

# Insect community composition and trophic guild structure in decaying logs from eastern Canadian pine-dominated forests

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## Abstract

Knowledge of the insect communities inhabiting different types of dead wood, and their responses to variation in its availability, is important in assessing the potential ecological impacts of changes in the quality and quantity of coarse woody debris (CWD) that may result from forest management activities. We collected all Diptera, Hymenoptera, and Coleoptera emerging from four decay classes of pine (*Pinus strobus*, *P. resinosa*, *P. banksiana*) logs collected from 22 sites within Algonquin Park, Ontario, Canada, in order to analyze variation in community composition and trophic structure as a function of log decay class, and to determine whether the abundance of wood-inhabiting insects in the logs was correlated with the amount of downed CWD in the surrounding area. Multivariate analyses revealed that community composition varied continuously across the four decay classes, and that our system of decay classes explained decomposition-related variation in insect communities relatively well compared to individual characteristics of the logs. Of 27 families that were classified as “common” (present in >25% of the logs from at least one decay class), 19 were found to vary significantly in rank-abundance across decay classes, with nearly all of these favouring logs that were either in an early (class I) or late (classes III–IV) stage of decomposition. These associations also reflected functional differences in trophic guild structure: xylophages and predators tended to be most abundant in fresh logs, whereas saprophages, fungivores, predators, and parasitoids tended to be most abundant in more highly decayed logs. When the community was considered as a whole, insect abundance generally did not appear to correlate with the volume of downed CWD in the surrounding 20 or 79 ha area, either within or across decay classes. When trophic guilds were considered separately though, we found that the average rank-abundance of fungivores was correlated with the surrounding volume of downed CWD. We conclude that wood-inhabiting insect biodiversity, and its associated ecological functions, may best be maintained through forest management practices that do not reduce overall amounts of CWD, and that ensure it is available in both early and late stages of decomposition.

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## 1. Introduction

Forest management activities can have strong impacts on the quality and quantity of coarse woody debris (CWD) in forest ecosystems (Spies et al., 1988; Sturtevant et al., 1997; Sippola et al., 1998; Pedlar et al., 2002). Dead wood represents an important habitat or substrate for numerous vertebrates, invertebrates, vascular plants, fungi, bryophytes, and lichens (Harmon et al., 1986; Samuelsson et al., 1994) and there is growing concern that reductions in CWD may lead to biodiversity loss in managed stands and landscapes (Hansen et al., 1991; Freedman et al., 1996; Huston, 1996; McComb and

Lindenmayer, 1999). Many organisms are currently threatened by the loss of this habitat (Berg et al., 1994), including a large number of saproxylic insect species (those dependent on dead wood, wood-inhabiting fungi, or other saproxylics) in northern Europe (Mikkola, 1991; Siitonen, 2001).

Insects inhabiting dead wood fall into a number of larval trophic guilds, including xylophages (wood-feeders), fungivores (fungal feeders), saprophages (scavengers and detrital feeders), predators, and parasitoids (Key, 1993; Grove, 2002a). They carry out important ecological functions by accelerating rates of wood decomposition (Zhong and Schowalter, 1989), exporting nutrients from woody detritus (Swift, 1977), dispersing fungal propagules (Muller et al., 2002), creating nesting, roosting, denning, and hibernation sites for vertebrates (Speight, 1989), and providing a food source for predators (Loeb, 1996). Knowledge of the insect communities that

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inhabit different types of dead wood, and their responses to variation in its availability, is thus important for assessing the potential ecological impacts of management-induced changes in the abundance of specific CWD resources.

Many physical and chemical changes occur during the course of wood decomposition (Lambert et al., 1980), and consequently a log's habitat value for different insects may vary as the resources within it change over time (Grove, 2002a). Several phases of decomposition are often recognized, with each supporting a distinct insect fauna (Savelly, 1939; Howden and Vogt, 1951; Esseen et al., 1997; Siitonen, 2001; Hammond et al., 2004). Though there is a long history of research on wood-inhabiting insects (see Dajoz, 2000 for review), many previous studies have tended to focus on species and groups whose biology and taxonomy are relatively well known (particularly Coleoptera) rather than undertake quantitative analyses of the larger insect community. A broader investigation into the insect fauna of decaying logs is thus important in order to understand and interpret the major sources of variation in the structure of CWD-inhabiting insect communities. In addition, few studies (e.g., Hammond et al., 2004) have examined changes in trophic guild structure as logs progress through different stages of decomposition. The guild concept can be useful for uncovering functional differences in insect communities as resources change over time (Hawkins and MacMahon, 1989), and represents a practical approach for summarizing taxon-specific associations of wood-inhabiting insects based on larval feeding habits.

Along with its stage of decomposition, wood-inhabiting insect communities may also be affected by the amount of CWD available to them within the surrounding area. If dead wood constitutes a limiting resource, then the abundance of saproxylic insects should vary in response to the availability of this resource (Wiens, 1984). Low amounts of CWD may further give rise to fragmentation effects whereby the richness and abundance of saproxylics decreases because poor dispersers are unable to maintain viable populations in isolated habitat patches (Andren, 1997). Such declines in saproxylic insect biodiversity are of particular concern in Scandinavia, where a long history of intensive forest management has drastically reduced supplies of CWD (Esseen et al., 1997). Many insect communities are consequently impoverished in areas where dead wood is scarce (Økland, 1994; Siitonen, 1994; Siitonen and Martikainen, 1994; Martikainen et al., 1996, 2000; Økland et al., 1996), although this is not universally the case (As, 1993; Sverdrup-Thygeson and Ims, 2002). Unfortunately, minimum habitat requirements of insects are not well known (Stubbs, 1991), and there are few data available from outside Europe (Grove, 2002a) to determine whether this problem is common to other forest regions and management systems.

Our objectives in the present study were to: (1) examine family-level insect community composition of natural pine logs in various stages of decay; (2) assess variation in larval trophic guild structure along this decomposition gradient; and (3) determine whether insect communities and trophic guilds vary in abundance according to the quantity of CWD in the surrounding area. In addressing these objectives, we aimed to provide insight

into the potential effects of management-induced changes in CWD supplies on wood-inhabiting insect biodiversity.

## 2. Materials and methods

### 2.1. Study area

The study was carried out in the eastern portion of Algonquin Provincial Park, Ontario, Canada (45°51'N, 78°00'W). The area lies within the Great Lakes–St. Lawrence forest region (Rowe, 1972), with soils comprised of sand and silty sand material deposited as post-glacial outwash (Hills, 1959). Forest cover is dominated by mature stands of eastern white pine (*Pinus strobus* L.) that often include red pine (*Pinus resinosa* Ait.), trembling aspen (*Populus tremuloides* Michx.), and red oak (*Quercus rubra* L.). Stands dominated by jack pine (*Pinus banksiana* Lamb.) also comprise a small percentage of the landscape. The area has been subjected to various partial harvesting practices since the mid 19th century, with forest management being carried out primarily under the uniform shelterwood system since the early 1970's (Corbett, 1994). Shelterwood harvesting does not tend to strongly affect the stand-level abundance of downed CWD in Algonquin Park, with levels in harvested stands being comparable to those found in unmanaged mature and old-growth stands within the region (Carleton, 2003). The distribution of CWD across decay classes, however, does appear to vary with time since harvest under this management system as harvest residues slowly decompose over time (Vanderwel, 2005).

Twenty-two sites were selected within in the study area that (1) had an overstory comprised of at least 50% pine (white, red, or jack pine), as judged from Forest Resource Inventory information (Ontario Ministry of Natural Resources, unpublished data); (2) had a closed canopy; (3) had not been harvested within the past seven years; and (4) were accessible by road. Sites were separated from each other by at least 1 km, and together spanned an area of approximately 1500 km<sup>2</sup>. Of these 22 sites, 10 had been harvested between 8 and 28 years ago, and 12 had not been harvested within the past 28 years.

### 2.2. Log collection and insect rearing

At each site we selected four logs from which to rear emerging insects. Logs were generally found within 250 m of the center of each site and were picked to meet criteria for decay class, expected species, and size as follows.

One log was chosen in each of four decay classes, which spanned a gradient from recently-dead trees through to material in an advanced stage of decomposition. Decay classes were similar to those described by Maser et al. (1979), and were specifically defined as: (I) bark firmly attached, fine branches and needles usually present; (II) needles absent, bark loose but still present, sapwood hard; (III) sapwood soft or decayed, log may be elevated above ground; and (IV) sapwood well decayed, log not elevated above ground. In addition to an assessment of overall decay class, a number of individual characteristics pertaining to a log's state of decomposition were recorded at the

time that the log was selected. These included: needles (firmly attached, loosely attached, or missing), branches (fine, coarse, or none), bark (firmly attached, loosely attached, or missing), sapwood (hard, soft, or well-decayed), heartwood (hard, soft, or well-decayed), colour (original, darkened, or lightened), shape (round or oval), colonization by moss (none, less than 50% of surface area, or more than 50% of surface area), and position relative to the ground (suspended more than 50 cm above ground, suspended less than 50 cm above ground, at ground level, or partially buried).

We only chose logs that we thought were white pine, red pine, or jack pine, but positive identification in the field was often difficult for the later decay classes. Subsequent species identification based on microscopic examination of cross-field pit structure (Panshin and de Zeeuw, 1980) showed that our initial assessments were correct in the great majority of cases: of the 88 log samples, 43 were white pine, 13 were red pine, 7 were jack pine, 15 were unidentifiable pines belonging to one of these three species, and only 3 were of non-pine species (2 spruce [*Picea* sp.], 1 eastern hemlock [*Tsuga canadensis* (L.) Carr.]). Seven samples were too highly decayed for identification. We retained all logs in our analyses.

A 75-cm-long section was cut from the base or middle of each log and transported to an indoor facility where it was placed into an emergence trap. Log sections ranged from 17 to 31 cm in average diameter and were approximately equal in size across decay classes (mean 24 cm). We constructed emergence traps from cardboard tubes 36–46 cm in diameter, covered at both ends with pieces of oriented strand board. A 7.6-cm-diameter circular opening was cut in the bottom of the front board, to which we attached a collecting bag containing 70% ethanol. We collected all adult insects that emerged from the logs between 6 June and 29 July 2003. In an earlier study, up to 80% of insects inhabiting dead wood were found to emerge during this period (Menard, 1982). An examination of some collections from later in the summer similarly showed that relatively few individuals emerged from our logs after July.

All insects from the major holometabolous orders (Diptera, Hymenoptera, and Coleoptera) were identified to family. Other orders of insects were not retained for analysis because they were less common both in our samples and in similar studies (Menard, 1982; Hammond, 1997; Koenigs et al., 2002), and because relatively few insect species from other orders are considered to be saproxylic (Siitonen, 2001). Accordingly, we felt that the three orders we examined represented the major components of the wood-inhabiting insect community in our study area. Each family was assigned to a larval trophic guild based on Teskey (1976), McAlpine et al. (1981, 1987), Arnett and Thomas (2001), Arnett et al. (2002) and Triplehorn and Johnson (2005). In cases where a family spanned more than one guild we based the assignment on the most common feeding habit of the constituent species that could be expected to occur within dead logs.

### 2.3. Downed coarse woody debris sampling

Relationships with woody debris are believed to be strongly scale-dependent (Økland et al., 1996), so we sampled fallen

CWD at two spatial scales. Six sampling points were randomly chosen between 30 and 250 m from the center of each site along equally spaced bearings, while another six points were similarly established at random distances between 250 and 500 m. A sampling point was also established at each site's center. At each of these sampling points, we laid out three 30 m transects oriented 120° from each other (Nemec and Davis, 2002) and calculated the volume of downed CWD  $\geq 7.5$  cm in diameter using line-intersect sampling (Van Wagner, 1968). Downed coarse woody debris volume was averaged by decay class for the 7 innermost points and for all 13 points together to estimate abundance at two spatial scales (20 and 79 ha).

### 2.4. Data analysis

We divided families into two sets for analysis, with those present in 25% of the log samples from at least one decay class classified as “common” and all others classified as “uncommon”. This distinction was made so that abundance data could be used for analyses involving common families, whereas those for uncommon families could make use of occurrence information. The abundance of each common family was rank-transformed across log samples for all analyses; this had the two-fold effect of alleviating problems with heavily-skewed abundance distributions within families, as well as converting abundances among families to a common scale.

We analyzed community composition across decay classes through a principal components analysis (PCA) on the correlation matrix of rank-transformed abundances of common families. A detrended correspondence analysis on this matrix revealed a maximum gradient length of only 0.8 standard deviation units, indicating that PCA's linear model was appropriate (Leps and Smilauer, 2003). The broken-stick criterion was used to select the appropriate number of components to retain and interpret (Jackson, 1993). Univariate analysis of variance (ANOVA) using a randomized block-design, with site as the blocking factor, was then performed on each of these PCA axes (Quinn and Keough, 2002). Ryan–Einot–Gabrel–Welsh (REGW) multiple comparison procedures ( $\alpha = 0.05$ ) were used to identify the decay classes of logs with significantly different insect communities.

To assess whether our decay class system adequately encapsulated decomposition-related variation in insect community composition, we tested whether individual log characteristics could explain significant variation in the correlation matrix of rank-transformed common insect families beyond that accounted for by the four decay classes. This was accomplished through a partial redundancy analysis (RDA), in which the variance explained by the decay classes was removed statistically before evaluating the effects of the individual log characteristics. A total of 18 dummy variables were created to represent the different levels of the nine nominal-scale characteristics of the logs. Forward variable selection was used to assess the significance ( $\alpha = 0.05$ ) of each variable, as determined by permutation tests in Canoco for Windows 4.5.

To examine taxonomic and functional variation in insect communities, we analyzed the decay class distributions of

Table 1

Mean abundances  $\pm$  S.E. of common families of Coleoptera, Diptera, and Hymenoptera and mean principal component scores from 22 log samples in each of four log decay classes

	Guild <sup>a</sup>	Decay class <sup>b</sup>				Probability <sup>c</sup>
		I	II	III	IV	
<b>Coleoptera</b>						
Cantharidae	Pred.	0 a	0.23 $\pm$ 0.23 a	0.64 $\pm$ 0.25 b	2.18 $\pm$ 0.52 c	<0.0001
Cerambycidae	Xylo.	2.00 $\pm$ 0.64 a	0.41 $\pm$ 0.19 b	0.32 $\pm$ 0.15 b	0.32 $\pm$ 0.32 b	<b>0.0002</b>
Melandryidae	Fun.	0.14 $\pm$ 0.10	0.27 $\pm$ 0.12	0.14 $\pm$ 0.07	0.64 $\pm$ 0.24	0.1633
Scolytidae	Xylo.	6.45 $\pm$ 3.08 a	0.23 $\pm$ 0.19 b	0.41 $\pm$ 0.22 b	0 b	<b>0.0007</b>
Staphylinidae	Pred.	1.91 $\pm$ 0.53 a	0.73 $\pm$ 0.24 b	0.41 $\pm$ 0.17 b	0.95 $\pm$ 0.26 ab	<b>0.0088</b>
Uncommon families		2.50 $\pm$ 0.94	2.41 $\pm$ 1.07	1.59 $\pm$ 0.34	2.64 $\pm$ 0.71	
Total Coleoptera		13.0 $\pm$ 4.1	4.27 $\pm$ 1.25	3.50 $\pm$ 0.59	6.73 $\pm$ 0.96	
<b>Diptera</b>						
Cecidomyiidae	Fun.	128.5 $\pm$ 52.0 a	82.6 $\pm$ 16.2 a	319.6 $\pm$ 46.6 b	514.2 $\pm$ 66.0 b	<0.0001
Ceratopogonidae	Sap.	16.0 $\pm$ 8.8 a	13.4 $\pm$ 5.0 a	35.2 $\pm$ 8.0 b	81.1 $\pm$ 28.2 b	<0.0001
Chironomidae	Sap.	0.09 $\pm$ 0.06 a	0.45 $\pm$ 0.21 ab	1.27 $\pm$ 0.72 b	3.86 $\pm$ 1.14 c	<0.0001
Clusidae	Sap.	0 a	1.05 $\pm$ 0.60 ab	0.91 $\pm$ 0.50 b	0.41 $\pm$ 0.24 ab	<b>0.0163</b>
Dolichopodidae	Pred.	16.1 $\pm$ 4.3 a	0.82 $\pm$ 0.39 b	0.05 $\pm$ 0.05 b	0.32 $\pm$ 0.17 b	<0.0001
Empididae	Pred.	0.95 $\pm$ 0.35 a	3.77 $\pm$ 1.28 ab	3.86 $\pm$ 0.74 bc	14.64 $\pm$ 7.22 c	<b>0.0003</b>
Lonchaeidae	Pred.	9.41 $\pm$ 4.00 a	0.05 $\pm$ 0.05 b	0.45 $\pm$ 0.23 b	0.36 $\pm$ 0.17 b	<0.0001
Milichiidae	Sap.	0 a	2.95 $\pm$ 1.51 a	16.7 $\pm$ 4.5 b	11.2 $\pm$ 3.5 b	<0.0001
Mycetophilidae	Fun.	7.45 $\pm$ 2.67 a	16.1 $\pm$ 4.0 b	7.68 $\pm$ 2.11 ab	18.7 $\pm$ 9.2 ab	<b>0.0351</b>
Phoridae	Sap.	4.86 $\pm$ 1.29 a	0.50 $\pm$ 0.28 b	2.00 $\pm$ 0.68 a	4.14 $\pm$ 1.73 a	<b>0.0008</b>
Sciaridae	Sap.	79.1 $\pm$ 28.6	25.0 $\pm$ 6.6	27.6 $\pm$ 8.0	54.9 $\pm$ 18.3	0.3870
Tipulidae	Fun.	2.50 $\pm$ 1.14	0.23 $\pm$ 0.15	0.14 $\pm$ 0.07	1.18 $\pm$ 0.59	0.0640
Uncommon families		13.82 $\pm$ 8.72	1.00 $\pm$ 0.60	0.68 $\pm$ 0.26	0.86 $\pm$ 0.24	
Total Diptera		278.7 $\pm$ 72.4	148.0 $\pm$ 22.3	416.2 $\pm$ 47.4	705.8 $\pm$ 79.2	
<b>Hymenoptera</b>						
Braconidae	Para.	0.86 $\pm$ 0.34	0.41 $\pm$ 0.20	2.14 $\pm$ 1.20	0.86 $\pm$ 0.32	0.4828
Ceraphronidae	Para.	2.41 $\pm$ 1.09 a	2.27 $\pm$ 0.52 a	6.41 $\pm$ 1.19 b	14.1 $\pm$ 2.5 c	<0.0001
Diapriidae	Para.	0.18 $\pm$ 0.11 a	0.55 $\pm$ 0.31 a	1.73 $\pm$ 0.51 b	2.82 $\pm$ 0.55 c	<0.0001
Eulophidae	Para.	0.55 $\pm$ 0.32	0.18 $\pm$ 0.08	0.36 $\pm$ 0.15	1.95 $\pm$ 0.71	0.0879
Formicidae	Oth.	10.2 $\pm$ 4.3	6.59 $\pm$ 4.09	16.6 $\pm$ 10.5	3.59 $\pm$ 1.29	0.1632
Ichneumonidae	Para.	0.86 $\pm$ 0.27 a	0.68 $\pm$ 0.19 a	1.82 $\pm$ 0.35 b	2.68 $\pm$ 0.39 b	<0.0001
Mymaridae	Para.	0.32 $\pm$ 0.17	0.45 $\pm$ 0.24	0.73 $\pm$ 0.24	1.59 $\pm$ 0.48	0.0663
Platygasteridae	Para.	0.95 $\pm$ 0.48 a	0.55 $\pm$ 0.29 a	6.91 $\pm$ 2.02 b	6.50 $\pm$ 1.45 b	<0.0001
Pteromalidae	Para.	0.73 $\pm$ 0.38	0	0.32 $\pm$ 0.14	0.41 $\pm$ 0.17	0.1039
Scelionidae	Para.	0.23 $\pm$ 0.19 a	0.41 $\pm$ 0.20 a	1.05 $\pm$ 0.48 a	3.36 $\pm$ 0.69 b	<0.0001
Uncommon families		1.23 $\pm$ 0.73	2.23 $\pm$ 1.01	1.68 $\pm$ 0.93	2.14 $\pm$ 1.01	
Total Hymenoptera		18.5 $\pm$ 4.4	14.3 $\pm$ 4.1	39.7 $\pm$ 10.4	40.0 $\pm$ 3.4	
Grand total		310.2 $\pm$ 75.7	166.5 $\pm$ 24.1	459.4 $\pm$ 47.2	752.6 $\pm$ 79.9	
<b>Principal component scores</b>						
First axis		-0.84 a	-0.63 a	0.38 b	1.09 c	<0.0001
Second axis		0.98 a	-0.40 b	-0.34 b	-0.23 b	<0.0001

<sup>a</sup> Larval trophic guild. Fun. = fungivore; Para. = parasitoid; Pred. = predator; Sap. = saprophage; Xylo. = xylophage; Oth. = other guilds (Formicidae).

<sup>b</sup> Small letters in common indicate lack of significant difference from REGW multiple comparison tests ( $\alpha = 0.05$ ).

<sup>c</sup> *P*-value of randomised block-design ANOVA on rank-transformed abundance. Values in bold are significant at  $\alpha = 0.05$ .

individual families and larval trophic guilds. For each common family we used analysis of variance (with site as a blocking factor) and REGW multiple comparison procedures to test for significant differences in rank-transformed abundances among the four decay classes. For each trophic guild, both the average rank-abundance of common families and the number of uncommon families present were calculated for each log sample. An ANOVA (again, blocked by site) was performed on

these indices for each guild, with REGW multiple comparison procedures used to identify significant differences among the decay classes.

Within each decay class of log samples, we used redundancy analysis to assess whether the amount of surrounding downed CWD in the same class was correlated with the abundance and composition of common insect families. Four predictor variables were derived that represented the volume of downed

CWD at two spatial scales (20 and 79 ha) and in two size ranges ( $\geq 7.5$  and  $\geq 20$  cm diameter). Permutation tests were used to determine whether decay-class-specific volumes of CWD at each site explained a significant amount of variation in the correlation matrices of common insect families ( $\alpha = 0.05$ ). We also averaged the rank-abundance of each family across log samples from each site and performed an RDA of this correlation matrix on the total volume of downed CWD (for both spatial scales and size ranges). In addition, Spearman's rank correlation was computed for these same CWD variables and each common family, both within individual decay classes and across all decay classes. Only those families present in at least 25% of the log samples from a given decay class were considered in the analysis of individual classes. Due to the large number of tests performed, we chose a relatively conservative significance level of  $\alpha = 0.01$  for these family-level correlations.

After determining decay class associations for each trophic guild, we employed Spearman's rank correlation to assess whether, within the classes in which they were most abundant, the average rank-abundance of common families or number of uncommon families belonging to that guild were related to the amount of surrounding CWD in those same decay classes. We also averaged both trophic guild indices across the log samples from each site and correlated them with the total volume of downed CWD. Again, relationships were tested separately for downed coarse woody debris volumes at 20 and 79 ha scales, and with 7.5 and 20 cm minimum diameters. A significance level of  $\alpha = 0.05$  was used for these guild-level analyses.

### 3. Results

#### 3.1. Insect community composition

In total 37,153 individuals were collected from 88 different families of Diptera, Hymenoptera, and Coleoptera. Although similar numbers of families were identified from the three orders (30 Diptera, 29 Hymenoptera, and 29 Coleoptera), dipterans comprised 91.7% of the total number of individuals (Table 1). Parasitic wasps, ants, and other hymenopterans accounted for a further 6.7%, and beetles (Coleoptera) accounted for only 1.6% of all individuals. Overall, the greatest number of individuals were found in decay class IV and the fewest in class II (Table 1). Twenty-seven families met the criteria to be considered common, whereas the remaining 61 families were classified as uncommon.

The first two axes of a principal components analysis (Fig. 1) explained a greater amount of variance in the rank-abundance of common families than expected according to the broken-stick criterion (22.8 and 12.7%, respectively). Both axes were strongly related to log decay class: the first axis significantly separated all decay classes except I and II, whereas the second significantly separated class I from all later classes (Table 1). Taken together, these two principal components therefore distinguished the average insect composition of each of the four decay classes. Vectors representing individual insect families generally loaded in the upper and right halves of the ordination diagram, signifying positive associations with early and late decay classes of logs, respectively. A partial RDA indicated that after accounting for

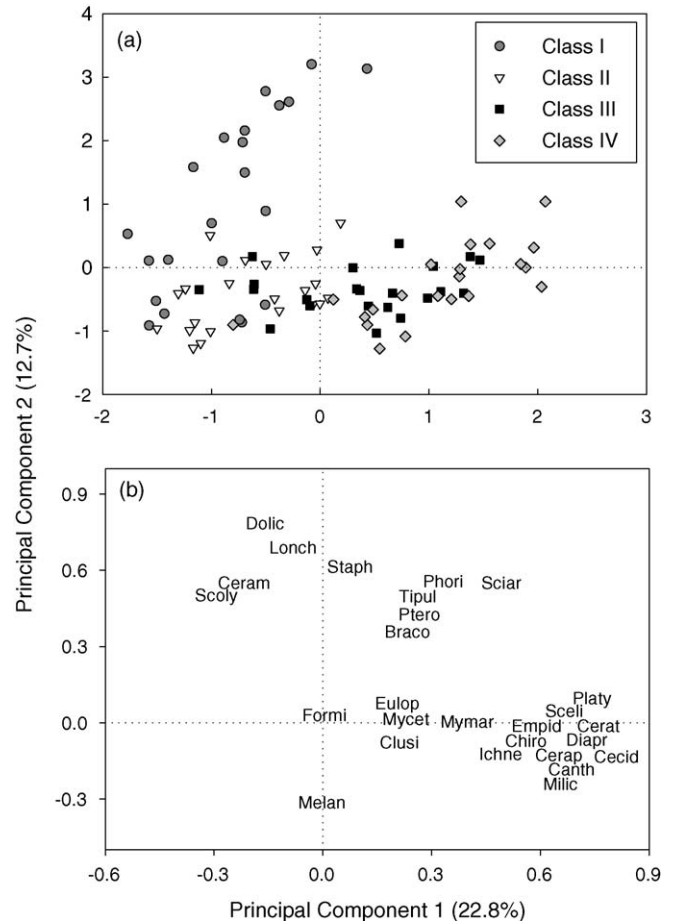


Fig. 1. Sample scores (a) and family loadings (b) from a principal component analysis on the rank-transformed abundance of 27 common insect families emerging from decaying logs in pine forests of eastern Algonquin Park, Canada. Families included were those that occurred in  $>25\%$  of the samples from at least one decay class. They are abbreviated using their first five letters and are listed in Table 1.

the variance explained by the decay classes, significant additional variation in insect composition could be explained based on the presence of loosely-attached needles ( $P = 0.002$ ), and on whether the log's heartwood was hard or not ( $P = 0.044$ ). These two variables together explained an additional 3.8% of the total variance in insect composition, compared with 21.0% accounted for by the four decay classes alone.

Family-level ANOVAs showed that 4 out of 5 common coleopteran families, 10 out of 12 common dipteran families, and 5 out of 10 common hymenopteran families varied significantly in abundance among decay classes (Table 1). Among these families, 6 were found in higher abundances in class I than in one or more later classes and 13 were found in higher abundances in classes III and/or IV than in one or both of the first two decay classes. One family (Phoridae) had a relatively high abundance in both early (I) and late (III, IV) decay classes, and was less abundant in class II. Decay class II log samples generally did not have a higher abundance of insects than other classes; of the 19 families that were found to vary in abundance across decay classes, only one was significantly more abundant in class II than in class I

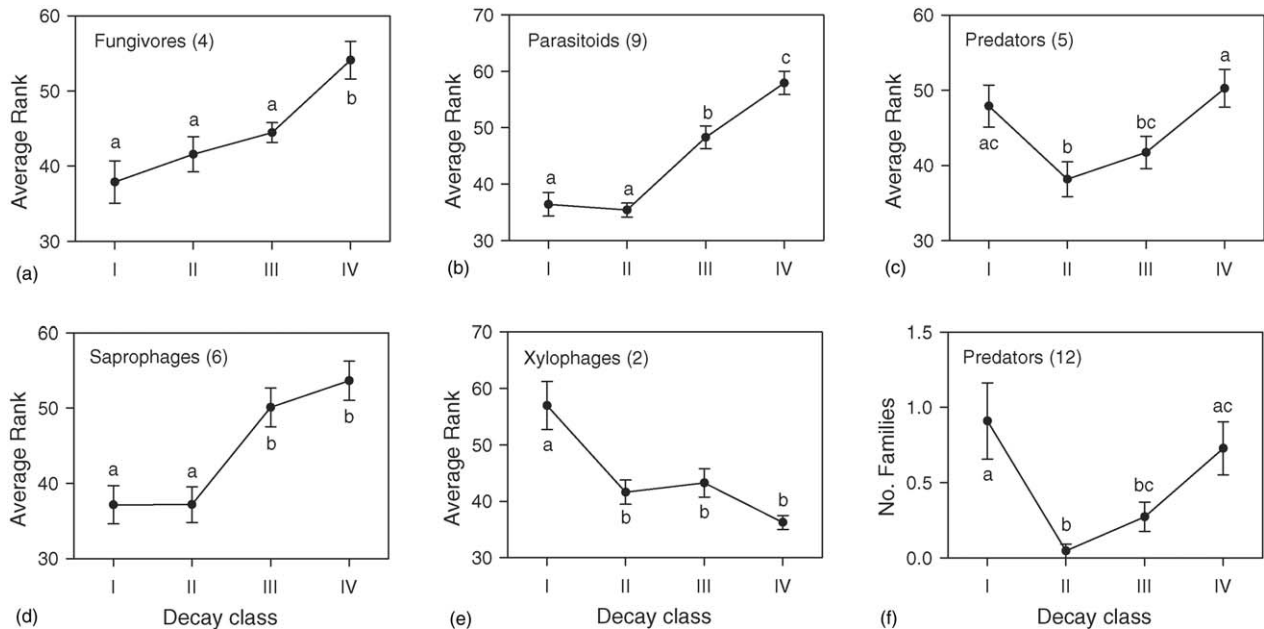


Fig. 2. Average rank-abundance of common families (a–e) and average number of uncommon families (f) in various trophic guilds, by decay class. The numbers of families included within each guild is indicated in brackets. Decay classes sharing a common letter were not significantly different ( $\alpha = 0.05$ ) based on REGW multiple comparison tests. Common families were defined as those that occurred in >25% of the samples from at least one decay class; all other families were defined as uncommon.

(Mycetophilidae) and none were significantly more abundant in class II than in classes III or IV.

### 3.2. Decay class distributions by trophic guild

We analyzed changes in the mean rank-abundance of common families and in the number of uncommon families for five trophic guilds: xylophages, fungivores, saprophages, predators, and parasitoids (guild assignments provided in Table 1 and Appendix A). Analysis of variance showed highly significant differences in the rank-abundance of common families across decay classes for each of these guilds (all  $P < 0.0001$  except predators,  $P = 0.002$ ; Fig. 2a–e). Xylophages and predators had relatively high abundances in class I logs whereas the other guilds had relatively low abundances in this class. Saprophages and parasitoids were significantly more abundant in decay class III and IV logs than in the earlier decay classes. In class IV logs, fungivores, predators, and parasitoids all had significantly greater mean abundances than in the previous class. Among uncommon taxa, predators were the only guild (of the five tested) to show significantly different numbers of families across decay classes ( $P = 0.001$ ; all others  $P > 0.05$ ). Their pattern mirrored that of common predator families, with the greatest number of families found in classes I and IV (Fig. 2f).

### 3.3. Effects of surrounding downed CWD

Mean volumes of downed coarse woody debris in decay classes I–IV were, respectively, 3.3 (range: 0.0–12.0), 9.8 (0.9–23.6), 14.4 (2.5–33.0), and 12.2 (2.4–24.5)  $\text{m}^3/\text{ha}$  at the 79 ha scale. At this same scale, total volume of downed CWD

averaged 39.6  $\text{m}^3/\text{ha}$  and ranged from 7.0 to 77.1  $\text{m}^3/\text{ha}$ . There were no significant differences in the volume of downed CWD in decay classes I, II, or IV between the sites that were harvested within the past 28 years and those that were not ( $t$ -tests for 79 ha scale; all  $P > 0.05$ ). The harvested sites did, however, have significantly more class III CWD than the others ( $P = 0.013$ ; mean  $\pm$  S.E. volume in harvested sites =  $18.4 \pm 2.5 \text{ m}^3/\text{ha}$ , in other sites =  $11.0 \pm 1.4 \text{ m}^3/\text{ha}$ ). Across all decay classes, the difference in total downed CWD volume was not significant ( $P = 0.070$ ).

Redundancy analysis showed that insect community composition within log samples in each of the four decay classes was unrelated to the volume of downed CWD in the same decay class in the surrounding 20 or 79 ha area (all  $P > 0.05$ ). Likewise, the total volume of downed CWD at each of these two scales failed to explain significant variation in insect community composition averaged across decay classes of log samples ( $P > 0.05$ ). In simple regressions performed on individual common families, only one family (Phoridae) showed a highly significant relationship between its rank-abundance within log samples and the volume of surrounding downed CWD in the corresponding decay class (DWD  $\geq 20$  cm within 20 ha area:  $r_s = 0.598$ ,  $P = 0.003$ ; within 79 ha area:  $r_s = 0.560$ ,  $P = 0.007$ ). Across decay classes, no families showed a highly significant relationship with the total volume of downed CWD at either scale (all  $P > 0.01$ ).

Although the common taxa in all five trophic guilds showed strong associations with one or two decay classes, none of these guilds showed significant relationships with the amount of surrounding downed CWD in these classes (all  $P > 0.05$ ). Among uncommon families, only predators had significantly

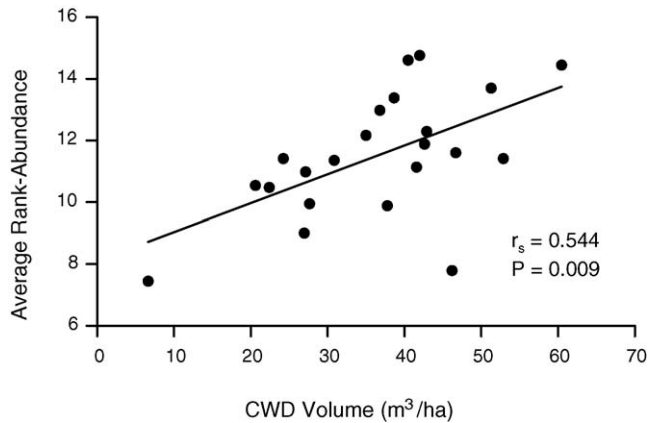


Fig. 3. Average rank-abundance of common fungivorous insect families (Cecidomyiidae, Mycetophilidae, Tipulidae, Melandryidae) emerging from pine log samples in eastern Algonquin Park, Canada, regressed against the total volume of downed CWD ( $\geq 7.5$  cm diameter) in the surrounding 20 ha area.

different numbers of families across decay classes, and the numbers of families present in classes I and IV were likewise unrelated to the amount of surrounding downed CWD in those same classes (both  $P > 0.05$ ). These findings held for DWD volume in both sizes ranges and spatial extents. When decay classes were combined, however, it was found that the abundance of common fungivores was well-correlated with the total volume of downed CWD  $\geq 7.5$  cm within the surrounding 20 ha ( $r_s = 0.544$ ,  $P = 0.009$ ; Fig. 3) and 79 ha areas ( $r_s = 0.542$ ,  $P = 0.009$ ). Total volumes of downed CWD were highly correlated between the two scales ( $r_s = 0.806$ ,  $P < 0.001$ ) and thus it was not possible to determine which scale was more relevant for wood-inhabiting fungivorous insects. No other guilds, either common or uncommon, were associated with the total abundance of downed CWD at either scale (all  $P > 0.05$ ).

## 4. Discussion

### 4.1. Successional patterns across decay classes

Principal components analysis revealed that each of four decay classes tended to support a distinctive insect community. While some additional variation could be independently explained by individual characteristics of the logs, the four decay classes succinctly captured the main patterns of insect community variation across the gradient in log decomposition. These analyses confirm that the habitat value of CWD changes over all stages of decomposition, and that our system of decay classes was useful for representing these habitat differences for many wood-inhabiting insect families. Among the individual common families, most showed a preference for either early or late decay classes of coarse woody debris. Only 8 out of 27 common families did not vary significantly in rank-abundance across the four decay classes.

Xylophages and predators both showed an affinity for logs in the earliest decay class. Xylophages, represented in our study by bark beetles (Scolytidae) and wood-boring beetles (Cerambycidae), feed on phloem and xylem tissues in trees

that have recently died, and subsequently disappear once these resources are depleted. It appears that they are accompanied by a number of associated predators (Dolichopodidae, Lonchaeidae, Staphylinidae), which leave the logs with them by the time decay class II is reached.

The abundances of saprophages and parasitoids were relatively high in decay class III logs. By this stage, the action of bacterial and fungal decomposers had undoubtedly created a log habitat rich in organic matter and other products of wood decay, upon which saprophages feed (Swift, 1977). The saprophages presumably acted as potential hosts for a rich complex of parasitic hymenopterans, which accordingly increased in abundance. Both groups remained abundant as decomposition progressed and CWD passed through to decay class IV.

Fungivores were most abundant in decay class IV CWD. Although many fungi are present in earlier decay classes (Bader et al., 1995), the fungivores did not show a numerical response until logs reached a highly advanced stage of decay (class IV). At this point, logs were undoubtedly colonized by fungi (and other organisms) characteristic of soil environments (Swift, 1977), and it is possible that these are the organisms upon which many of the fungivores feed. Also, predators and parasitoids further increased in abundance in this decay class, likely as a response to the greater availability of potential prey/hosts. However, as no sampling of the soil was conducted, it is uncertain to what degree the insect fauna of class IV logs overlapped with that of the soil itself.

Although we found strong differences among decay classes for insect guilds represented by common families, this generally was not the case for those classified as uncommon. Four of the five trophic guilds did not have significantly different numbers of uncommon families in the four decay classes, with predators being the only exception. There were only a small number of uncommon families included in the saprophages and xylophages (five and three, respectively), and it is not surprising that we failed to detect any differences within these groups (on average there was less than one family from each of these guilds in every 10 log samples, and such low occurrence rates are subject to a great deal of random variation). Fungivores and parasitoids included more families (11 and 17, respectively), but still showed more-or-less equal counts across the decay classes.

The distribution of uncommon predator families mirrored that of common ones, with the greatest number of families being found in logs in decay classes I and IV. A number of families (e.g., Ephidryidae, Nitidulidae, Stratiomyidae) were likely predators of bark beetles in class I, while others (e.g., Carabidae, Scydmaenidae) likely preyed upon invertebrates associated with highly-decayed logs. The parallel distributions of common and uncommon predators across decay classes lends good support to their affinity for CWD in both early and very advanced stages of decay.

The successional changes revealed by the four log decay classes differed in several respects from patterns that have been reported previously, though comparisons are complicated to some extent because we did not undertake species-level

analyses. Many authors have described several phases of community turnover, each dominated by a number of characteristic species (Savelly, 1939; Howden and Vogt, 1951; Heliövaara and Vaisanen, 1984; Stubbs, 1991). In contrast, we found that there were families and trophic guilds associated with either early or late decay classes, but no groups that specialized upon logs in the intermediate stages of decay. Logs in decay class II generally contained a paucity of insects relative to other classes. At this stage, most of the early wood-feeders had left and the saprophages and fungivores associated with later classes had yet to become abundant.

The absence of stronger community turnover may partly be an artifact of the decay class system that we used. Many of the early phases of faunal succession are short in duration (Heliövaara and Vaisanen, 1984), and our first decay class may have incorporated several of these together. We found, for example, that the presence of loosely-attached needles, as a proxy variable for time since death, could explain variation not accounted for by the decay class system. More intensive sampling within decay class I might be required to distinguish brief phases of faunal succession in recently-dead fallen trees.

Our results also showed a significant increase in fungivores, predators, and parasitoids in logs that were in a very advanced stage of decay. We are not aware of any other studies that report these functional changes in the insect fauna. These findings emphasize the potential value of a broad community-level approach, even at a relatively coarse scale of taxonomic resolution.

#### 4.2. Effects of surrounding downed CWD

Redundancy analysis showed that the volume of surrounding downed coarse woody debris was not a major correlate of insect community composition or abundance either within or across log decay classes. These results were largely corroborated by regressions for individual families, which failed to uncover highly significant relationships with downed CWD (at  $\alpha = 0.01$ ) for 26 of 27 common insect families. Current levels of downed CWD therefore did not seem to be limiting to the majority of wood-inhabiting insects.

In contrast to the community- and most family-level results, the abundance of the fungivorous insect guild within log samples was positively related to the total volume of downed CWD in the surrounding area (Fig. 3). The richness and abundance of an array of fungal taxa have been found to correlate with CWD supplies (Bader et al., 1995; Gomez et al., 2003; Rubino and McCarthy, 2004; Sippola et al., 2004), suggesting that lower amounts of CWD could limit numbers of fungivorous insects through reduced food availability. In Norway, Økland (1996) reported that the abundances of one-quarter of mycetophilid species were significantly influenced by the number of species of wood-inhabiting fungi present. The occurrence of certain fungivorous insects has also been found to be affected by the spatial proximity of wood-decaying fungal fruiting bodies (Jonsell et al., 1999; Kehler and Bondrup-Nielsen, 1999). Thus, the relationship we observed between fungivores and CWD availability is consistent with previous

findings that reductions in CWD can adversely affect fungal communities, and that such declines may have consequent effects on the fungivorous insect fauna.

To date, most research on saproxylic insect conservation has been carried out in northern Europe, and in particular Scandinavia, where the saproxylic insect fauna has declined dramatically as a result of sharp reductions in coarse woody debris in managed stands. Although the total volume of downed CWD was much higher at our sites (average of 40 m<sup>3</sup>/ha at the 79 ha scale; range: 7–77 m<sup>3</sup>/ha) than in managed landscapes in Fennoscandia (average of 2–10 m<sup>3</sup>/ha of CWD; Siitonen, 2001), it still appeared that at least part of the wood-inhabiting insect community responded to variation in CWD abundance. Outside of Europe, Grove (2002b) found that saproxylic beetle species richness (but not abundance) in Australian lowland rainforests was correlated with CWD volume, which ranged from 4 to 45 m<sup>3</sup>/ha. Work et al. (2004) reported that, within deciduous-dominated stands in Alberta, Canada, four species of carabid beetles had higher abundances in stands with more than 43 m<sup>3</sup>/ha of CWD than in stands with less CWD. In bottomland hardwood forests of South Carolina, Ulyshen et al. (2004) found a greater richness and abundance of woodboring and clerid beetles in 1-year-old forest gaps with nearly 25% CWD ground cover than in 6-year-old gaps with little CWD. Our study adds to the growing list of regions in which researchers have documented relationships between CWD abundance and saproxylic insects, and in conjunction with the findings of Grove (2002b) and Work et al. (2004), suggests that reductions in CWD resources may have negative impacts on this fauna even where levels exceed those presently found in Fennoscandian managed forests. Continued research should help further uncover the range of conditions under which saproxylic insect communities respond to variation in CWD availability.

## 5. Conclusions

This study revealed that insect community composition and trophic structure within downed coarse woody debris varied according to the stage of CWD decomposition, and that the abundance of fungivores within decaying logs was correlated with the amount of surrounding downed CWD. In order to avoid potential losses in biodiversity, it may be important not only to maintain adequate total amounts of downed CWD, but also to ensure that it is distributed across different decay classes. Wood-inhabiting insect biodiversity, and its associated ecological functions, may therefore best be maintained through forest management practices that do not reduce overall amounts of CWD, and that ensure it is available in both early and late stages of decomposition over time.

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## Appendix A

List of uncommon families (present in less than 25% of the log samples from each decay class) that emerged from decaying logs in eastern Algonquin Provincial Park, Canada, by order and trophic guild.

Coleoptera	Diptera	Hymenoptera
Fungivores	Fungivores	Fungivores
Cerylonidae	Synneuridae	None
Colydidae		Parasitoids
Endomychidae	Parasitoids	Aphelinidae
Laemophloeidae	Bombyliidae	Bethylidae
Lathrididae	Tachynidae	Chalcididae
Leiodidae		Chrysididae
Lycidae	Predators	Dryinidae
Mycetophagidae	Carabidae	Embolemidae
Ptiliidae	Cucujidae	Encyrtidae
Tenebrionidae	Elateridae	Eupelmidae
	Monotomidae	Figitidae
Parasitoids	Nitidulidae	Megaspilidae
None	Scydmaenidae	Mutillidae
Predators		Perilampidae
Carabidae	Saprophages	Proctotrupidae
Cucujidae	Heleomyzidae	Tiphiidae
Elateridae	Muscidae	Trichogrammatidae
Monotomidae	Syrphidae	
Nitidulidae		Predators
Scydmaenidae	Xylophages	None
	None	Saprophages
Saprophages	Other	None
Dermestidae	Agromyzidae	Xylophages
Melyridae	Scathophagidae	Siricidae
	Simulidae	
Xylophages		Other
Anobidae	Unknown	Sphecidae
Buprestidae	Chyromidae	Tenthredinidae
	Dryomyzidae	
Other	Scatopsidae	Unknown
Chrysomelidae		Sierolomorphidae
Curculionidae		
Mordellidae		
Unknown		
Aderidae		

## References

- Andren, H., 1997. Habitat fragmentation and changes in biodiversity. *Ecol. Bull.* 46, 171–181.
- Arnett, Jr., R.H., Thomas, M.C. (Eds.), 2001. *American Beetles*, vol. 1. CRC Press, Boca Raton, FL.
- Arnett, Jr., R.H., Thomas, M.C., Skelley, P.E., Frank, J.H. (Eds.), 2002. *American Beetles*, vol. 2. CRC Press, Boca Raton, FL.
- As, S., 1993. Are habitat islands islands? Woodliving beetles (Coleoptera) in deciduous forest fragments in boreal forest. *Ecography* 16, 219–228.
- Bader, P., Jansson, S., Jonsson, B.G., 1995. Wood-inhabiting fungi and substratum decline in selectively logged boreal spruce forests. *Biol. Conserv.* 72, 355–362.
- Berg, A., Ehnstrom, B., Gustafsson, L., Hallingback, T., Jonsell, M., Weslien, J., 1994. Threatened plant, animal, and fungus species in Swedish forests—distribution and habitat associations. *Conserv. Biol.* 8, 718–731.
- Carleton, T.J., 2003. Old growth in the Great Lakes forest. *Environ. Rev.* 11, S115–S134.
- Corbett, C.M., 1994. White pine management and conservation in Algonquin Park. *For. Chron.* 70, 435–436.
- Dajoz, R., 2000. *Insects and Forests: The Role and Diversity of Insects in the Forest Environment*. Intercept Ltd., Paris.
- Esseen, P., Ehnstrom, B., Ericson, L., Sjöberg, K., 1997. Boreal forests. *Ecol. Bull.* 46, 16–47.
- Freedman, B., Zelazny, V., Beaudette, D., Flemming, T., Flemming, S., Forbes, G., Gerrow, J.S., Johnson, G., Woodley, S., 1996. Biodiversity implications of changes in the quantity of dead organic matter in managed forests. *Environ. Rev.* 4, 238–265.
- Gomez, D.M., Anthony, R.G., Trappe, J.M., 2003. The influence of thinning on production of hypogeous fungus sporocarps in Douglas-fir forests in the northern Oregon Coast Range. *Northwest Sci.* 77, 308–319.
- Grove, S.J., 2002a. Saproxyllic insect ecology and the sustainable management of forests. *Annu. Rev. Ecol. Syst.* 33, 1–23.
- Grove, S.J., 2002b. Tree basal area and dead wood as surrogate indicators of saproxyllic insect faunal integrity: a case study from the Australian lowland tropics. *Ecol. Indic.* 1, 171–188.
- Hammond, H.E.J., 1997. Arthropod biodiversity from *Populus* coarse woody material in north-central Alberta: a review of taxa and collection methods. *Can. Entomol.* 129, 1009–1033.
- Hammond, H.E.J., Langor, D.W., Spence, J.R., 2004. Saproxyllic beetles (Coleoptera) using *Populus* in boreal aspen stands of western Canada: spatiotemporal variation and conservation of assemblages. *Can. J. For. Res.* 34, 1–19.
- Hansen, A.J., Spies, T.A., Swanson, F.J., Ohmann, J.L., 1991. Conserving biodiversity in managed forests: lessons from natural forests. *Bioscience* 41, 382–392.
- Harmon, M.E., Franklin, J.F., Swanson, F.J., Sollins, P., Gregory, S.V., Lattin, J.D., Anderson, N.H., Cline, S.P., Aumen, N.G., Sedell, J.R., Lienkaemper, G.W., Cromack Jr., K., Cummins, K.W., 1986. Ecology of coarse woody debris in temperate ecosystems. *Adv. Ecol. Res.* 15, 133–302.
- Hawkins, C.P., MacMahon, J.A., 1989. Guilds: the multiple meanings of a concept. *Ann. Rev. Entomol.* 34, 423–451.
- Heliovaara, K., Vaisanen, R., 1984. Effects of modern forestry on northwestern European forest invertebrates: a synthesis. *Acta For. Fenn.* 189, 1–32.
- Hills, G.A., 1959. *A Ready Reference to the Description of the Land of Ontario and its Productivity*. Ontario Department of Lands and Forests, Maple, Ont.
- Howden, H.F., Vogt, G.B., 1951. Insect communities of standing dead pine (*Pinus virginiana* Mill). *Ann. Entomol. Soc. Am.* 44, 581–595.
- Huston, M.A., 1996. Models and management implications of coarse woody debris impacts on biodiversity. In: McMinn, J.W., Crossley Jr., D.A. (Eds.), *Biodiversity and Coarse Woody Debris in Southern Forests*. General Technical Report SE-94. USDA Forest Service, Southern Research Station, Asheville, NC, pp. 139–143.
- Jackson, D.A., 1993. Principal components analysis: how many components are nontrivial and interpretable? *Ecology* 74, 2204–2214.
- Jonsell, M., Nordlander, G., Jonsson, M., 1999. Colonization patterns of insects breeding in wood-decaying fungi. *J. Insect Conserv.* 3, 145–161.
- Key, R., 1993. What are saproxyllic invertebrates? In: Kirby, P., Drake, C.M. (Eds.), *Dead Wood Matters: The Ecology and Conservation of Saproxyllic Insects*. English Nature Science, No. 7, Peterborough, UK, p. 5.
- Kehler, D., Bondrup-Nielsen, S., 1999. Effects of isolation on the occurrence of a fungivorous forest beetle, *Bolitotherus cornutus*, at different spatial scales in fragmented and continuous forests. *Oikos* 84, 35–43.
- Koenigs, E., Shea, P.J., Borys, R., Haverty, M.I., 2002. An investigation of the insect fauna associated with coarse woody debris of *Pinus ponderosa* and *Abies concolor* in Northeastern California. In: Laudenslayer Jr., W.F., Shea, P.J., Valentine, B.E., Weatherspoon, P., Lisle, T.E. (Technical Coordinators), *Proceedings of the Symposium on the Ecology and Management of Dead Wood in Western Forests*. General Technical Report PSW-181. USDA Forest Service, Pacific Southwest Research Station, Albany, CA, pp. 97–110.

- Lambert, R.L., Lang, G.E., Reiners, W.A., 1980. Loss of mass and chemical change in decaying boles of a subalpine balsam fir forest. *Ecology* 61, 1460–1473.
- Leps, J., Smilauer, P., 2003. *Multivariate Analysis of Ecological Data using CANOCO*. Cambridge University Press, Cambridge.
- Loeb, S.C., 1996. The role of coarse woody debris in the ecology of south-eastern mammals. In: McMinn, J.W., Crossley Jr., D.A. (Eds.), *Biodiversity and Coarse Woody Debris in Southern Forests*. General Technical Report SE-94. USDA Forest Service, Southern Research Station, Asheville, NC, pp. 108–118.
- Martikainen, P., Siitonen, J., Kaila, L., Punttila, P., 1996. Intensity of forest management and bark beetles in non-epidemic conditions: a comparison between Finnish and Russian Karelia. *J. Appl. Entomol.* 120, 257–264.
- Martikainen, P., Siitonen, J., Punttila, P., Kaila, L., Rauh, J., 2000. Species richness of Coleoptera in mature managed and old-growth boreal forests in southern Finland. *Biol. Conserv.* 94, 199–209.
- Maser, C., Anderson, R.G., Cromack Jr., K., Williams, J.T., Martin, R.E., 1979. Dead and down woody material. In: Thomas, J.W. (Ed.), *Wildlife Habitats in Managed Forests: The Blue Mountains of Oregon and Washington*. USDA Forest Service Agriculture Handbook, vol. 553, pp. 78–95.
- McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockerth, J.R., Wood, D.M. (Coordinators), 1981. *Manual of Nearctic Diptera*, vol. 1. Agriculture Canada Monograph No. 27. Biosystematics Research Institute, Ottawa, Canada.
- McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockerth, J.R., Wood, D.M. (Coordinators), 1987. *Manual of Nearctic Diptera*, vol. 2. Agriculture Canada Monograph No. 28. Biosystematics Research Institute, Ottawa, Canada.
- McComb, W., Lindenmayer, D., 1999. Dying, dead and down trees. In: Hunter, Jr., M.L. (Ed.), *Maintaining Biodiversity in Forest Ecosystems*. Cambridge University Press, Cambridge, pp. 335–372.
- Menard, E.A., 1982. Insects associated with dead elm trees (*Ulmus americana* Linnaeus) in Southern Ontario. M.Sc. Thesis. University of Guelph, Guelph, Canada.
- Mikkola, K., 1991. The conservation of insects and their habitats in northern and eastern Europe. In: Collins, N.M., Thomas, J.A. (Eds.), *The Conservation of Insects and their Habitats*. Academic Press, London, pp. 109–120.
- Muller, M.M., Varama, M., Heinonen, J., Hallaksela, A.M., 2002. Influence of insects on the diversity of fungi in decaying spruce wood in managed and natural forests. *For. Ecol. Manage.* 166, 165–181.
- Nemec, A.F.L., Davis, G., 2002. Efficiency of six line intersect sampling designs for estimating volume and density of coarse woody debris. BC Forest Service Technical Report TR-021, Nanaimo, BC, 12 pp.
- Økland, B., 1994. Mycetophilidae (Diptera), an insect group vulnerable to forestry practices? A comparison of clearcut, managed and semi-natural spruce forests in southern Norway. *Biodivers. Conserv.* 3, 68–85.
- Økland, B., 1996. Unlogged forests: important sites for preserving the diversity of mycetophilids (Diptera: Sciaroidea). *Biol. Conserv.* 76, 297–310.
- Økland, B., Bakke, A., Hagvar, S., Kvamme, T., 1996. What factors influence the diversity of saproxylic beetles? A multiscaled study from a spruce forest in southern Norway. *Biodivers. Conserv.* 5, 75–100.
- Panshin, A.J., de Zeeuw, C., 1980. *Textbook of Wood Technology: Structure, Identification, Properties and Uses of the Commercial Woods of the United States and Canada*, fourth ed. McGraw-Hill, NY.
- Pedlar, J.H., Pearce, J.L., Venier, L.A., McKenney, D.W., 2002. Coarse woody debris in relation to disturbance and forest type in boreal Canada. *For. Ecol. Manage.* 158, 189–194.
- Quinn, G.P., Keough, M.J., 2002. *Experimental Design and Data Analysis for Biologists*. Cambridge University Press, Cambridge.
- Rowe, J.S., 1972. *Forest Regions of Canada*. Canadian Forest Service, Ottawa, Canada.
- Rubino, D.L., McCarthy, B.C., 2004. Composition and ecology of macrofungal and myxomycete communities on oak woody debris in a mixed-oak forest of Ohio. *Can. J. For. Res.* 33, 2151–2163.
- Samuelsson, J., Gustafsson, L., Ingflog, T., 1994. Dying and Dead Trees: A Review of their Importance for Biodiversity. Swedish Threatened Species Unit, Uppsala, Sweden.
- Savely, H.E., 1939. Ecological relations of certain animals in dead pine and oak logs. *Ecol. Monogr.* 9, 323–385.
- Siitonen, J., 1994. Decaying wood and saproxylic Coleoptera in two old spruce forests: a comparison based on two sampling methods. *Ann. Zool. Fenn.* 31, 89–95.
- Siitonen, J., 2001. Forest management, coarse woody debris and saproxylic organisms: Fennoscandian boreal forests as an example. In: Jonsson, B.G., Krus, N. (Eds.), *Ecology of Woody Debris in Boreal Forests*. *Ecol. Bull.* 49, pp. 11–41.
- Siitonen, J., Martikainen, P., 1994. Occurrence of rare and threatened insects living on decaying *Populus tremula*: a comparison between Finnish and Russian Karelia. *Scand. J. For. Res.* 9, 185–191.
- Sippola, A.-L., Siitonen, J., Kallio, R., 1998. Amount and quality of coarse woody debris in natural and managed coniferous forests near the timberline in Finnish Lapland. *Scand. J. For. Res.* 13, 204–214.
- Sippola, A.-L., Simila, M., Monkkonen, M., Jokimaki, J., 2004. Diversity of polyporous fungi (Polyporaceae) in northern boreal forests: effects of forest site type and logging intensity. *Scand. J. For. Res.* 19, 152–163.
- Speight, M.C.D., 1989. Saproxylic invertebrates and their conservation. *Nature and Environment Series No. 42*. Council of Europe, Strasbourg, France.
- Spies, T.A., Franklin, J.E., Thomas, T.B., 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. *Ecology* 69, 1698–1702.
- Stubbs, A.E., 1991. Insects in dead wood in standing and fallen trees. In: Fry, R., Lonsdale, D. (Eds.), *Habitat Conservation for Insects—A Neglected Green Issue*. Amateur Entomologists Society, Brentwood, UK, pp. 58–67.
- Sturtevant, B.R., Bissonette, J.A., Long, J.N., Roberts, D.W., 1997. Coarse woody debris as a function of age, stand structure, and disturbance in boreal Newfoundland. *Ecol. Appl.* 7, 702–712.
- Sverdrup-Thygesen, A., Ims, R.A., 2002. The effect of forest clearcutting in Norway on the community of saproxylic beetles on aspen. *Biol. Conserv.* 106, 347–357.
- Swift, M.J., 1977. The ecology of wood decomposition. *Sci. Prog.* 64, 175–199.
- Teskey, H.J., 1976. Diptera larvae associated with trees in North America. *Mem. Entomol. Soc. Can.* 100, 1–53.
- Triplehorn, C.A., Johnson, N.F., 2005. *Borror and DeLong's Introduction to the Study of Insects*, seventh ed. Thompson Books/Cole, Belmont, CA.
- Ulyshen, M.D., Hanula, J.L., Horn, S., Kilgo, J.C., Moorman, C.E., 2004. Spatial and temporal patterns of beetles associated with coarse woody debris in managed bottomland hardwood forests. *For. Ecol. Manage.* 199, 259–272.
- Van Wagner, C.E., 1968. The line intersect method in forest fuel sampling. *For. Sci.* 14, 20–26.
- Vanderwel, M.C., 2005. *Modelling the dynamics of coarse woody debris in central Ontario*. M.Sc.F. Thesis. University of Toronto, Toronto, Ont.
- Wiens, J.A., 1984. Resource systems, populations, and communities. In: Price, P.W., Slobodkinoff, C.N., Gaud, W.S. (Eds.), *A New Ecology: Novel Approaches to Interactive Systems*. John Wiley and Sons, NY, pp. 397–436.
- Work, T.T., Shorthouse, D.P., Spence, J.R., Volney, W.J.A., Langor, D., 2004. Stand composition and structure of the boreal mixedwood and epigeaic arthropods of the ecosystem management emulating natural disturbance (EMEND) landbase in northwestern Alberta. *Can. J. For. Res.* 34, 417–430.
- Zhong, H., Schowalter, T.D., 1989. Conifer bole utilization by wood boring beetles in western Oregon. *Can. J. For. Res.* 19, 943–947.