to moisture and temperature gradients in the wood (Vanlaerhoven and Stephen 2002; Ulyshen et al. 2011).

Our working question was how forest management influences the diversity of key functional groups in logs and snags of the boreal forest. Our overall goal was to examine the response of saproxylic assemblages to

Table 1 Mean volume (m³/ha) of early and late decay (early = classes 1–3; late = classes 4–5; sensu Fischer et al. 2012) coniferous and deciduous downed wood in sites that were horse-logged, machine-logged or unlogged in the boreal forest of central Canada. Forest ages at the sites are also shown

Site type	Site name	Conifer		Deciduous		Forest age in 2006
		Early decay	Late decay	Early decay	Late decay	
Horse-logged	HL12PG	27.7	5.0	25.6	1.2	63
Horse-logged	HL14PG	10.2	0.0	34.8	13.9	47
Horse-logged	HL20PG	32.9	3.9	17.8	4.4	51
Horse-logged	HL24PG	12.4	4.3	3.9	0.5	60
Horse-logged	HL28PG	–	–	–	–	62
Machine-logged	ML02PG	5.4	2.5	27.1	23.8	33
Machine-logged	ML04PG	2.0	3.6	44.3	23.7	31
Machine-logged	ML10PG	8.6	3.1	64.1	9.9	33
Machine-logged	ML11PG	11.5	23.3	49.9	84.4	39
Machine-logged	ML29PG	1.1	1.6	22.3	9.8	34
Unlogged	UL01PG	25.3	17.8	19.3	11.6	155
Unlogged	UL03PG	16.6	14.0	23.7	21.5	115
Unlogged	UL06PG	53.7	28.9	9.7	8.2	155
Unlogged	UL07PG	30.3	16.2	15.0	24.9	140
Unlogged	UL20PG	14.4	5.9	29.5	10.8	82

different logging histories and dead wood quality (species, stage of decay, and posture), using a high-taxon level approach. Specifically, we examined differences in the abundance of selected saproxylic insects emerging from logs of different logging history (horse-logged, machine-logged, and unlogged), tree species (*Populus* and *Picea*), stage of wood decay (early and late decay stages), and wood posture (standing snags and downed logs) in the boreal forests of central Canada. We predicted that these parameters would account for observed differences between insect assemblages at the high-level taxa. All arthropod orders were examined in order to have an overview of the insect communities emerging from dead wood. However, we chose to focus on dipteran and parasitic hymenopteran families because: (1) they show high diversity in dead wood (Siitonen 2001; Stokland et al. 2012); (2) they contain many taxa that have been shown to be sensitive to forest management practices (i.e., Finnamore 2000; Deans et al. 2005; Maleque et al. 2007; Smith et al. 2012); (3) they are known to be extinction prone (La Salle and Gauld 1991; Shaw and Hochberg 2001); and (4) they rarely have been studied in boreal forests.

Materials and methods

Study area

The study was conducted in the Gordon Cosens Forest in northeastern Ontario, Canada. The study area comprises over two million hectares of forest in the “Northern Clay”

section of the Canadian boreal forest (Rowe 1972), where logging began in 1926 (Radforth 1987). The generally low-lying, flat topography of the Northern Clay section has resulted in large stretches of black spruce-dominated forests, with deciduous or mixed coniferous-deciduous forests dominated by trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), balsam fir (*Abies balsamea* (L.) Mill), white spruce (*Picea glauca* (Moench) Voss) and black spruce (*Picea amariana* (Mill.)) in locations with better drainage. Black spruce and white cedar (*Thuja occidentalis* L.) are found at swamp edges, and jack pine (*Pinus banksiana* Lamb.) dominates the driest sites (Rowe 1972). Based on aerial photo interpretation (OMNRF unpublished), composition of the forest canopy in the stands was 30–70% poplar (including trembling aspen and balsam poplar; mean 44%) and 10–50% spruce (including black and white spruce; mean 23%). Other common tree species included balsam fir (20% on average) and white birch (*Betula papyrifera* Marsh.) (10% on average); rarer species included white cedar and jack pine (< 2% on average).

Site selection

We sampled 15 sites, five of each were either horse-logged, machine-logged or unlogged. Sites were selected to span a range of volumes of downed dead wood within each logging treatment, and to sample various logging histories (Table 1). Unlogged sites were most recently disturbed by fire in either 1924 (one site) or the mid to late 1800s (four sites). Horse-logged stands were harvested in 1943–1959 and machine-logged stands were harvested in 1967–1975.

We chose different logging histories because they were expected to affect the quantity and quality of dead wood volume (Table 1). At each site except one, we quantified the volume of coniferous and deciduous early- (decay classes 1–3) and late-decay (decay classes 4 and 5) downed wood. We chose dead wood volume as the key variable because it is correlated with species richness of saproxylic assemblages, especially in the boreal forest (Lassauce et al. 2011). Volume was based on sampling wood in a 120×120 -m area at each site, using seven 120-m transects spaced 15 m apart per area, and included all downed wood ≥ 7 cm diameter (see Fischer et al. 2012 for details). Typically, unlogged stands had more woody debris and species (especially *Picea*), and decay class representation was more evenly distributed than in logged sites. The distribution of decay classes was also affected by time since harvesting: horse-logged stands had a low volume of heavily decayed wood and recent additions of relatively small-diameter wood, whereas machine-logged sites have a relatively large volume of heavily decayed wood (from the logging event itself) and relatively little recently decayed wood from self-thinning (see also Fischer et al. 2012).

Study design

We conducted two experiments in a split-plot ANOVA design. The three logging treatments (horse-logged, machine-logged and unlogged), with five replicates (sites) each, represented “whole-plot” factors. Within each of the 15 sites, we examined the effects of two “within-plot” factors: tree species (*Picea* and *Populus*) and stage of decay (early and late decay stage) in 2005, and tree species (*Picea* and *Populus*) and dead wood posture (standing snag and downed log) in 2006.

In the summer of 2005, we sampled eight log sections of *Populus* sp and eight log sections of *Picea* sp at each of the 15 study sites. We sampled two log sections per tree species for each of two decay classes (early- and late-decay). Thus, we had 10 log sections for each combination of logging treatment, tree species, and stage of decay for a total of 120 log Sects. (5 sites \times 3 logging treatments \times 2 log sections \times 2 tree species \times 2 stages of decay). Early-decay and late-decay wood were classified as either Class 1 or Class 4, respectively (from Vanderwel et al. 2006b). In each site, we established a 120×120 -m plot and walked the plot along the same transects, 15 m apart, selecting the first log that met the criteria and was at least 15 m away from other selected logs. Log sections were 50 cm long, 12–31 cm in diameter (mean 16.7 cm), and were approximately equal in size across decay classes. In the summer of 2006, a similar experimental design was set, but we collected two log sections per tree species for each of standing (snag) or downed (log) dead wood, with 10

replicates for each combination of logging treatment, tree species and wood posture. All log sections were Decay Class 1. Log sections from snags were cut at 1–2 m above the ground. All log and snag sections were 50 cm long and 12–31 cm in diameter.

Insect sampling and identification

Each collected log was placed in a cardboard tube and stored on shelving in an unheated storage building with natural lighting. Tubes were 75-cm long and sealed at both ends with black corrugated plastic (Coroplast[®]) and tape. One end of each tube had a hole, ca. 7 cm in diameter, through which insects could exit. A Whirl-Pak[®] bag filled with 70% alcohol was secured to this hole so emerging insects were killed and preserved for later identification. Emergent insects were collected over 8 weeks from June to August 2005 and 2006. All arthropods were identified to order, and all dipterans (using McAlpine et al. 1987) and parasitic hymenopterans (using Goulet and Huber 1993) were identified to family.

Habitat sampling

Downed woody debris volume was quantified as described above, and diameter, decay class, and species (where possible) of all downed wood intercepting each transect line within the 120×120 -m area was quantified every 15 m. The number of variables for analysis was reduced by undertaking a principal components analysis on the correlation matrix of these data. Further analyses were undertaken using the scores from the first three principal components of this analysis (93% of the total variation). The principal components captured: (1) variation in the total quantity of wood among the plots (all woody debris variables loaded positively on the first axis and variables measuring total woody debris volume had the greatest loadings); and (2) variation in woody debris quality (relative to other plots, unlogged plots tended to have large volumes of coniferous dead wood whereas machine-logged sites tended to have large quantities of heavily decayed deciduous wood).

Data analysis

We combined insect abundances from the 2 log sections per species and considered this combination as one sample resulting in a total number of 60 log sections. Univariate split-plot ANOVAs were performed in SAS v. 8.2 on the abundance of the most frequently-collected taxa (i.e., caught in at least 33% of traps). In addition, multivariate split-plot analyses were applied to matrices of abundances in the various taxonomic groups by use of redundancy

analyses (RDAs; 9999 iterations) in Canoco v. 4.51 on the correlation matrices. Data were log-transformed. Although analyzing the correlation matrices essentially upweights rare taxa, some taxa were much more abundant than others and hence would dominate analyses on the covariance matrix. By combining insects from the sampling periods and by analyzing them on different taxonomic levels, the effects of rare taxa were reduced. In addition to main effects, in the split-plot analyses we tested for all possible two-way interactions. To identify the strongest effects and because of multiple tests, we used $\alpha = 0.01$ instead of 0.05 as the threshold for significance in the RDAs. Because results from the multivariate analysis did not provide much additional information to the univariate analysis, the biplots are not shown.

Results

Differences by logging technique, tree species, and stage of decay

A total of 16,471 arthropods emerged from the 120 log sections in 2005. Diptera was the most abundant insect order (7788 individuals), followed by parasitic Hymenoptera (parasitoids; 1932), non-parasitic Hymenoptera (1322), and Coleoptera (255). Twelve orders comprised the remaining 33% of arthropods caught in emergence traps. Among dipterans, Cecidomyiidae was the most abundant family (65.3%), followed by Sciaridae (15.7%), Ceratopogonidae (8.7%), Phoridae (2.9%), and Chironomidae (2.2%). The remaining 16 dipteran families represented approximately 5% of the total dipterans collected. Among the parasitoid families, Scelionidae (28.7%) and Ceraphronidae (27.4%) had the most individuals emerge, followed by the Ichneumonidae (13.2%), Diapriidae (10%), and Eulophidae (6.6%). The remaining 12 parasitoid families represented less than 15% of total parasitoids.

None of the permutation tests on the insect matrices were significant (9999 iterations, all P values > 0.11) for variation in dead wood quantity and quality (as measured

by the three principal components), including whole-plot effects (three principal components) and their interactions with the within-plot factors decay class and wood species (Table 2).

Logging treatment and tree species showed little effect on insects at the high taxonomic level of Order in the split-plot ANOVA (Table 3); in contrast, many Orders showed significant responses to the stage of wood decay. Araneae, Diptera, and hymenopteran parasitoids were all more abundant in late-decay wood; no arthropods at the taxonomic level of Order were strongly associated with early-decay dead wood. Non-parasitic hymenopterans emerged in significantly greater numbers from *Populus* decay wood in horse-logged sites than from either unlogged or machine-logged sites. Acarina and Coleoptera were significantly more abundant in *Picea* than *Populus* dead wood.

Decay stage showed the strongest influence on the Cecidomyiidae, Ceratopogonidae, and Chironomidae families, and a weaker effect on the Phoridae and Sciaridae families, all of which were more abundant in late- than in early-decay wood (Table 3). None of the families was most abundant in early-decay dead wood. There was greater abundance of Cecidomyiidae in *Populus* than in *Picea* ($P < 0.03$); with interaction effects in the Ceratopogonidae (emergence from late-decay logs collected from horse-logged sites was greater than from other plots) and in the Milichiidae (late-decay *Picea* accounted for more emergence than late-decay *Populus*).

Most of the common parasitoid families were significantly more abundant in late- than in early-decay wood, including the Ichneumonidae, Ceraphronidae, Scelionidae, Braconidae, Diapriidae, Eulophidae, Mymaridae, and Platygastriidae (Table 3). Early-decay dead wood was not associated with greater abundance of any parasitoid family. Platygastriidae was more abundant in *Picea* than in *Populus*. Parasitoid families showing interactions were Mymaridae (abundance in late-decay wood from unlogged sites was greater than from other sites, and abundance in late-decay *Populus* from unlogged sites was greater than in other combinations), Scelionidae (fewer individuals emerged from late-decay wood on machine-logged sites

Table 2 P values of RDAs that were performed on the correlation matrices of log-transformed insect emergence data. The whole-plot factors were the three principal components found in an RDA performed on woody debris volume data from each site

	Constrained (RDA)		
	Whole-plot (PC)	Interaction (PC*D)	Interaction (PC*S)
Orders	0.4269	0.1257	0.2128
Diptera	0.3452	0.1146	0.1721
Parasitoids	0.8944	0.3348	0.1153
Scelionidae	0.7201	0.1304	0.3271
Diapriidae	0.3027	0.5044	0.7016

PC principal component, D decay stage, S tree species

Table 3 Mean abundance of arthropods per log section for different tree species (S) and decay stage (D; early = classes 1–3; late = classes 4–5; sensu Vanderwel et al. 2006a) collected from sites with different logging history (L) in the boreal forest of central Canada during the summer of 2005

	Unlogged				Horse-logged				Machine-logged				Sig. tests treat (<i>P</i>)
	<i>Populus</i>		<i>Picea</i>		<i>Populus</i>		<i>Picea</i>		<i>Populus</i>		<i>Picea</i>		
	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	
<i>Order</i>													
Acarina	88.4	87.0	58.4	32.0	21.6	58.8	64.6	58.8	34.4	10.2	61.8	75	S (0.0034)
Aranaea	6.0	7.0	2.2	1.4	0.4	8.6	5.8	6.6	2.8	10.8	2.4	9.8	D (< 0.0001)
Chilopoda	0	0	0	0	0	0	0	0	0	0	0.2	0	
Coleoptera	4.2	2.0	3.8	2.8	1.2	4.6	17.6	4.8	2.0	3.2	2.8	2.0	S (0.017)
Collembola	33.0	7.0	8.2	7.8	57.4	37.4	18.2	13.0	30.0	14.2	37.6	13.2	L (0.0493)
Diptera	170.4	203.4	70.0	41.0	74.2	339.4	48.8	142.8	72.6	195.0	48.6	151.4	D (< 0.0001)
Heteroptera	0	1.6	0	0	0.2	0.6	0	0.4	0	0	0	0.2	
Homoptera	0.2	2.4	0	0	0.2	2.0	0.2	1.8	0	0.8	1.2	2.2	
Hymenoptera (non-parasitic)	48.8	2.2	14.0	0.8	43.6	81.8	5.0	0.2	39.6	7.0	3.0	18.4	L*S (0.0009)
Hymenoptera (parasitic)	32.0	47.2	9.0	5.0	16.6	60.8	14.6	68.4	25.4	49.6	7.6	50.2	D (< 0.0001)
Lepidoptera	2.4	1.4	0.2	0	1.6	0.8	0.2	1.4	0.6	2.8	0	2.2	
Neuroptera	0.4	0	0.2	0	0	0.2	0	0	0.2	0.8	0.2	0.4	
Pseudoscorpiones	0.4	0.4	0	0	0.2	0.6	0	0.6	0	0.4	0	0.2	
Psocoptera	0.2	0.6	0	0	0.2	0.4	0.4	0.4	0	0.6	0	0	
Thysanoptera	0.4	0.6	2.6	0	0	1.2	1.0	0.2	0.4	0.2	0	0.6	
<i>Diptera</i>													
Anthomyiidae	0	0	0	0.2	0	0	0	0	0	0	0	0	
Cecidomyiidae	21.0	117.0	27.2	119.8	37.4	226.8	9.6	86.4	13.6	119.2	17.4	91.4	S (0.0272) D (< 0.0001)
Ceratopogonidae	4.4	23.4	4.2	4.8	4.8	40.8	4.6	17.4	2.8	6.4	1.6	3.8	D (0.0013) L*D (0.027)
Chironomidae	0.2	9.2	0.8	2.0	0	11.4	0	3.2	0	3.2	0.2	0.8	D (0.0081)
Clusiidae	0	0	0	0	0	0	0	0	0.2	0	0	0	
Dolichopodidae	0	0	0.2	0	0	0	2	0	0	0	0	0	
Dryomizidae	0	0	0	0	0	0	0	0	0	0	0.2	0	
Empididae	1.6	1.2	2.2	0.6	2.0	1.0	1.0	1.8	0.2	0.4	0.6	0.2	
Hybotidae	0	0	0.2	0.2	0	0	0.2	0.2	0	0	0	0	
Lonchaeidae	0.4	0	0	0	0	0	0.4	0	0	0	0	0	
Milichiidae	1.4	0.2	1.8	6.2	0.2	0	0	5.8	0	1.6	0	3.6	S*D (0.027)
Mycetophilidae	0.4	0.2	0	0.4	0.2	3.4	0.2	0.6	0.4	0.4	0.2	0	
Oдиниidae	0.2	0.2	0	0	0	0.2	0	0	0	0.2	0.2	0.4	
Phoridae	0.8	7.6	3.4	3.6	0.8	6.2	0.8	2.2	5.4	2.0	2.8	3.2	D (0.0147)
Scatopsidae	0.2	0	0	0	0.8	0	0.4	0	0	0	0	0.2	
Sciaridae	6.8	22.6	26.2	9.0	6.2	23.6	17.6	14.4	26.2	25.8	15.0	19.2	D (0.0461)
Synneuridae	0	0	3.6	0	0	0	0	0	0	0	0	0	
Syrphidae	0	0	0	0.2	0	0	0	0	0	0	0	0	
Tachinidae	0	0	0	0	0.2	0	0	0.4	0	0	0	0	
Tipulidae	0	0.6	0	0	0	0.2	0	0	0	0	0	0	
Xylophagidae	0	0	0	0	0	0	0	0	0	0.4	0	0	
<i>Hymenoptera (parasitic)</i>													
Aphelinidae	0.4	0	0	0	0	0	0	0.2	0	0	0	0	
Braconidae	0	0.4	0	0.6	0.2	0	0.2	1.6	0.4	1.0	0.2	0.8	D (0.024)
Ceraphronidae	1.4	20.0	1.6	11.2	0.8	13.4	3.2	14.8	6.2	13.2	3.6	8.4	D (< 0.0001)

Table 3 continued

	Unlogged				Horse-logged				Machine-logged				Sig. tests treat (<i>P</i>)
	<i>Populus</i>		<i>Picea</i>		<i>Populus</i>		<i>Picea</i>		<i>Populus</i>		<i>Picea</i>		
	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	Early	Late	
Charipidae	0.2	0.2	0	0	0	0	0	0	0	0	0	0	
Diapriidae	0.8	3.2	1.4	1.8	0.2	3.2	3.0	5.6	8.2	0.6	0.4	7.2	D (0.0262) L*S*D (0.0029) L*S (0.0306) L*S*D (0.0084)
Platygastridae	0	0.6	0.4	3.2	0	1.0	0.2	2.6	0.2	1.8	0	2.6	S (0.0111) D (0.0019)
Pteromalidae	0.8	0.4	0	0.2	0	0.4	3.2	0.8	0.4	0.2	0	1.4	
Scelionidae	3.6	18.6	2.0	9.0	1.8	15.0	1.8	21.4	6.8	11.2	2.8	8.4	D (< 0.0001) L*D (0.0206)
Tetracampidae	0	0	0	0	0.2	0	0	0	0	0	0	0	
Trichogrammatidae	0	0	0	0	0	0	0.6	0	0	0	0	0	

Significant results from split-plot ANOVAs are reported

than on other sites) and Diapriidae (greater emergence from late-decay *Picea* wood on machine-logged sites than other combinations).

Differences by logging technique, tree species, and wood posture

A total of 8,537 individual arthropods emerged from the downed log and snag sections in 2006. Diptera was the most abundant order (3719 individuals), followed by parasitic Hymenoptera (723), Coleoptera (714) and non-parasitic Hymenoptera (289). Nine orders comprised the remaining 36% of collected arthropods. Among dipteran families, Cecidomyiidae accounted for 65.2% of the complete collection, Sciaridae 14.4%, Ceratopogonidae 7.2%, Phoridae 5.5%, and the remaining 21 families 7.7%. Of the collected parasitoids, Scelionidae was most abundant (31.0%) followed by Ceraphronidae (16.9%), Braconidae (11.9%), Mymaridae (8.9%), Diapriidae (8.4%),

Ichneumonidae (8.2%), and Eulophidae (5.7%); 12 families accounted for the remaining parasitoids.

Considering insect abundance as a function of variation in site-specific dead wood quantity and quality, none of the permutation tests was significant (9999 iterations, $P_s > 0.11$), including the whole-plot effects (three principal components) and their interaction with the within-plot factors tree species and wood posture (Table 4).

Results showed there was no response to the logging treatments in the abundance of insects at the taxonomic level of Order, but some responded to wood species and posture (Table 5). More Diptera emerged from *Populus* than from *Picea* wood, and Coleoptera showed the opposite pattern. Diptera and Collembola were significantly affected by wood posture, emerging in greater numbers from downed logs than from snags (Table 5). Significant interactions shown by parasitoids were between logging treatment and wood posture (higher numbers emerged from snags on horse-logged sites than from other sites) and tree species and wood posture (higher numbers emerged from

Table 4 *P* values from multivariate split-plot analyses on the correlation matrices of insect emergence data. The whole-plot factors were the three principal components found in an RDA performed on woody debris variables from each site

	Constrained (RDA) (<i>P</i> values)		
	Whole-plot (PC)	Interaction (PC*P)	Interaction (PC*S)
Orders	0.8331	0.2102	0.2287
Diptera	0.6349	0.2881	0.2352
Parasitoids	0.5125	0.1186	0.8410
Scelionidae	0.5387	0.1066	0.9993
Diapriidae	0.2032	0.4865	0.6542

No whole-plot or interaction factor had significant effects on insect emergence
PC principal component, *P* wood posture, *S* tree species

Table 5 Mean abundance of arthropods per log section of different tree species (S) and wood posture (P) (standing or downed) collected from sites with different logging history (L) in the boreal forest of central Canada during the summer of 2006

	Unlogged				Horse-logged				Machine-logged				Sign. tests treat (<i>p</i> value)
	<i>Populus</i>		<i>Picea</i>		<i>Populus</i>		<i>Picea</i>		<i>Populus</i>		<i>Picea</i>		
	Log	Snag	Log	Snag	Log	Snag	Log	Snag	Log	Snag	Log	Snag	
<i>Orders</i>													
Acari	43.8	31.2	24.0	44.8	9.2	3.6	159.6	5.0	44.2	29.6	20.8	9.6	
Araneae	1.2	0.8	1.2	1.8	2.6	2.4	3.2	2.0	0.4	0.8	1.2	1.2	
Coleoptera	3.8	9.4	27.0	12.0	3.0	2.8	11.4	7.0	4.2	2.4	33.8	26.0	S (0.0314)
Collembola	34.8	1.2	16.6	3.8	4.2	3.0	11.2	21.2	8.8	17.6	11.2	2.0	P (0.0057)
													L*S*T (0.0317)
Diptera	67.0	225.2	44.4	30.6	58.0	9.2	76.4	14.4	107.8	38.0	71.8	3.2	S (0.0157)
													P (0.0089)
Heteroptera	0.6	0	0.2	0	0	0	0	0	0	0	0	0	
Homoptera	0.4	0	0.2	0.2	1.0	0.6	2.6	0.8	0	0.2	1.4	0.2	
Hymenoptera (non-parasitic)	2.8	0.2	6.4	2	1.8	0	2.0	0	7.0	0.2	34.6	0.8	
Hymenoptera (parasitic)	15.2	4.4	9.0	8.6	4.8	8.6	7.2	47.6	8.0	9.0	12.2	12.4	L*P (0.0196)
													S*P (0.0471)
Lepidoptera	0.4	0.2	1.0	0.6	0.2	0.2	0.4	0.6	4.4	0	0	1.0	
Neuroptera	0	0	0	0	0	0	0	0	0.2	0	0	0	
Psocoptera	4.6	2.4	1.0	0.4	0	0	0.2	0	0	1.0	0.4	0	
Thysanoptera	0.4	0	0.4	0	1.6	0.4	0.8	0.6	0.4	0.4	0.6	0.8	
<i>Diptera</i>													
Anthomyiidae	0.2	0	0	0	0	0	0	0	0.2	0	0	0	
Asilidae	0	0	0.2	0	0	0	0	0.2	0	0	0	0	
Cecidomyiidae	41.0	195.0	26.6	7.0	30.6	6.6	35.0	9.2	48.4	31.8	53.2	0.8	S (0.0067)
													P (0.0165)
Ceratopogonidae	8.2	0.6	3.2	2.0	9.0	1.2	1.0	1.0	25.2	1.4	1.0	0	S (0.0056)
													P (0.0228)
Chironomidae	0.6	1.0	0.2	0	0.8	0	0	0	0.2	0	1.8	0.2	
Chloropidae	0.4	0.2	0	0	0.2	0.6	0	0.2	0.4	0.2	0	0	
Clusiidae	0	0	0	0	0	0	0	0.2	0	0	0	0	
Dolichopodidae	0.2	0.4	3.6	0	0.8	0.2	0.6	0	1.8	1.2	0.2	0.2	
Drosophilidae	0.4	0	0.2	0	0	0	0	1.2	0	0	0.2	0	
Dryomyzidae	0.2	0	0	0	0	0	0	0	0	0	0	0	
Empididae	0.8	0.2	1.8	0	0.2	0	0.2	0	2.2	0.6	1.4	0	P (0.0061)
Lauxaniidae	0	0	0	0	0	0	0.4	0	0.2	0	0	0	
Lonchaeidae	0.6	1.0	0	0	0	0	1.8	0	0.6	0	0.2	0	
Milichiidae	2.4	0	0	0	1	0.2	0.2	0	0	0.4	0	0	
Muscidae	0.4	0	0	0	0	0	0	0	0.2	0	0.2	0	
Mycetophilidae	1.0	0.2	1.8	0.4	1.0	0	0.8	0	1.4	0.2	0.4	0	P (0.0187)
Odiniidae	0	0.2	0	0	0	0	0	0	0	0	0	0	
Phoridae	2.8	3.6	0.8	19.4	0.4	0	1.6	0	4.4	1.0	6	1.2	
Pipunculidae	0	0.2	0	0.2	0	0	0	0.2	0	0	0	0	
Rhagionidae	0	0	0	0	0	0	0	0	0	0	0	0	
Scathophagidae	0.2	0	0.2	0	0	0	0	0	0.4	0	0	0	
Scatopsidae	0.2	0.2	0	0	1.6	0	0	0	0.2	0	0.2	0	

Table 5 continued

	Unlogged				Horse-logged				Machine-logged				Sign. tests treat (<i>p</i> value)
	<i>Populus</i>		<i>Picea</i>		<i>Populus</i>		<i>Picea</i>		<i>Populus</i>		<i>Picea</i>		
	Log	Snag	Log	Snag	Log	Snag	Log	Snag	Log	Snag	Log	Snag	
Sciariidae	7.0	27.0	6.2	1.0	15.2	0.6	36.2	1.0	3.0	1.0	8.8	0.2	P (0.0031) S*P (0.0298) L*S*P (0.0239)
Syrphidae	0	0	0	0	0.4	0	0	0	0	0	0	0	
Tipulidae	0.6	0.2	0	0	0	0	0	0	4.6	0	0	0	
Xylophagidae	0	0	0	0	0	0	0	0	0	0	0.2	0	
<i>Hymenoptera (parasitic)</i>													
Braconidae	0.4	0.8	2.4	1.8	0.2	1.2	0	2.2	1.2	2.2	1.8	3.0	
Ceraphronidae	8.8	1.0	1.6	1.2	0.2	0.2	1.0	6.6	0.2	1.0	2.2	0.4	L*S*P (0.0342)
Diapriidae	1.0	0	1.2	3.6	1.2	0	2.0	0	1.6	0.4	1.2	0	T (0.0312)
Encyrtidae	0	0	0.2	0	0	0	0	0.6	0	0	0	0	
Eucoilidae	0	0.2	0.6	0	0	0	0.2	0	0	0	0.6	0	
Eulophidae	2.0	0	0.4	0	0.6	3.6	0.2	0.2	0.4	0.4	0.2	0.2	
Eurytomidae	0	0	0	0	0.0	0	0	0.6	0.0	0	0	0	
Ichneumonidae	2.4	0	1.2	0.6	1.0	0	1.8	0.4	2.2	0.4	0.8	1.0	P (0.032)
Megaspilidae	0.2	0	0	0	0	0	0	0	0	0	0	0	
Mymaridae	0.8	2.0	0	0.2	0.2	4.2	0	2.8	0.4	1.8	0.2	0.2	S (0.0018) P (0.0067)
Perilampidae	0	0	0	0	0	0	0	0	0.4	0	0	0	
Platygastridae	0.2	0	0.2	0	0	0	0	0.2	0.2	0	0.2	0.2	
Proctotrupidae	0	0	0	0	0.2	0	0	0	0	0	0	0	
Pteromalidae	0.2	0.4	0	0	0.2	0	0	0	0.2	0.4	0.6	0	
Scelionidae	0.6	0.2	1.0	0.2	0.2	0.2	1.2	32.2	0.8	2.4	1.4	4.4	
Tiphiidae	0.2	0	0	0.4	0	0	0	0.2	0	0.8	0	0	
Torymidae	0	0	0	0	0	0	0	0	0	0	0	0.2	
Trichogrammatidae	0	0	0	0	0	0	1.4	1.0	0.2	0	0	1.2	

Significant results from split-plot ANOVAs are reported

Picea snags than from any posture of dead *Populus*). Collembola showed a three-way interaction (higher numbers emerged from *Picea* snags on horse-logged sites than from any other sites).

Only two dipteran families (Cecidomyiidae and Ceratopogonidae) showed significant univariate effects for species of dead wood, with both showing greater emergence from *Populus* than *Picea* (Table 5). Cecidomyiidae, Ceratopogonidae, Empididae, Mycetophilidae, and Sciariidae were all significantly more abundant in downed than in standing dead wood, while no other dipteran families showed significantly higher emergences from snags. Sciariidae showed interactions between dead wood species and posture (higher numbers emerged from downed *Picea* logs than from *Populus* dead wood of any posture) and among the three factors (more insects emerged from *Populus*

snags on unlogged sites than from any other three-way combination).

ANOVA showed that Mymaridae was more abundant in snags than in downed wood, whereas Diapriidae and Ichneumonidae had significantly more individuals emerge from downed logs than from snags (Table 5). Mymaridae was the only parasitoid family significantly affected by tree species, with higher numbers emerging from *Populus* than from *Picea*. Ceraphronidae showed a significant three-way interaction (significantly more emerged from *Picea* snags on horse-logged sites than from any other treatment).

Discussion

Our objective was to analyze responses of saproxylic insects to dead wood characteristics at high taxonomic levels. We found that some taxa responded whereas others did not. Undoubtedly, additional differences would be seen at lower taxonomic levels, such as genus or species; however our study is one of the first to show common habitat attributes for many of the species-rich families found in dead wood. The taxonomy of the two most abundant orders we collected (Diptera and Hymenoptera) continues to advance at the species level, and thus, detailed identification could later prove unreliable for many of the important saproxylic groups we found (i.e. parasitoid families). Furthermore, differences at high taxonomic levels are particularly useful for biodiversity monitoring and conservation purposes as they allow for the identification of key substrate habitats that must be retained during forest harvesting.

Our results show no evidence for an effect of logging history on the abundance of saproxylic insect assemblages, suggesting convergence with age between treatments. Stenbacka et al. (2010) working in northern Scandinavian boreal forests found that saproxylic beetle species occurring in late successional stages were present in 53-year old stands but not in 30-year old stands, also suggesting community convergence with stand age. In our case, assemblage convergence would be even more apparent using the high-level taxa approach.

It is also possible that the lack of strong response in saproxylic insect communities to logging history may be due to our study design. We selected sites to provide a range of decayed wood volume within each treatment; i.e. generally, less dead wood was found in horse-logged sites relative to machine-logged or unlogged sites (Table 1). The significant interaction involving horse-logging we observed might therefore have been due to habitat limitation. For example, more non-parasitic Hymenoptera emerged out of *Populus* dead wood on horse-logged sites than on unlogged or machine-logged sites (2005). The majority of these non-parasitic Hymenoptera were saproxylic ants, which are well known to rely on dead wood for nesting in the boreal forest (Higgins 2006). This group appears to show no preference for different dead wood taxa, and thus in our study, the non-parasitic Hymenoptera (ants) may have used dead wood regardless of tree species on the horse-logged sites, even though most dead wood on these sites was *Populus* (as the *Picea* had already been logged). This would have obscured any statistical differences.

In contrast to logging history, we found that many high taxonomic levels of saproxylic arthropods responded differentially depending on tree species. Previous studies

showed contrasting results with respect to insects emerging from different species of dead wood. For example, Selby (2006) found that both the dominant cecidomyiid species and species assemblages of Cecidomyiidae differed between beech (*Fagus grandifolia* Ehrh) and maple (*Acer saccharum* Marsh.) dead wood, while Ulyshen et al. (2011) found no difference in the abundance of saproxylic parasitoids among sweet gum (*Liquidambar styraciflua* L), pine (*Pinustaeda* L), and oak (*Quercus rubra* L) dead wood. In our study, the abundance of all coleopterans and cecidomyiids emerging from dead wood differed by tree species consistently in both years. More coleopterans emerged from spruce (*Picea*) than from poplar (*Populus*), and this was again consistent with previous studies in North American boreal forests (Jacobs et al. 2007; Saint-Germain et al. 2007). We saw no significant association between Cecidomyiidae and *Populus* dead wood; however we did find that Platigastridae was more abundant in *Picea* than *Populus* dead wood in 2005 (low numbers emerged in 2006). The latter supports the work of Vanderwel et al. (2006a) who reported platygastrid associations with another heavily decayed conifer, *Pinus*. In contrast, significantly more mymarids emerged from *Populus* than from *Picea* logs in our 2006 experiment; to our knowledge, this is the only documented evidence for an association with dead wood by this parasitic family.

We found the stage of wood decay was a common factor associated with the abundance of many insect taxa; parasitoid families were more abundant in the late rather than in the early stages of wood decomposition. These results are consistent with previously observed associations for insects emerging from dead *Pinus* in mixed coniferous-deciduous forests from central Canada (Vanderwel et al. 2006a). Our results reinforce the growing body of knowledge that downed dead wood is a critical substrate for saproxylic parasitic wasps in the Nearctic boreal forests, and that such forests should be managed to provide enough dead wood for this key functional group.

The lack of distinct insect associations with early-decay wood was unexpected, even at the high taxonomic level. Decay is known to progress quickly once a tree dies, and insect community turnover has been shown to be relatively more rapid and distinct in early-decay rather than late-decay stages (Hammond et al. 2001). These authors also found early succession to be very fast by saproxylic beetles in *Populus* dead wood, with some of the first colonizing insects abandoning the substrate after only 1 year following tree death. Although the early-decay wood in our study was of unknown age, it was estimated to be between 1 and 11 years old (Vanderwel et al. unpubl.). The fact that we saw no insect assemblages associated with this early-decay wood might be because the wood, although considered early decay, was in fact older. Most xylophagous

saproxylic insects are beetles associated with early-decay dead wood, at both the family (Vanderwel et al. 2006a) and species (Hammond 1997; Hammond et al. 2001) levels. Coleopterans in our study were only classified to order, but further family-level classification might show more wood decay associations. For example, Vanderwel et al. (2006a) found that wood decay had significant effects on the abundance of predatory beetles of the families Cantharidae and Staphylinidae.

We found differences in the abundance of many saproxylic insect taxa between downed and standing dead logs. Our results are consistent with previous work reporting high between-habitat differentiation in saproxylic assemblages for snags and downed logs (Jonsell and Weslien 2003; Hilszczański et al. 2005; Ulyshen et al. 2011). Dipteran families that emerged significantly more from downed logs than from standing snags had varied functional roles, including saprophages (Ceratopogonidae and Sciaridae), fungivores (Cecidomyiidae and Mycetophilidae), and predators (Empididae). These results illustrate differences in both the quality and quantity of decay wood and fungal colonies present in downed logs and snags, with logs providing a broader resource than snags. Presumably, because downed logs fostered more saprophages and fungivores, they also produced more predacious dipterans than did snags. Dipterans, diaphids, and ichneumonids were all strongly associated with downed logs while mymarids were associated with snags. Hilszczański et al. (2005) also found that downed logs produced the greatest number of ichneumonid wasps. While we found no association of braconids with wood posture at the family level, there was evidence of species responding to and being stratified in snags (Ulyshen et al. 2011). We also found no literature on saproxylic Mymaridae and dead wood, although Krugner et al. (2008) showed that host specificity in this family is relatively broad.

Finally, our study provides evidence that some insects at a high taxonomic level respond to different dead wood attributes that are significantly affected by forest management practices. We found clear associations between some high-level insect taxa and dead wood attributes (tree species, stage of decay, and wood posture) suggesting that the quality of dead wood is a strong determinant of the saproxylic assemblage structure. Significant loss of biodiversity has become increasingly linked to the removal of natural woody debris during intensive forest harvesting especially in Europe; i.e. forest management practices are considered the main reason for the threatened status of 46 saproxylic beetle species listed on the IUCN Red List (Nieto and Alexander 2010). Forest practices that support the retention of dead wood during timber harvesting will encourage biodiversity and its associated ecological

functions for healthier forest ecosystems. Our work adds to the growing body of knowledge that shows saproxylic dipterans and parasitoids have great potential to be used as indicators for sustainable forest management, especially if high-level taxa can act as a surrogate for more taxonomically difficult species-level studies in monitoring biodiversity for conservation (Margules and Pressey 2000; Timms et al. 2013).

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