Early colonization of *Populus* wood by saproxylic beetles (Coleoptera)

H.E. James Hammond, David W. Langor, and John R. Spence

Abstract: The early colonization of newly created coarse woody material (CWM) by beetles was studied in aspen mixedwood forests at two locations in north-central Alberta. Healthy trembling aspen (*Populus tremuloides* Michx.) trees, in old (>100 years) and mature (40–80 years) stands, were cut to provide three types of CWM: stumps, bolts on the ground (logs), and bolts suspended above the ground to simulate snags. Over 2 years, 1049 Coleoptera, representing 49 taxa, were collected. Faunal structure differed little between the two locations. Species diversity was higher in old than in mature stands, and higher in stumps and logs than in suspended bolts; however, these "snags" tended to have higher abundance when compared with stumps and logs. Overall beetle abundance and the catch of wood-boring beetles was significantly higher in the first year post-treatment, mainly because of the ambrosia beetle (*Trypodendron retusum* (LeConte)) and one of its predators, *Rhizophagus remotus* LeConte; however, beetle diversity was higher in the second year, suggesting that early wood-boring species may "precondition" the wood for a number of succeeding species. The high turnover rate of taxa and spatial or temporal variation in faunal structure suggests that effort focused on habitat classification of CWM will facilitate management to conserve saproxylic faunal diversity.

Résumé : La colonisation initiale, par les coléoptères, de débris ligneux grossiers fraîchement produits a été étudiée sur deux sites dans des forêts mixtes dominées par le peuplier faux-tremble (*Populus tremuloides* Michx.) et situées dans le centre-nord de l'Alberta. Des tiges saines de peuplier faux-tremble ont été abattues et débitées dans de vieux peuplements (>100 ans) et dans des peuplements matures (40–80 ans), de façon à créer trois types de débris ligneux grossiers : des souches, des billes au sol (billots) et des billes suspendues au-dessus du sol pour simuler des chicots. Plus de 1049 coléoptères appartenant à 49 taxa ont été récoltés au cours d'une période de 2 ans. La structure faunique des deux sites différait très peu. La diversité des espèces était plus grande dans les vieux peuplements que dans les peuplements matures, et plus grande dans les souches et les billots que dans les billes suspendues. Cependant, ces dernières tendaient à présenter une abondance plus élevée que les souches et les billots. L'abondance globale des coléoptères et les captures de perceurs de l'écorce étaient significativement plus élevées au cours de la première année après le traitement, surtout à cause du scolyte d'Ambrosie, (*Trypodendron retusum* (LeConte)), et de l'un de ses prédateurs, *Rhizophagus remotus* LeConte. Cependant, la diversité des coléoptères était plus élevée au cours de la deuxième année, ce qui suggère que les espèces les plus hâtives de perceurs de l'écorce pourraient préparer le bois pour plusieurs des espèces qui viennent par la suite. Le taux de rotation élevé des taxa et la variation spatio-temporelle de la structure faunique suggèrent que des efforts consentis à la classification des habitats que procurent les débris ligneux grossiers pourraient faciliter l'aménagement visant à conserver la diversité de la faune qui se développe sur le bois mort.

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Introduction

A large percentage of biomass in boreal aspen–mixedwood forests is made up of submerchantable timber and coarse woody material (CWM) in various states of decay. For example, it is estimated that healthy trembling aspen (*Populus tremuloides* Michx.) forest stands contain between 10 and 20 Mg·ha^{-1} (Harmon et al. 1986) or up to 29% of above- and below-ground biomass, as snags, logs, stumps, and other forms of dead woody material (Peterson and Peterson 1992). CWM has many important structural roles in forest ecosystems, including provision of habitat for autotrophs and heterotrophs and regulation of geomorphic processes such as soil erosion and the downslope movement of water and litter (Harmon et al. 1986). Dead wood is also important in nutrient dynamics as it contributes nitrogen, carbon, phosphorus, potassium, calcium, magnesium, and other nutrients to forest soils (Ausmus 1977; Swift 1977; Hendrickson 1988; Hendrickson et al. 1989). Woody material decomposes rather slowly and is low in nutrient quality compared with needles and foliage but rather is a long-term source of nutrients (Larsen et al. 1978; Vogt et al. 1986; Alban and Pastor 1993; Kauffman et al. 1993).

Decomposition of CWM is influenced by "saproxylic" invertebrates associated with this resource (Ausmus 1977;

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Swift 1977). Saproxylic species are those that depend upon dead wood for at least part of their life cycle (Speight 1989). These species are functionally important to forest ecosystems, both because of their crucial involvement in breakdown of CWM and nutrient cycling (Ausmus 1977; Reichle 1977; Swift 1977; Shaw et al. 1991) and because of their significance as food for valued species like woodpeckers (Martikainen et al. 1998). Generally, wood-boring beetles are the first to colonize weakened or newly dead trees, attracted to them by volatiles such as ethanol and terpenes emanating from dying or recently dead trees (Roling and Kearby 1975; Millar et al. 1986; Witcosky et al. 1987; Ytsma 1989; Schroeder 1992). Also, symbiotic relationships between some beetle species and fungi increase the ability of these organisms to colonize and use woody material. The best known examples include bark and ambrosia beetles and their associated staining and ambrosia fungi (e.g., Abrahamson et al. 1967; Wood 1982; Paine et al. 1997). Some beetles gain nutrients directly from fungi (e.g., ambrosia beetles and ambrosia fungi), but many other beetle species are simply vectors of decay fungi. The close association between insects and decay fungi strongly influences the rate of wood decay (Gardiner 1957; Wallis et al. 1971; Zhong and Schowalter 1989; Lowell et al. 1992).

Recent work on the saproxylic arthropod fauna associated with *Populus* CWM has shown that the fauna is highly diverse in terms of both species and trophic roles (Hammond 1996, 1997). Given the functional importance of the saproxylic fauna in forest ecosystems, and its sensitivity to forest harvesting and other management activities (Heliövaara and Väisänen 1984; Siitonen and Martikainen 1994; Väisänen et al. 1993; Hammond 1996, 1997; Martikainen 2001), a better understanding of its structure, function, and spatiotemporal dynamics in boreal mixedwood ecosystems can contribute to development of forest management strategies that minimize impacts on ecosystem structure and function.

We investigated the dynamics of early colonization of *Populus* CWM by arthropods. Specifically, we were interested in (*i*) identifying what arthropod assemblages are the first to colonize recently dead wood; (*ii*) how various landscape features such as geographic region, stand age, CWM type (i.e., snags, logs, stumps) influenced species assemblages, diversity, and abundance; and (*iii*) how time after tree death influenced assemblage turnover. The earliest stage of faunal succession in coarse woody debris (CWD) is unique, short lived (1–2 years), and is dominated by insects and their associates that require fresh phloem and wood. Although we provide basic data about arthropods at the ordinal level, we focus here on the Coleoptera, because it is a dominant insect order in CWM (Speight 1989; Hammond 1997); the taxonomy of many beetle families is relatively well known and beetles are easy to collect, preserve, and store for later identification. Furthermore, the distribution of many beetle species in Canada is relatively well known and has recently been documented (Bousquet 1991). The Coleoptera is diverse with respect to species and trophic role, and many previous studies of the CWM fauna elsewhere have focused on beetles (e.g., Fager 1968; Speight 1989; Väisänen et al. 1993; Käila et al. 1994; Jonsell and Nordlander 1995; Martikainen et al. 1999, 2001), providing a basis for analysis and comparison.

Materials and methods

Stand descriptions and experimental design

Living aspen trees were cut to create new CWM in the spring of 1993 at two sites in northern Alberta, near Lac la Biche (54°51′N, 111°27′W) and near Eureka River (56°35′N, 118°37′W). Study sites were dominated (>80% of trees) by trembling aspen and balsam poplar (*Populus balsamifera* L.), but also contained some white spruce (*Picea glauca* (Moench) Voss) and birch (*Betula* spp.).

The experiment was replicated in three old (>100 years) and three mature (40–80 years) stands near Lac la Biche, and two old and two mature stands near Eureka River. In each replicate, increment core samples were extracted at breast height from the heartwood of standing live trees to determine the amount of fungal infection in apparently healthy trees. We controlled for the amount of heart rot in trees by selecting only trees with <20% of the core sample having fungal stain. In each replicate, three dominant aspen trees were cut so as to leave a 120 cm high stump in the ground. Two 120 cm long sections were cut from the base of each felled tree; one was left on the ground to serve as a log, and the second was suspended with rope 1–2 m above the ground and thus oriented to simulate a "snag." The diameters of the trees selected from old stands ranged from 24.1 to 44.5 cm (mean 33.8 cm), and trees in mature stands ranged from 15.8 to 28.6 cm (mean 22.9 cm). The exposed faces of the wood were sealed with paraffin wax to slow down moisture loss.

In early spring of 1994, a 60 cm long wood bolt was cut from each snag, log, and stump section in each replicate for rearing. The newly exposed face of each wood section was then resealed with paraffin. Each sample was labeled, placed in a plastic bag to prevent insect escape, immediately transported to the laboratory and placed in an individual 1-m^3 cardboard box for rearing. The bottom of each box was covered with tape to minimize crevices in which arthropods could crawl. After the bolts were placed in the boxes they were sealed. A clear plastic jar was attached to the bottom of each box by hot gluing the lid to the cardboard. A 3 cm diameter hole cut through the box and lid facilitated collection of arthropods as they were attracted to light emanating from the hole. Rearings were checked weekly from mid-May to mid-October 1994. In mid-October, bolts were removed and the containers searched for any remaining arthropods. The length and diameter of each bolt was measured to the nearest centimetre. The wood sections remaining in the field were similarly handled and arthropods were reared over the same general time frame in 1995.

Data analysis

All analyses were done in SAS unless otherwise indicated. All analysis of variance (ANOVA), and multivariate analysis of variance (MANOVA), utilized a general linear model consisting of a four-way comparison in a split-plot design with the main effects of region and stand age (tests of hypotheses used the mean square of stands nested within the region × age interaction), wood section (tests of hypotheses used the mean square of the type × stand interaction nested within region × age interaction), and year of rearing (tests of hypotheses used the mean square of the year × stand interaction nested within the region × age interaction). Examination of residual values from the ANOVA using the Shapiro–Wilk statistic, stem leaf and box plots, normal probability plot, and plot of the residual values against predicted values indicated that the number of species collected from each wood bolt followed a normal distribution ($N = 180$, $W = 0.98$). However, the total raw abundance (i.e., beetle counts) from each wood bolt was not ($N = 180$, $W = 0.57$); therefore, beetle abundance from each wood bolt was transformed to log(abundance + 1), which normalized the abundance data ($N = 180$, $W = 0.98$). Because the diameter of each wood bolt varied widely across stand ages, we used wood volume as a covariate in

analysis. A test of homogeneity of slopes for the volume covariate and the main effects in the model were nonsignificant, indicating that volume is an appropriate covariable. Separate analyses using bolt surface area and squared bolt diameter as a covariate were identical to that using volume. Main effects with greater than two means were compared using the "pdiff tables" option in SAS.

Mean species richness and overall log transformed abundance of Coleoptera from each wood bolt was compared across spatiotemporal scales using ANOVA. A number of species diversity and evenness indices were calculated to minimize possible bias associated with a single measure. SAS was used to generate the following diversity indices (where p_i is the proportional abundance of the ith species, and S is the total number of species): the compliment of Simpson's index ($1 - C = 1 - \Sigma_i p_i^2$, where $i = 1, 2, …, S, 0 \leq C \leq 1$), Shannon index ($H = -\Sigma_i p_i \ln(p_i)$, where $i = 1, 2, …, S, 0 \leq H \leq \infty$), Hill's diversity ($N_1 = \exp[\Sigma_i p_i \ln(p_i)]$, where $i = 1, 2, …, S, 0 \leq N_1 \leq \infty$), Hill's reciprocal of Simpson's index ($N_2 = (\Sigma_i p_i^2)^{-1}$, $i = 1, 2, …, S, 0 \leq N_2 \leq S$); and evenness indices: Pielou's index ($J = H/\ln(S)$), Hurlbert's index ($V = \Sigma_i p_i^2/(1/S)$), and Hill's index ($E = N_2/N_1$) (Simpson 1949; Hurlbert 1971; Hill 1973; Peet 1974; Pielou 1975; Magurran 1988). Rarefaction, which corrects for uneven beetle counts among samples by estimating the number of species expected in a random subsample of individuals drawn from the original sample, was also used as a diversity index (Simberloff 1978). Rarefaction was calculated using a Web-based program (www.gause.biology.ualberta.ca/jbrusto).

To analyze trophic composition of the beetle assemblage, each beetle taxon was assigned one of four trophic roles (predator, fungivore, wood borer, and scavenger), based on the biology of the predominant life stage found in dead wood. If the trophic role of a species was uncertain, it was assigned to an "unknown" category. The log-transformed abundance of each trophic role for each bolt was compared across spatial and temporal scales using ANOVA, and the abundance of all trophic groups were analyzed together using MANOVA.

Results

A total of 5799 arthropods were collected over the 2 years of this study. The six most abundant orders accounted for 99% of the overall catch: Diptera (41%), Acari (22%), Coleoptera (18%), Collembola (8%), Psocoptera (6%), and Hymenoptera (3%). Except for the Lepidoptera and Araneae, which had total catches of <30 individuals, the remaining orders, which included the Hemiptera, Thysanoptera, and Trichoptera, had catches of <5 individuals each. A total of 1049 specimens and 49 identified taxa (genera or species) of Coleoptera were collected (Table 1).

Region and stand age

Saproxylic beetle catch, species richness, and diversity were similar for both regions (Table 2); however, 16 of 40 beetle taxa collected at Lac la Biche and 9 of 32 at Eureka River were exclusively captured in the respective regions (Table 1). Beetle trophic structure at each regional site was dominated by fungivores and predators (Table 3). There was a significantly higher wood borer abundance at Lac la Biche (Table 3) ($F = 6.21, P = 0.04$); however, when all trophic groups were analyzed together there were no significant differences between regions (MANOVA, $F_{[5,2]} = 4.69, P = 0.18$).

Although there was no effect of stand age on mean beetle species richness and catch, diversity and evenness estimates tended to be higher in old stands (Table 2). Seven of 25 beetle taxa collected in mature stands and 24 of 42 collected in old stands were exclusively captured in the respective stand ages (Table 1). Overall trophic abundance did not vary significantly with stand age (MANOVA, $F_{[5,2]} = 4.67, P = 0.19$) (Table 3).

CWM type

Neither species richness or catch of saproxylic beetles was affected by wood type; however, species diversity and evenness measures showed that assemblages in snags were less diverse than in either stumps or logs (Table 2). Twelve of 36 beetle taxa collected from stumps, 5 of 28 beetles from logs, and 6 of 24 from snags were exclusively captured in the respective CWM types (Table 1). Overall beetle trophic structure was significantly influenced by wood type (MANOVA $F_{[10,16]} = 2.58, P = 0.04$); wood borers and fungivores were more abundant in snags, while scavengers and predators were more abundant in stumps and logs. There was also a significant type × region interaction ($F = 5.14, P = 0.02$), with fungivores significantly more abundant in snags from Eureka River.

Temporal variation

Saproxylic beetle species richness was not influenced by year of collection, but diversity and evenness were much higher in samples from the second year (1995). Beetle catch was significantly higher in 1994 ($F = 9.61, P = 0.02$) (Table 2), mostly as a result of the greater catch of Scolytidae and Rhizophagidae in that year. There was a significant year × age interaction for species richness ($F = 7.42, P = 0.04$) with richness significantly lower in 1995 mature stands. Significant year × CWM type interactions were observed for species richness ($F = 4.06, P = 0.05$), which was lowest in 1995 snags, and for catch ($F = 5.47, P = 0.02$), which was highest in 1994 snags. Thirteen of 29 taxa collected in 1994 and 19 of 36 taxa in 1995 were collected in only one year (Table 1). In general, trophic structure did not change across years (MANOVA, $F_{[5,2]} = 5.89, P = 0.15$). When groups were individually analyzed, however, fungivore abundance showed a year × CWD type effect with higher abundance in snags collected in 1994 ($F = 6.33, P = 0.01$); scavengers showed a year × region interaction with higher abundance from Lac la Biche stands in 1994 ($F = 6.94, P = 0.04$); and wood borers exhibited a significant year effect, with a higher a catch in 1994 ($F = 21.85, P < 0.01$) (Table 3), and year × region effect, with higher abundance catch in 1994 at Lac la Biche ($F = 13.02, P = 0.01$).

Discussion

The numerical dominance of Diptera, Acari, Coleoptera, and Collembola in new *Populus* CWM is also evident in more advanced decay classes (Hammond 1997). Notably, Hymenoptera were less dominant in new CWM than in other decay classes, largely because ants, such as *Camponotus* and *Formica*, which are usually abundant in more decayed wood, were not well represented during the early stages of decay. Also, Psocoptera comprised a larger proportion of overall arthropod abundance in new CWM than in other decay classes, perhaps reflecting food sources (e.g., algae, lichens, and molds on and beneath the bark surface) or oviposition

Table 1. The catch of Coleoptera collected from new coarse woody material from boreal mixedwood forests in northern Alberta.

Family	Species	Role[a]	Stump 1994	Stump 1995	Log 1994	Log 1995	Snag 1994	Snag 1995	Eureka River	Lac la Biche	Old	Mature
Bostrichidae	*Endecatomus rugosus* (Randall)	WB					*			*		*
Buprestidae	*Agrilus liragus* Bart.& Brwn.	WB			*		*			*	*	
Carabidae	*Agonum obsoletum* Say	P		*					*		*	
	Platynus decentis (Say)	P		*				*	*	*	*	
	Trichocellus cognatus (Gyllenhal)	P					*			*		*
Cerambycidae	*Trachysida mutabilis* (Newman)	WB					*		*			*
Cerylonidae	*Cerylon castaneum* Say	F		*		*				**	*	*
Corylophidae	*Molamba biguttata* (LeConte)	F	**	*	***	*	****	*	****	***	****	****
	Orthoperus scutellaris LeConte	F			*	*			*	*	*	*
Cryptophagidae	*Atomaria ephippiata* Zimmerman	F		**		*		*	*	***	***	
	Atomaria (*Anchicera*) spp.	F	**	*	*			*		**	**	*
	Atomaria (*Atomaria*) spp.	F		*					*		*	
	Antherophagus ochraceus Melsheimer	F		*	*	*		*	*	*	*	
	Cryptophagus acutangulus Gyllenhal	F	*		*				*	*	*	*
	Cryptophagus tuberculosis Maklin	F		*				*	*	*	*	
	Henoticus spp.	F				*			*	*	*	*
Cucujidae	*Cucujus clavipes* Fab.	P		*		*		*	*	**	*	*
	Laemophloeus biguttatus (Say)	P			*				*		*	
Dermestidae	*Dermestes lardarius* L.	S	*			*			*	*	*	*
	Trogoderma sinistrum Fall	S			*					*		*
Histeridae	*Platysoma lecontei* Marseul	P	*						*		*	
Lampyridae	*Pyractomena borealis* (Randall)	P	*							*	*	
Lathridiidae	*Corticaria* spp.	F	*	*	*	**	*	**	**	***	***	**
	Enicmus sp. A	F	*							*		*
	Lathridius sp. A	F					*			*		*
	Melanopthalma pumilla (LeConte)	F	*			*				*	*	
Leiodidae	*Agathidium* spp.	F	*			*			*	*	*	
Lymexylidae	*Hylecoetus lugubris* Say	WB		*						*	*	
Melandryidae	*Enchodes sericea* (Haldeman)	S	*							*	*	
Micropeplidae	*Micropeplus laticollis* Maklin	F				*				*	*	
Nitidulidae	*Epuraea* spp.	F	*	*		*	*		*	*	*	*
	Glischrochilus moratus Brown	F	*				*		*	*	*	*
Pselaphidae	*Batrisodes* spp.	P		*						*	*	
	Euplectus duryi Casey	P		**		*			**	*	**	*
Ptiliidae	*Acrotrichus* spp.	F		*					*		*	
Pyrochroidae	*Dendroides testaceus* LeConte	F		*					*		*	
Rhizophagidae	*Rhizophagus bruneus* Horn	P	*	*	**	***	*		***	**	***	**
	Rhizophagus remotus LeConte	P	***	**	***	**	***	*	***	****	****	****
Scolytidae	*Procryphalus mucronatus* (LeConte)	WB						**	**		**	
	Trypodendron retusum (LeConte)	WB	***		***		****		**	****	****	****
Staphylinidae	Aleocharinae spp.	?	*	**	*	***	*	*	***	***	***	**
	Carphacis nepigonensis (Bernhauer)	P	*						*		*	
	Nudobius cephalus (Say)	P		*	*	*			**	*	**	*
	Phloeonomus lapponicus (Zetterstedt)	S	*		*	*	*		*	*	*	*
	Pseudopsis sagitta Herman	P			*	*				*	*	
	Quedius plagiatus Mannerheim	P	*			*			*	*	*	
	Quedius velox Smetana	P		*		*			*	*	*	
	Sepedophilus littoreus (L.)	F		*						*	*	
Trogossitidae	*Thymalus marginicollis* Chevrolat	P					*			*		*

Note: Asterisks show the numbers of individuals captured as follows: *, 1–5 individuals; **, 6–20 individuals; ***, 21–75 individuals; ****, >75 individuals.

[a]F, fungivore; P, predator; S, scavenger; WB, wood borer; ?, unknown or uncertain of the stage(s) found in dead wood.

Table 2. Species richness, diversity, and catch of saproxylic beetles in new coarse woody material from boreal mixedwood forests in northern Alberta.

	Species richness[a]	Catch[b]	Rarefaction[c]	Shannon index (H)	Simpson index ($1 - C$)	Hill index (N_1)	Hill index (N_2)	Hurlbert evenness (V)	Pielou evenness (J)	Hill evenness (E)
Region										
Eureka River	1.6±0.4	1.2±0.2	31.4±0.7 (400)	1.95	0.72	7.02	3.64	0.75	0.56	0.52
Lac La Biche	1.4±0.3	1.1±0.2	32.5±2.2 (400)	1.96	0.71	7.07	3.49	0.73	0.53	0.49
Stand age										
Old	1.5±0.5	1.2±0.3	37.4±1.8 (400)	2.55	0.87	12.80	7.73	0.89	0.68	0.60
Mature	1.5±0.5	1.1±0.3	22.5±1.4 (400)	1.63	0.72	5.11	3.53	0.74	0.51	0.69
Type										
Stump	1.6±0.2	1.1±0.2	30.8±1.9 (200)	2.44	0.84	11.43	6.36	0.87	0.67	0.56
Log	1.6±0.2	1.1±0.2	25.7±1.3 (200)	2.41	0.88	11.12	8.08	0.91	0.72	0.73
Snag	1.3±0.2	1.3±0.2	15.2±2.0 (200)	1.55	0.69	4.70	3.28	0.73	0.49	0.70
Year										
1994	1.6±0.2	1.4±0.1a	16.2±2.1 (250)	1.56	0.70	4.77	3.37	0.73	0.46	0.71
1995	1.4±0.2	0.9±0.1b	35.4±0.7 (250)	2.83	0.91	16.88	11.37	0.94	0.79	0.67

Note: Means followed by different letters are significantly different at $P < 0.05$ (see text for statistical details).
[a]Values are mean number of species ± SE; the mean is based on catches from individual wood bolts.
[b]Values are mean catch (log(abundance + 1)) ± SE; the mean is based on catches from individual wood bolts.
[c]Values are the expected number of species ± SD in a subsample of n individuals; n is given in parentheses.

sites (branches and trunks) were more abundant on new CWM.

Regional and age effects

The diversity and trophic structure of beetles was remarkably similar among regions but clearly varied with stand age. This study and other work in these same forest stands (Hammond 1996) revealed higher beetle diversity in new CWM in old as opposed to mature stands; however, when all decay classes were considered together, beetle diversity was similar among stand ages (Hammond 1996; Spence et al. 1997). Most of the higher diversity in old stands can be attributed to the higher number of generalist predator species, especially Carabidae and Staphylinidae collected there. This trend of higher diversity of predatory insect groups in older stands has also been shown for the litter fauna from aspen mixedwood stands (Spence et al. 1996, 1997), as well as from old montane lodgepole pine (*Pinus contorta* Dougl. ex Loud.) stands (Spence et al. 1996). It may be that the larger diameter of CWM in old stands provides more suitable habitat for predators or that significant populations of these species require long periods to develop, as suggested in the work of Niemelä et al. (1993).

Most of the beetles collected exclusively in one region or in one stand age-class were relatively rare, and their apparent geographic or habitat restriction is probably a sampling artefact. Even most of the more common species caught in one region or age-class during this study were captured in both regions or both age-classes during other sampling (Hammond 1996). Thus, our data illustrate that even relatively abundant taxa may be missed with limited sampling and that accurate inventories of the saproxylic fauna within a region or stand will require large effort and substantive resources.

Distributions of two species appear to be either regionally restricted or prefer old-growth stands, as distribution patterns found in this study corroborate other work in Alberta. The wood-boring bostrichid, *Endecatomus rugosus* (Randall),

Table 3. Least squares means ± SE log(abundance + 1) of beetle trophic groups colonizing newly created sections of coarse woody material in aspen mixedwood stands in northern Alberta.

	Trophic group			
	Fungivore	Predator	Scavenger	Wood borer
Region				
Eureka River	0.7±0.1	0.6±0.2	0.02±0.02	0.1±0.1a
Lac La Biche	0.4±0.1	0.5±0.1	0.04±0.02	0.5±0.1b
Age				
Old	0.6±0.2	0.5±0.2	0.01±0.03	0.3±0.2
Mature	0.5±0.2	0.6±0.2	0.05±0.03	0.3±0.2
CWM type				
Stump	0.5±0.1	0.6±0.1	0.04±0.02	0.2±0.1
Log	0.5±0.1	0.6±0.1	0.04±0.02	0.2±0.1
Snag	0.7±0.1	0.4±0.1	0.01±0.02	0.5±0.1
Year				
1994	0.7±0.1	0.6±0.1	0.04±0.01	0.6±0.1a
1995	0.4±0.1	0.4±0.1	0.02±0.01	0.06±0.1b

Note: Means followed by different letters are significantly different at $P < 0.05$ (see text for statistical details). Means are based on catches from each individual wood bolt.

was collected exclusively at Lac la Biche (Hammond 1996, 1997) and is thought to have a more eastern distribution (Bousquet 1991). The transcontinental predaceous staphylinid, *Pseudopsis sagitta* Herman, was found only in old stands at Lac la Biche (Hammond 1996). Spence et al. (1997) also found that *P. sagitta* was almost exclusively collected in litter samples taken from old stands, furthering the evidence that this species may be an old-growth specialist.

CWM type and modes of colonization

Although there were no statistically significant differences in number of beetles collected among wood types, there tended to be more beetles collected from the "hanging" snag

sections compared with woody material in contact with the ground. Lower beetle diversity in snags than in other CWM types, however, likely reflects their inaccessibility to epigaeic taxa that colonize mainly by walking. Although overall beetle trophic structure was significantly influenced by CWM type, individual trophic groups were not. Wood borers tended to be more abundant in snags than in logs and stumps suggesting that they colonize mainly by flight; however, they were also collected in the other wood types. Others have pointed out that many wood- and bark-boring beetles are attracted to dark, vertical silhouettes (Raffa and Berryman 1980; Amman and Cole 1983). Although stumps also present such silhouettes, beetles probably fly and search for hosts at higher levels above the ground and, thereby, minimize exposure of their young stages to the many predatory taxa found closer to the litter layer. Predators were more abundant in logs and stumps than in snags, suggesting that many taxa, especially carabids and staphylinids, disperse more by walking or may require more cover as is offered on the ground.

Faunal succession

There was a notable succession in arthropod faunal composition over the first 2 years (Table 1). Beetles, mainly *Trypodendron retusum* (LeConte) and it's associated rhizophagid predators, dominated the fauna in the first year and accounted for approximately 52% of the overall beetle catch. Scolytidae and other bark- and wood-borers precondition CWM for colonization by creating many access routes into the phloem and wood for other arthropods and fungi (Zhong and Schowalter 1989). Groups such as Collembola, Acari, and Diptera, many of which are fungivorous or saprophagous, greatly increased in abundance in the second year. Howden and Vogt (1951) and Fager (1968) also showed that the abundance and diversity of arthropods entering CWM increased during, or just after, initial colonization by woodboring beetles. Unfortunately, much of the work focusing on wood decay has looked exclusively at the effects of woodboring pests and their symbiotic fungi (e.g., Wallis et al. 1971; Edmonds and Eglitis 1989; Zhong and Schowalter 1989; Lowell et al. 1992; Schowalter et al. 1992), and little is known about the complex interactions occurring within assemblages of wood-boring beetles and other saproxylic taxa.

A clear succession of Coleoptera was also reflected in the turnover of 65% of the taxa between years. It is well known that weakened and newly dead wood has a unique Coleoptera fauna, which is rare or absent in more decayed material (Simandl 1993; Hammond 1996; Irmler et al. 1996). Many wood- and bark-boring beetles such as cerambycids, buprestids, and scolytids require fresh host material (Wood 1982; Brewer et al. 1989) and are among the first insects to attack new CWM (Samuelsson et al. 1994). Most of these insects disperse well and have excellent host-finding capabilities mediated by long-range attraction to odors, such as ethanol and terpenes, emanating from weakened and newly dead trees (Chapman 1963, 1966; Witcosky et al. 1987). In this study, for example, both the buprestid, *Agrilus liragus* Bart. & Brwn., and *T. retusum* were abundant in 1-year-old CWM, and absent in 2-year-old dead wood. In fact, the significant decrease in beetle catches and overall wood borer abundance

over the 2-year study reflected the decrease in abundance of *T. retusum*. The explanation for this is unclear. The ambrosia fungi cultured in the galleries of this beetle and eaten by its larvae may be unable to compete with other fungi that eventually invade the wood (Boddy 1992), or perhaps, the fungi alter the under-bark environment so as to preclude their own further growth after a year.

Several fungivorous species, the most abundant being *Molamba biguttata* (LeConte), were caught much more often in 1994 than 1995. However, most of these species do not strictly specialize in fresh CWM as they have been commonly recovered in rearings from more advanced decay classes (Hammond 1996). Of the species considered here, only the nitidulid *Glischrochilus moratus* Brown seems to have a true preference for fresh CWM, as it was only collected in 1994 in this study and was absent in more advanced decay classes in other work (Hammond 1996). Larvae and adults of *Glischrochilus* are known to live beneath the bark of recently dead trees (Cuppen and de Oude 1996), feeding upon fermenting sap or fungi from the walls of scolytid beetle galleries (Koch 1989; Audisio 1993). They are apparently attracted to recently dead wood via wood volatiles (Lindelow et al. 1992). Overall, the number of fungivorous species increased by over 50% from 1994 to 1995, accounting for a large portion of the overall temporal increase in diversity. Temporal changes in the arthropod fauna inhabiting CWM may be tightly linked to changes in fungal community structure over time (Crowson 1984; Newton 1984; Wheeler and Blackwell 1984).

Saproxylic insects, habitat classification, and forest management

The arthropod assemblages associated with CWM are highly diverse and constitute a major and functionally significant proportion of overall biodiversity in Canadian forests. Hammond (1996) estimated that over 2000 saproxylic insect species (including Coleoptera) occur in *Populus* snags and logs at just two locations in Alberta. Furthermore, many saproxylic species are highly sensitive to forest disturbances and management regimes (Heliövaara and Väisänen 1984; Speight 1989; Martikainen 2001) and, thus, can serve a useful role as indicators of sustainability and ecosystem recovery following disturbance. To effectively predict the effects of harvest related disturbances on saproxylic arthropods and incorporate conservation of this fauna as a management objective, it is necessary to understand assemblage composition, structure, and its variability in time and space. Our work has contributed new knowledge about early faunal succession in *Populus* CWD in Alberta, but such work is a daunting task in the broader Canadian context largely because of the relatively poor taxonomic knowledge of this diverse assemblage. Clearly, increased investment in arthropod systematics will help, but this must be viewed as a long-term goal. In the meantime, forest management should be guided by the best existing knowledge, and at this time, conservation of saproxylic assemblages can be best addressed by focusing on conservation of habitats.

To date there has been relatively slow progress with characterization of CWM habitats, mainly in the form of anecdotal observations. In North America, CWM in forests is usually partitioned into snags and logs and assigned to a de-

cay class, ranging in number from three (e.g., Hammond 1996), five (e.g., Cline et al. 1980; Dingledine and Haufler 1983), to seven (McCullough 1948; Crites and Dale 1995). Assignment to decay classes is based mainly on physical characters such as numbers of twigs or branches and percent of bark remaining, amount of decay, and coverage by mosses and other vascular and nonvascular plants. Such classifications, however, have relatively low biological relevance as any class may span several to many years within the decay life of CWM and encompass a great deal of succession in the associated fauna (and flora). Biologically meaningful classification systems of CWM should also incorporate other variables such as size, degree and type of heart rot, presence and number of cavities, degree of sun exposure (e.g., forest edge versus interior), species, and abundance of fungal conks. A short-term investment in development of a CWM classification that better reflects saproxylic arthropod associations could soon yield tools to clearly identify CWM habitat features that are most endangered by forestry practices and, thereby, contribute to adaptive management.

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