# Community Composition of Longhorned Beetles (Coleoptera: Cerambycidae) in the Canopy and Understorey of Sugar Maple and White Pine Stands in South-Central Ontario

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**ABSTRACT** Insects of forest canopies are poorly known, especially in temperate forests of eastern North America. From June to August 2001, we sampled Cerambycidae using paired canopy and understorey flight-interception traps in nine pine and nine maple sites in south-central Ontario. Canopy traps were set using a simple ground-based bow-and-arrow method, and averaged 24.5 m in height at pine sites and 20.5 m at maple sites. In total, 297 individuals from 28 species were collected during 6 wk of sampling. *Clytus ruricola* (Olivier) accounted for 37% of all individuals. Pine sites had more species and higher expected richness than maple sites but significantly fewer individuals. Ten species were unique to pine, six to maple, and 12 occurred in both forest types. The two trap heights had similar observed richness, but expected richness was higher for canopy than understorey traps. Understorey traps accumulated significantly higher abundances than canopy traps. Eleven species were unique to canopy traps, 11 to understorey traps, and six occurred at both heights. Species accumulation was much faster when both heights were sampled compared with either alone. *Anthophylax attenuatus* (Newman), which has been rarely caught in other studies, was collected only in the canopy and was relatively abundant. Top collecting bottles on traps yielded similar observed richness as bottom bottles but had higher expected richness. Several species showed strong associations with either top or bottom collecting bottles. Species accumulation rates appeared to be higher than in other studies. Our results emphasize the necessity of including the canopy fauna in diversity studies.

**KEY WORDS** Cerambycidae, white pine, temperate forest, canopy diversity, flight-interception traps

LOGGING AND FIRE SUPPRESSION since the 1700s have transformed the Great Lakes-St. Lawrence forest of Canada's mixedwood temperate region from one containing many white pine forests to one composed mainly of hardwoods (Carleton 2000, Thompson 2000). Unfortunately, despite this change in forest composition, little information exists on the distribution and ecology of arthropods in this forest zone, particularly in the canopy. Research in tropical and western temperate forest canopies has revealed a surprisingly high abundance and diversity of arthropods (Erwin 1983, Winchester and Ring 1996), and in North American old-growth forests, arthropods are thought to comprise 80%–90% of known species (Asquith et al. 1990). However, this result may underestimate the true percentage because little research has been performed in the canopy of these forests, especially in the east (Lowman and Wittman 1996).

The long-horned beetles (Cerambycidae: Coleoptera) are an insect group of particular interest, partly because of their potential for biomonitoring (Yanega 1996, Bond and Philips 1999). The use of this family as a potential indicator group for forest management is based on three characteristics. First, they are strongly associated with forested lands and, in many cases, require dead or decaying wood for larval development (Linsley 1961). Thus, cerambycids are potential indicators of the logging-induced erosion of downed woody debris that has been proposed to have a negative effect on forest biodiversity (Hale et al. 1999). Second, they show diverse adult-feeding behavior, including sap, twigs, pollen, nectar, and leaves, and, hence, have the potential to indicate changes in a variety of ecological processes. Finally, they are easily identified: almost all North American species can be identified by eye or with a hand lens (Yanega 1996).

Although they represent an ideal group in some regards, their ecology is poorly known. For example, in his review of the biology of North American Cerambycidae, Hanks (1999) was able to discuss only 81 of 1,580 species in detail. This paucity of information is a result of relatively low economic importance, nocturnal habits, and rarity of many taxa (Hanks

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1999). Although certain cerambycid species display preferences for specific regions of trees (e.g., roots versus canopy) to which maturation, mating, or oviposition may be restricted, only one study has sampled the cerambycid fauna in forest canopies (Krinsky and Godwin 1996). The investigators collected cerambycids by fogging the canopy, but they did not compare the revealed community structure with that of the understorey. Studies that include samples from both the understorey and canopy provide three main advantages over those that sample at one height only: they avoid a vertical-bias, which is usually understorey-based, in inter-site comparisons of arthropod fauna (Su and Woods 2001), they allow comparisons between understorey and canopy communities, and they may provide a more representative sample of the community. By comparing the composition of ecological guilds between the canopy and the understorey, information also can be obtained on the vertical stratification of ecological processes in the forest.

We present information on the abundance, diversity, and community composition of Cerambycidae at sites in the Great Lakes-St. Lawrence mixedwood forest of south-central Ontario based on flight-interception trapping in both the canopy and understorey. In addition, we compare cerambycid communities between two major forest types in the region: white pine (*Pinus strobus* L.) and sugar maple (*Acer saccharum* Marsh.), and investigate several habitat variables as correlates of cerambycid community structure. This article is one of the first to collect insects in flight-interception aerial traps according to methods outlined in the Ecological Monitoring and Assessment Network protocols for sampling canopy arthropod biodiversity (Finnamore et al. 1998). As such, we also were interested in the overall efficiency of the trap used; specifically, comparing capture success between the upper and lower collecting bottles of the trap. During the course of the research, we developed a rapid and inexpensive technique for placing flight-interception traps in the forest canopy.

## Materials and Methods

**Study Area and Trapping.** The study was performed in The Haliburton Forest and Wildlife Reserve (45°15′N, 78°35′W), a 22,005-ha privately owned area in the Great Lakes-St. Lawrence temperate mixedwood forest of south-central Ontario. The region is primarily upland and is on moderately rolling rocky hills covered by shallow to moderately deep stony, silt, and sand on the Precambrian shield (Hills 1959). Tolerant hardwoods (*Acer saccharum* and *Fagus grandifolia* Ehrh.) tend to dominate upland sites. Numerous hemlock stands (*Tsuga canadensis* [L.] Carrière) are also present. Because of past logging, white pine (*Pinus strobus*) is sparsely scattered throughout the forest, with remnant stands being rare and small ($< 1$ ha).

Insects were collected using a type of malaise trap modified for sampling in the canopy, termed an "aerial malaise trap" or flight-interception trap (Finnamore et al. 1998). This trap is similar to a traditional Malaise trap (Townes 1962) because insects are sampled passively in the top of the trap by intercepting their flight. However, insects that drop upon interception are also collected in a bottle at the bottom of the trap.

**Survey Design.** The study was designed as a split-split block design, in which the main design factor was stand type (pine or maple), the first split factor was trap height (canopy or understorey), and the second split factor was bottle location (top or bottom collecting bottle). Within each of three forest blocks, we sampled three pine sites and three maple sites. To our knowledge, they were old-growth sites that had never been logged. However, it is possible that the maple stands were subjected to some high-grading in the past. Within each block, the three sites per forest type were located within a single forest stand because of the rarity of pine stands in the region. However, the sites were always at least 50 m from each other and are considered independent samples. At each site, one trap was placed in the canopy and one in the understorey. Thus, a total of 36 traps were sampled (three blocks × two stands/block (maple/pine) × three sites/stand × two traps/site), with two bottles per trap.

Previous cerambycid studies in temperate zones found highest activity during the months of June and July (Yanega 1996, Bond and Philips 1999). Hence, insects were sampled in the first 2 wk of June, July, and August 2001. Bottles were usually collected at the end of each week. However, they were sometimes collected after five, six, or eight collecting d (113 of 394, 1-wk samples). Of the total expected 432, 1-wk samples, only 394 were obtained, primarily due to wind damage early in the study and bear depredation.

**Canopy Access.** Traps were set in the canopy by first locating a gap between two large conspecific canopy trees (pine or maple). From the center of the gap, a bow was used to shoot an arrow with attached fishing line (9.1-kg [20 lb] test) over the highest point of the canopy of one tree (Fig. 1A). One or two 1.7 cm steel nuts were taped to the arrowhead to provide additional weight. After the shot, the arrow was untied and a thicker line (2-mm diameter) was tied to the fishing line. The 2-mm rope was pulled over the canopy by reeling in the fishing line. This 2-mm rope was subsequently used to pull an even thicker (7-mm diameter) line over the canopy. This process was repeated for the other canopy tree. The two 7-mm lines were tied together at ground level in the center of the gap, and a pulley (and associated pulley-rope) was attached near the knot. By pulling on the untied ends, a horizontal line (with pulley) was thus placed across the gap (Fig. 1B). The pulley-rope was used to raise and lower the flight-interception trap. Using this technique, we were able to set each site in two-four h. Average trap height in the pine canopies was 24.5 m (range, 21.0–27.6 m) and in the maple canopies was 20.5 m (range,18.2–23.3 m).

**Insect Handling.** Insects were collected and stored in 70% ethanol. Cerambycids were identified to species using Yanega (1996) and a 40× dissecting micro-

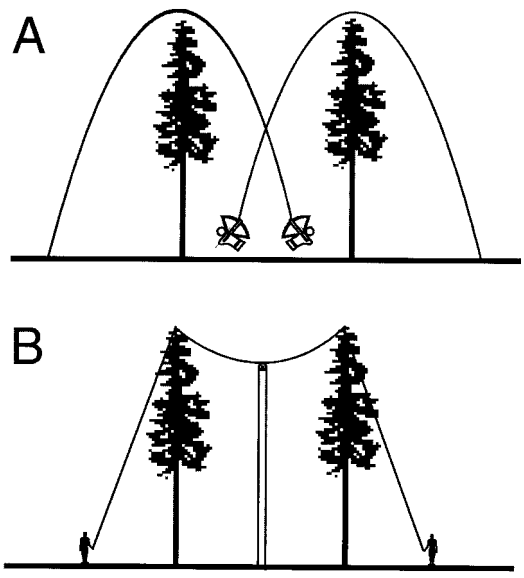


**Fig. 1.** Bow-and-arrow method for setting flight-interception traps in the upper canopy of the forest. (A) From a gap between two trees, a line was shot over each of the two tree canopies and used to pull stronger ropes over. (B) A horizontal rope in the canopy was created by tying together the two rope ends in the gap, attaching a pulley with an associated pulley-rope nearby, and pulling the nongap rope ends to suspend the pulley. The rope ends were then tied to nearby trees, and the trap was raised by the pulley-rope.

scope. Identifications were verified using collections at the Royal Ontario Museum (Toronto, Ontario, Canada), which also is where voucher specimens were deposited.

**Habitat Variables.** Sixteen habitat variables were measured at each site. Topography was scaled from one-three, where one was bottom slope, two was midslope, and three was top slope. Digital photographs were taken with a camera (Nikon, Melville, NY) affixed with a fisheye lens and a 90° field of view. Photographs were subsequently analyzed using computer software (Regent Instruments, Quebec, Canada) to quantify canopy openness, the estimated total (direct + diffuse) photosynthetic photon flux density (PPFD, mol/$m^2$/d) under the canopy, and leaf area index. Understorey vegetation plots consisted of 10 contiguous 2 by 2-m subplots forming a 20-m-long plot, with the center point of the plot located in the same position as the canopy flight-interception trap. In each subplot, percentage cover of vegetation was calculated, and flowering plants in genera known to be fed upon by adult cerambycids were identified. These were *Cornus*, *Rubus*, *Viburnum*, *Sambucus*, *Acer*, *Prunus*, *Aralia*, and *Trillium* (Gardiner 1970, Gosling and Gosling 1977, Gosling 1986, Bond and Philips 1999). The percentage cover of each of these species was summed across subplots to give an overall measurement of percentage flowering host-plant cover. Leaf litter depth was measured to the nearest cm at 0, 10, and 20 m along the plot. Basal area of conifers, hardwoods, and snags were each calculated from a 1000-$m^2$ circular stem-map survey centered at the flight-interception trap. We also calculated percentage cover of downed woody debris > 7.5 cm in diameter along four 17.8-m-long transects (radius 1000-$m^2$ circular plot) branching out in the four cardinal directions from the center point. Downed woody debris was categorized into five decomposition classes following Hayden et al. (1995).

### Data Analysis

**Species Abundance and Richness.** Because of missing samples and variation in the number of days that a trap was set, we standardized effort by dividing the total number of captures per month of each cerambycid species by the total monthly trap effort (in trap days). An entire month's effort was missing for five bottles. We replaced these missing data with the average for that month from all other bottles. We used this procedure because of variation in abundances of some species from month to month. The monthly abundances were then averaged over the three sampling months.

Variation in total abundance was tested using a randomized-block split-split plot analysis of variance (ANOVA), with forest block as the blocking factor. Due to the large number of zeroes in the data set, we used a Fisher exact test for comparing the abundances of individual species between forest types, with the exception of the abundant *Clytus ruricola* (Olivier), for which we used ANOVA. We also conducted nonparametric paired tests to evaluate differences in abundances between the two bottles of a trap and between the two trap heights (canopy or understorey). Specifically, the effort-corrected number of individuals in top bottles was subtracted from that in bottom bottles, and the frequency of positive versus negative differences was then tested using a binomial test (Siegel 1956). The same was done for the effort-corrected number of individuals in canopy and understorey traps. A $P$ value of 0.05 was considered significant in all tests, and all analyses were conducted using statistical software (SAS Institute 2000).

As a rarefaction procedure (Ludwig and Reynolds 1988), raw species richness (i.e., uncorrected for effort) was compared using a split-split plot analysis of covariance (ANCOVA) with total number of individuals as the covariate. This linear model provided a reasonable fit to species accumulation over the range of abundances obtained.

Species accumulation curves were computed using statistical software (Colwell 1997) for each treatment using 100 randomizations of sample pooling order. Input data were the captures during each of the six sampling weeks at each site (uncorrected for effort). Estimators of species richness (Jackknife two and Chao 2) were subsequently compared among treatments using paired $t$-tests for collection bottle and trap height, and a two-sample $t$-test for tree species.

**Multivariate Community and Habitat Analyses.** To investigate variation in species composition by tree

species, trap height, location of collecting bottle, and variation in habitat variables, we used multivariate analyses with statistical software (CANOCO 1998). Effort-standardized species abundances were square-root transformed, and rare species were down-weighted before analysis (ter Braak and Šmilauer 1998). A gradient length of 5.6 and 3.1 for the first two axes in a Detrended Correspondence Analysis (DCA) indicated that unimodal models were suitable (Legendre and Legendre 1998). DCA by second order polynomials was performed on the 10 most abundant species (> 5 individuals collected), focusing on inter-species chi-square distances and using Hill biplot scaling (ter Braak and Šmilauer 1998). After constraining species with habitat variables, gradient lengths were 1.27 and 1.34 for the first two axes, respectively, so we used a linear model to explore habitat relations instead of a unimodal model. Correlations with habitat variables were investigated using Redundancy Analysis (RDA) on the correlation matrix. Before analysis, we reduced the number of habitat variables to four by using scores from the first four axes of a Principal Components Analysis (PCA) on the habitat variables. Step-wise permutation tests (999 iterations) were used to determine which axes contributed significantly to species variance. To aid in interpretation, we included the original habitat variables in the analysis "passively" (ter Braak and Šmilauer 1998) and also conducted stepwise permutation tests to evaluate the significance of the raw habitat variables.

## Results

**Abundances.** A total of 2,662 trap-days yielded 297 individuals of 28 cerambycid species in 24 genera (Table 1). Overall, significantly more cerambycids were found in maple traps than in pine traps (ANOVA, $F = 436.73$; df = 1,2; $P = 0.002$). However, there was significant interaction between tree species and trap height, with trap success being approximately equal at the two heights in maple stands but greater in the understorey than the canopy of pine stands (Fig. 2; ANOVA, $F = 61.57$; df = 1,2; $P = 0.016$). More cerambycids were collected in the top bottle of a trap than in the bottom bottle (ANOVA, $F = 405.3$; df = 1,2; $P = 0.003$), but again, there was a significant trap height-bottle interaction, with more always being caught in the top than bottom bottles, except in the pine canopy (ANOVA, $F = 249.31$; df = 1,2; $P = 0.004$).

*Clytus ruricola* accounted for 37% of all individuals collected. There was some evidence of higher abundances in maple stands than pine stands (ANOVA, $F = 8.62$; df = 1,2; $P = 0.099$). This species was significantly more common in top rather than bottom bottles (ANOVA, $F = 234$; df = 1,2; $P = 0.004$) and more common in the canopy than in the understorey (ANOVA, $F = 40.8$; df = 1,2; $P = 0.024$), although there was evidence of a three-way interaction (ANOVA, $F = 43.9$, df = 1, $P = 0.022$). For pine stands, canopy top bottles collected approximately the same number of individuals as understorey top bottles, but in maple stands, canopy top bottles collected more than understorey top bottles. When this species was removed from the analysis, there was no significant tree species effect on the total number of individuals collected (ANOVA, $F = 3.24$; df = 1,2; $P = 0.22$). However, the significant interactions between height and tree species (ANOVA, $F = 1899$; df = 1,2; $P < 0.001$) and height and bottle location (ANOVA, $F = 21.1$; df = 1,2; $P = 0.044$) remained.

Of the 10 next most abundant species, only *Neoalosterna capitata* (Newman) had a significant association with tree species because they were more common in maple than pine stands (Fisher test, chi-square = 3.6; df = 1; $P = 0.044$). *Anthophylax attenuatus* (Haldeman) was collected in the canopy more than the understorey (binomial, $P = 0.008$), and *Evodinus monticola* (Randall), *Leptura subhamata* Randall, *Microgoes oculatus* (LeConte), *Pidonia rufi-collis* (Say), and *Strangalepta abbreviata* (Germar) were associated more with the understorey than the canopy (binomial $P = 0.046, 0.019, 0.09, < 0.001, 0.016$, respectively). Of those species more abundant in the understorey, *E. monticola* was collected more in bottom bottles than top bottles (binomial, $P = 0.004$) and *S. abbreviata*, *M. oculatus*, and *Gaurotes cyanipennis* (Say) were collected more in top bottles than bottom bottles (binomial, $P = 0.016$; $< 0.001$; 0.003, respectively). Of the species that were abundant in the canopy, *N. capitata* and *A. attenuatus* were more often collected in bottom bottles than top ones (binomial, $P = 0.008$ and 0.008, respectively).

**Species Richness.** The total number of species captured was slightly higher in pine than maple sites (22 versus 18 species). However, the difference was not significant either without or with the number of individuals as a covariate (ANOVA, $F = 1.23$; df = 1,2; $P = 0.38$; ANCOVA, $F < 0.01$; df = 1,2; $P = 0.99$, respectively). Of the 28 species identified, 12 were collected both in pine and maple stands, six in maple only, and 10 in pine only. Species accumulation curves showed that species richness in pine increased more quickly than in maple, and that observed and expected richness were higher in pine sites than maple (Fig. 3; Table 2). The pine species accumulation curve was quite similar to that obtained when both tree species were sampled equally, indicating relatively little compositional difference between the two forest types (Fig. 3).

Differences in species richness between trap heights were not significant, either without or with number of individuals as a covariate (ANOVA, $F = 8.83$; df = 1,2; $P = 0.097$; ANCOVA, $F = 13.4$; df = 1,2; $P = 0.067$, respectively). However, there was considerable evidence of species associations to height. Only six of 28 species were collected at both heights, 11 in the canopy only, and 11 in the understorey only. Canopy and understorey strata had similar rates of species accumulation and similar observed richness. However, species accumulation was considerably faster when both heights were sampled, indicating compositional differences (Fig. 3). Expected richness was significantly higher in the canopy than the understorey (Table 2).

**Table 1. Average abundances ± SEM per 1,000 trap-days and total number of individuals of Cerambycidae collected in the Great Lakes–St. Lawrence forest of south-central Ontario using flight-interception traps in two forest types, at two heights (canopy and understorey), and at two collecting locations within the flight-interception trap (top or bottom collecting bottle)**

| Species | Maple | | | | Pine | | | |
|---|---|---|---|---|---|---|---|---|
| | Canopy | | Understorey | | Canopy | | Understorey | |
| | Top (TN = 351) | Bottom (TN = 345) | Top (TN = 345) | Bottom (TN = 324) | Top (TN = 276) | Bottom (TN = 303) | Top (TN =352) | Bottom (TN = 366) |
| Cerambycinae | | | | | | | | |
| *Anelaphus villosus* (F.) | 7.4 ± 7.4 (2) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Clytus ruricola* (Olivier) | 156.7 ± 42.9 (49) | 6.9 ± 4.2 (2) | 87.3 ± 25.2 (29) | 5.7 ± 5.7 (2) | 33.0 ± 11.8 (11) | 1.0 ± 0.7 (0) | 43.0 ± 19.1 (15) | 5.5 ± 3.6 (2) |
| *Cyrtophorus verrucosus* (Olivier) | 0 | 0.1 ± 0.1 (0) | 0 | 0 | 0 | 0.1 ± 0.1 (0) | 2.6 ± 2.6 (1) | 2.6 ± 2.6 (1) |
| *Microclytus compressicollis* (LaPorte & Gory) | 0 | 0.1 ± 0.1 (0) | 0 | 0 | 0 | 0.1 ± 0.1 (0) | 5.3 ± 2.5 (2) | 0 |
| *Molorchus b. bimaculatus* Say | 0 | 10.7 ± 8.0 (4) | 0 | 0 | 0 | 0.2 ± 0.2 (0) | 0 | 0 |
| *Pronocera c. collaris* (Kirby) | 0 | 0.1 ± 0.1 (0) | 0 | 0 | 5.3 ± 5.3 (1) | 0.1 ± 0.1 (0) | 0 | 0 |
| *Sarosesthes fulminans* (F.) | 0 | 0 | 2.8 ± 2.8 (1) | 0 | 0 | 0 | 0 | 3.7 ± 3.7 (1) |
| *Xylotrechus colonus* (F.) | 0 | 6.6 ± 4.4 (2) | 0 | 0 | 0 | 0 | 0 | 0 |
| Lepturinae | | | | | | | | |
| *Anthophylax attenuatus* (Haldeman) | 0 | 5.6 ± 3.3 (2) | 0 | 0 | 0 | 26.2 ± 15.9 (5) | 0 | 0 |
| *Anthophylax cyaneus* (Haldeman) | 0 | 2.7 ± 2.6 (1) | 0 | 2.6 ± 2.6 (1) | 0 | 0.1 ± 0.1 (0) | 0 | 0 |
| *Anthophylax viridis* (LeConte) | 0 | 0.2 ± 0.2 (0) | 0 | 0 | 0 | 12.7 ± 8.6 (4) | 0 | 0 |
| *Evodinus m. monticola* (Randall) | 0 | 5.8 ± 3.4 (2) | 2.5 ± 2.5 (1) | 13.1 ± 7.0 (4) | 0 | 0.5 ± 0.5 (0) | 0 | 15.7 ± 3.9 (6) |
| *Gaurotes cyanipennis* (Say) | 24.0 ± 18.2 (7) | 6.1 ± 3.6 (2) | 29.1 ± 9.5 (11) | 5.7 ± 5.7 (2) | 0 | 3.5 ± 2.8 (1) | 24.4 ± 10.9 (9) | 0 |
| *Leptura plebeja* Randall | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 5.7 ± 3.8 (2) |
| *Leptura subhamata* Randall | 0 | 0 | 9.4 ± 4.8 (3) | 2.6 ± 2.6 (1) | 0.1 ± 0.1 (0) | 0 | 17.3 ± 8.6 (6) | 6.6 ± 4.4 (2) |
| *Lepturopsis biforis* (Newman) | 0 | 0 | 0 | 0 | 0.2 ± 0.1 (0) | 0.1 ± 0.1 (0) | 0 | 5.3 ± 3.5 (2) |
| *Neoalosterna capitata* (Newman) | 2.6 ± 2.6 (1) | 45.6 ± 21.4 (17) | 2.6 ± 2.6 (1) | 2.6 ± 2.6 (1) | 0 | 0.8 ± 0.8 (0) | 0 | 5.1 ± 3.4 (2) |
| *Pidonia ruficollis* (Say) | 0 | 1.5 ± 1.5 (0) | 67.2 ± 39.7 (16) | 18.5 ± 13.6 (6) | 0 | 1.5 ± 1.5 (0) | 10.6 ± 4.2 (4) | 10.6 ± 8.0 (4) |
| *Pygoleptura n. nigrella* (Say) | 0 | 0 | 0 | 0 | 0 | 5.9 ± 3.9 (2) | 0 | 0 |
| *Sachalinobia r. rugipennis* (Newman) | 0 | 0 | 0 | 0 | 2.6 ± 2.6 (1) | 0 | 0 | 0 |
| *Stictoleptura c. canadensis* (Olivier) | 0 | 0 | 0 | 0 | 0.1 ± 0.1 (0) | 0 | 0 | 2.6 ± 2.6 (1) |
| *Strangalepta abbreviata* (Germar) | 0 | 0 | 17.1 ± 8.5 (6) | 0 | 0 | 0 | 14.2 ± 11.4 (5) | 0 |
| *Trachysida mutabilis* (Newman) | 0 | 0.2 ± 0.2 (0) | 7.6 ± 5.3 (3) | 0 | 0 | 0.2 ± 0.2 (0) | 2.6 ± 2.6 (1) | 2.5 ± 2.5 (1) |
| Lamiinae | | | | | | | | |
| *Astylopsis macula* (Say) | 2.8 ± 2.8 (1) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Microgoes oculatus* (LeConte) | 5.5 ± 3.6 (2) | 0 | 28.5 ± 6.5 (10) | 0 | 0.5 ± 0.3 (0) | 0.3 ± 0.2 (0) | 28.9 ± 14.9 (9) | 0 |
| *Monochamus s. scutellatus* (Say) | 3.1 ± 3.1 (1) | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Saperda imitans* Felt & Joutel | 0 | 0 | 0 | 0 | 2.8 ± 2.8 (1) | 0 | 0 | 0 |
| *Urgleptes querci* (Fitch) | 0 | 0 | 2.6 ± 2.6 (1) | 0 | 0.2 ± 0.1 (0) | 0.1 ± 0.1 (0) | 0 | 2.6 ± 2.6 (1) |

Each mean is based on effort-corrected samples from nine traps (see text for details). Raw abundances (total number of individuals captured) are listed in parenthesis. TN = Trap nights.

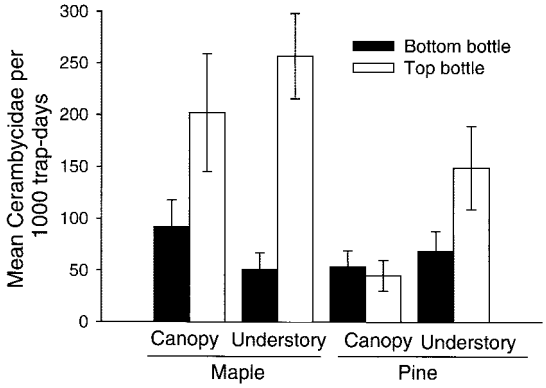


**Fig. 2.** Mean number of cerambycid adults (±SEM) per 1,000 flight-interception trap-days in maple or pine, canopy or understorey, and top or bottom collecting bottles in Great Lakes-St. Lawrence forests of South-Central Ontario. Each mean is based on a sample of nine flight-interception traps.

Top bottles had a higher species richness than bottom bottles, whether the number of individuals was considered as a covariate or not (ANCOVA, $F = 17.8$; df = 1,2; $P = 0.052$; ANOVA, $F = 61.71$; df = 1,2; $P = 0.012$, respectively). However, there were height-bottle interactions for species richness, with top bottles showing greater richness than bottom bottles in understorey traps, but both bottles showing approximately equal richness in the canopy (ANOVA, $F = 76.0$; df = 1,2; $P = 0.013$). Ten species were collected in both bottles, while nine species were caught in top bottles only and nine in bottom bottles only. Bottom bottles acquired species much more quickly than top bottles (Fig. 3), but expected richness was higher for top bottles than bottom ones (Table 2).

**Multivariate Tests.** The first two axes from a DCA on the 10 most abundant species represented 24.1% and 14.0%, respectively, of the total variance (Fig. 4). The first axis showed partial separation of top (high scores) and bottom bottles (low scores), but this was primarily due to the occurrence of *A. attenuatus* and, to a lesser extent, *N. capitata* in lower canopy bottles, as also indicated in the univariate tests. The second axis distinguished understorey traps (high scores) from canopy traps (low scores). Species associated with understorey traps included *E. monticola*, *P. ruficollis*, *Trachysida mutabilis* (Newman), and *L. subhamata*, while species associated with canopy traps included *C. ruricola*, *N. capitata*, and *A. attenuatus*.

The four PCA-derived composite habitat variables explained 23% of the total variance. The first variable was close to significant in the RDA (permutation test, $F = 1.66$; $P = 0.07$), but the other three were not ($F = 1.14$; $P = 0.32$; $F = 0.66$; $P = 0.74$; $F = 0.47$, $P = 0.95$, respectively). In step-wise permutation tests of the original habitat variables, three that loaded highly on the first composite PCA axis were significant: photon photosynthetic flux density ($F = 2.24$, $P = 0.009$), basal area of conifers ($F = 2.16$, $P = 0.013$), and basal area of hardwoods ($F = 2.013$, $P = 0.019$). The first axis of the RDA (11.3% of the species variance) clearly separated pine and maple sites, as indicated by the vectors representing basal area of conifers and hardwoods at opposite ends of the axis (Fig. 5). Not surprisingly, maple sites had more leaf area than pine sites and a higher percentage cover of flowering species. Pine sites were more open, had higher levels of light intensity (PPFD), were further up the slope, and had higher basal area of snags than maple sites. Downed woody debris of all decomposition classes was associated more with pine than maple sites. *E. monticola* and *L. subhamata* were more common in pine sites, as expected, because of their use of conifers as hosts. *Strangalepta abbreviata*, a species able to use either host, tended to be about equally abundant in both forest types. Species known to have hardwood hosts (*G. cyanipennis*, *C. ruricola*, *N. capitata*, and *P. ruficollis*) were associated with maple sites; the exception was *A. attenuatus*, which showed no correlation with either axis.

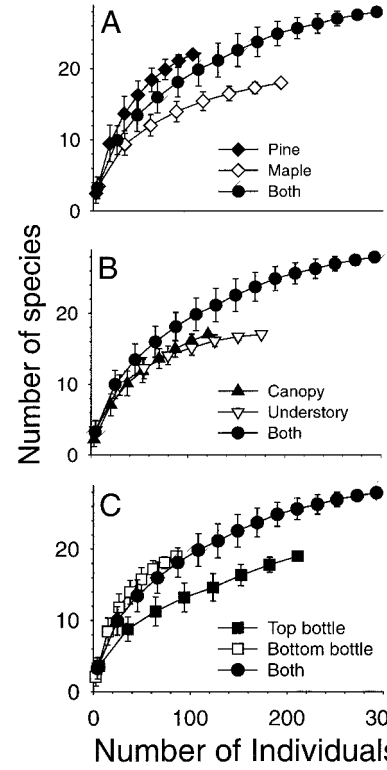


**Fig. 3.** Species accumulation curves for adult cerambycids collected in flight-interception traps in Great Lakes-St. Lawrence forests of south-central Ontario. Curves plot the observed number of species as a function of the number of pooled individuals. (A) For maple and pine sites. (B) For canopy and understorey traps. (C) For top or bottom-collecting bottles. Error bars are SD, and only every fifth point is shown. Each point is based on 100 randomizations of sample accumulation order.

**Table 2. Estimated total species richness (± SD) of Cerambycidae in the Great Lakes–St. Lawrence forest of south-central Ontario, based on two estimators (Chao 2 and Jackknife 2)**

| Treatment | Trap location | Chao 2 | *t* | df | *P* | Jackknife 2 | *t* | df | *P* |
|---|---|---|---|---|---|---|---|---|---|
| Tree Species | Maple | 19.8 ± 2.7 | −5.3 | 70 | <0.001 | 21.9 ± 1.9 | −3.5 | 70 | <0.001 |
| | Pine | 24.4 ± 2.8 | | | | 27.8 ± 2.2 | | | |
| Height | Canopy | 20.3 ± 3.9 | −3.9 | 35 | <0.001 | 22.8 ± 2.6 | −3.2 | 35 | 0.003 |
| | Understorey | 17.3 ± 0.8 | | | | 18.9 ± 1.4 | | | |
| Collection bottle | Bottom | 21.3 ± 3.0 | −5.5 | 35 | <0.001 | 23.9 ± 2.1 | −3.5 | 35 | 0.001 |
| | Top | 30.6 ± 12.5 | | | | 27.8 ± 2.9 | | | |
| All treatments | – | 29.7 ± 2.1 | – | – | – | 33.9 ± 2.3 | – | – | – |

## Discussion

Community composition differed substantially between the top and bottom collecting bottles, especially for understorey traps (e.g., as indicated by the first DCA axis). On average, top-collecting bottles captured significantly more species than bottom-collecting bottles, and expected richness was higher in the top than in the bottom bottles. Certain species (*C. ruricola*, *S. abbreviata* and *M. oculatus*) were collected significantly more in the top bottles, while others (*E. monticola*, *A. attenuatus*, and *N. capitata*) were collected more in the bottom bottles. A higher abundances in one or the other of the two collecting bottles presumably reflects differential behavioral responses, with some species clinging and climbing upward after striking an interception panel, and others dropping. Although abundance was much higher in top than bottom collecting bottles, bottom bottles acquired more species per individual and collected nine species not found in the top bottles.

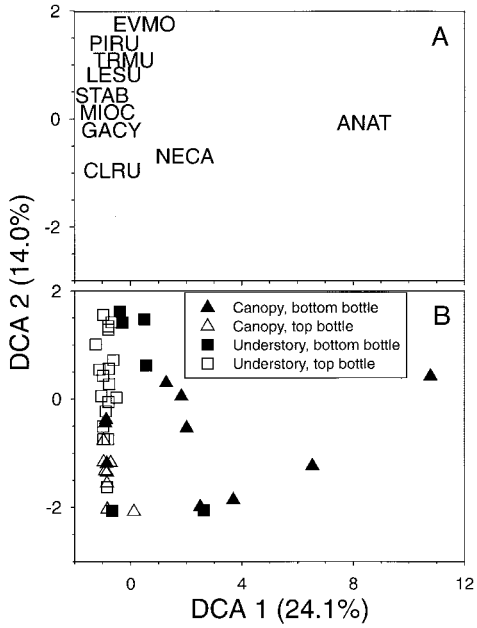


**Fig. 4.** Correlation biplots from a detrended correspondence analysis on the 10 most abundant species of adult cerambycids captured in flight-interception traps from a mixedwood temperate forest. (A) Site scores. (B) species scores. Four-letter species acronyms are the first two letters of the genus and the first two letters of the species.

By placing the flight-interception traps both in the canopy and in the understorey, we increased our representation of the cerambycid community. Even stronger compositional differences were exhibited between the two heights than between the two collecting bottles, with *E. monticola*, *S. abbreviata*, *P. ruficollis*, *L. subhamata*, and *M. oculatus* more abundant at understorey level, and *A. attenuatus* and *N. capitata* more common in the canopy. Only six of 28 species were captured at both heights. Although cerambycids are considered to be strong active flyers, Bense (1995) argued that some species (e.g., *Clytus tropicus*) live their entire adult lives in the tops of host trees, where all their feeding and oviposition requirements are met. Our data support this idea for at least one species, *A. attenuatus*, which was exclusively captured in the canopy in lower collection bottles. This species rarely has been collected in understorey-based surveys (Gosling 1986). It has a feeding preference for pine cones (Yanega 1996), which are more abundant high in the crowns of pine trees. Similarly, *N. capitata* was collected more frequently in the canopy, perhaps in search of catkins from its host, yellow birch (*Betula alleghaniensis* Britt.). Although there were no significant differences in species richness between the two heights, canopy traps collected 11 species not collected in the understorey, and vice versa. The species accumulation curve was also much higher if traps from both heights were used, rather than from one or the other. Thus, flight-interception trapping in the canopy increased species richness over trapping in the understorey traps alone. Ideally, both should be included in future studies.

Our data suggest, albeit less strongly, that the structure of the cerambycid community varied significantly with forest type. Thus, by including tree species as a third factor in our sampling design, species richness increased. Differences in the structure of the cerambycid community were correlated with several environmental features in the two forests, including a high percentage cover of flowering host plants and a high leaf area index in the maple sites, and high levels of light intensity (PPFD) and steep topography in the pine sites (Fig. 5). Pine sites were associated strongly with higher snag density and amounts of downed wood, both of which are important variables for cerambycid larval development (Gosling and Gosling 1977).

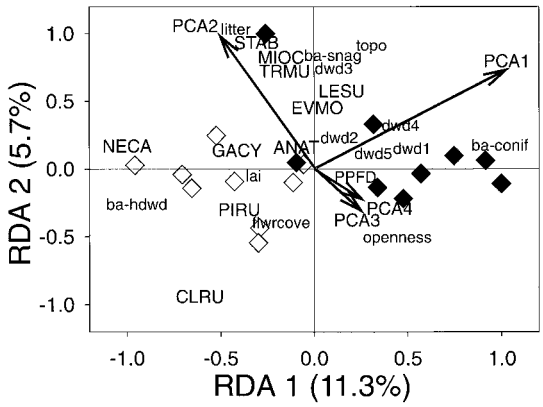


**Fig. 5.** Redundancy analysis of the adult cerambycid fauna in maple (open diamond) and pine (filled diamond) sites in temperate mixedwood forest. Species vectors are represented by upper-case, four-letter species acronyms (first two letters of the genus and the first two letters of the species). Habitat vectors are represented by lower-case acronyms. ba, basal area; dwd1–5, downed woody debris in each of five decomposition classes; flwrcove, ground cover by genera of flowering plants known to be fed upon by cerambycids; lai, leaf area index; litter, depth of leaf litter; openness, canopy openness; topo, slope position.

We expected to find more cerambycids in the pine sites because of the relatively high levels of available brood material compared with the maple sites, but this was not the case. This result may be explained in part by larval feeding behavior. Of the 28 species we collected, 14 have a preference for hardwoods, while only seven prefer conifers (Yanega 1996). Alternatively, because most adult cerambycids are strong flyers and spend much time feeding on flowers away from sites where they developed as larvae (Linsley 1961), it may be that the adults we collected had left their natal coniferous sites and were more active in neighboring maple sites, where a higher percentage of the forest floor was covered with flowering plants. This result appears true for at least two species in our study, *E. monticola* and *L. subhamata*, both flower-feeding Lepturinae whose preferred hosts are white pine and hemlock, respectively. Both species were equally abundant in pine and maple sites. However, potential hosts and feeding sources do not provide an entire explanation because other factors also contribute to species abundances, including microclimate, competition, predation, and parasitism (Yanega 1996). Also, caution must be used interpreting our data because a single species, the most abundant (*C. ruricola*), alone accounted for the significantly higher abundance of cerambycids in maple sites.

Our richness estimators (Chao 2 and Jackknife 2) suggested that we would find only a few more cerambycid species if sampling continued into following years. It is possible that we were close to accumulating the maximum richness obtainable by using this single trap type (Longino et al. 2002). Multiple sampling methods and extensive effort are required to obtain relatively complete inventories of species-rich arthropod communities (Winchester and Ring 1996, Longino et al. 2002, Simon and Linsenmair 2001). However, it is interesting that we recorded a similar number of anthophilous species in 6 wk of sampling as did Bond and Phillip (1999) over a 4-yr period of timed observations in forests and along road edges in southeastern Ohio, despite catching only one-fifth as many individuals. In the subfamilies Cerambycinae and Lepturinae, they recorded 22 species, and here we recorded 23 species. Only a few more species were captured during five years in similar mixed northern hardwood stands in Michigan by Gosling (1986) (34 species using direct observation, branch beating, UV light traps and malaise traps) and in New England by Krinsky and Godwin (1996) (30 species by fogging). Because of the high species richness we observed after only one summer of sampling, the Ecological Monitoring and Assessment Network protocol may represent an especially useful one for forest cerambycids. Alternatively, it is possible that population levels of many species were high during the year of our sampling.

The new bow-and-arrow method that we developed allowed us to set canopy traps rapidly. It also was easy: accuracy in shooting was an asset, but the technique required no special skills. Upper canopies of tall forest trees traditionally have been reached using methods such as preconstructed platforms, aerial flotation devices, or single rope climbing techniques (Perry 1978; Simon and Linsenmair 2001). All these techniques are relatively expensive, time-consuming, and require special skills, including no fear of heights. To our knowledge, the bow-and-arrow has not been used as a stand-alone method to sample forest canopies but rather to set traps over lower branches or vines, or to pull climbing ropes up into the canopy (Moffett and Lowman 1995). Our technique allowed us to set traps at heights ranging from 18 to 28 m in the mid to upper canopies of temperate forests. With a more powerful bow or crossbow, higher canopies could be sampled easily.

This study is the first to inventory the community of Cerambycidae in temperate mixedwood forests in both the forest understorey and canopy. It also sheds light on two important issues relevant to forest insect conservation. First, it lends support to the recommendation that vertical sampling should be included when sampling forest insect faunas (Su and Woods 2001), especially if rapid estimates of diversity are desired. We suspect that this result will hold true for other insect groups as well. Second, and of broader impact, these results support the practice of managing temperate forests to maintain tree species diversity and, particularly, to increase the representation of white-pine stands in maple-dominated forests. We collected 10 cerambycid species only in pine, and the expected species richness was higher overall in pine than maple. This result suggests that pine stands are potentially valuable for maintaining cerambycid diversity, and raises the possibility that further losses and fragmentation of pine ecosystems in this region could lead to local species losses. Quantitative studies of ceramby-

cid communities in other mature forest types could be very useful for understanding and conserving insect species as natural components of forest ecosystems.

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