Differences Between Forest Type and Vertical Strata in the Diversity and Composition of Hymenpteran Families and Mymarid Genera in Northeastern Temperate Forests

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ABSTRACT Most insects' assemblages differ with forest type and show vertical stratification. We tested for differences in richness, abundance and composition of hymenopteran families and mymarid genera between sugar maple (*Acer saccharum*) and white pine (*Pinus strobus*) stands and between canopy and understory in northeastern temperate forests in Canada. We used flight interception traps (modified malaise traps) suspended in the canopy and the understory in a split-split block design, with forest type as the main factor, forest stratum as the first split factor, and collection bottle location as the second split factor. Hymenopteran families and mymarid genera differed in their diversity depending on forest type and stratum. Both family and genera richness were higher in maple than in pine forests, whereas family richness was higher in the canopy and top bottles and generic richness was higher in the understory and bottom bottles. Multivariate analysis separated samples by forest type, vegetation stratum, and bottle location. Family composition showed 77% similarity between forest types and 73% between the canopy and understory. At the lower taxa level, mymarid genera showed only 47% similarity between forest types and 40% between forest strata, indicating vertical stratification and relatively high β-diversity. Our study suggests that hymenopteran diversity and composition is strongly dependent on forest type and structure, making flying members of this order particularly vulnerable to forest management practices. It also shows that insect assemblage composition (especially at low-taxon levels), rather than relative abundance and richness, is the community attribute most sensitive to forest type and vertical stratification.

KEY WORDS canopy insects, high-taxa level, insect conservation, forest management

Insect communities and their associations with forest stand characteristics are becoming increasingly important in forest management and conservation plans; however, our current state of knowledge about these relationships is surprisingly low, especially where forest canopies are concerned. Although May (1990) and Stork (1993) subsequently derived more conservative estimates, Erwin (1982) originally calculated that twice as many insect species could be found in the world's forest canopies as in their understories. Despite many recent studies describing insects in canopies, especially in the tropics (Lowman and Wittman 1996, Storke et al. 1997, Basset et al. 2003b), considerable work remains to be done because of the wide variety of forest types and insect groups. For example, relatively few studies have examined insect diversity in canopies of northeastern temperate forests in North America.

Richness, relative abundance, and composition of several insect assemblages have been shown to vary according to forest type (Schulz and Wagner 2002), tree species (Didham 1997, Schowalter and Zhang 2005), and in some cases, among congeneric tree species (Tovar-Sánchez et al. 2003). Similar patterns are beginning to be deciphered from work in temperate forests, where canopy insect assemblages may also differ between forest types (Vance et al. 2003) and even between congeneric tree species (Le Corf and Marquis 1999). Maple and pine forests are major forest types in northeastern forests of North America and show different structural, physiological, and site characteristics, differences that may be reflected in their insect assemblages.

Environmental and biological variability influence the vertical distribution of insects in the forest and, as improved methods for accessing the canopy are made available, it is becoming increasingly clear that arthropods are sensitive to these vertical gradients (Basset et al. 2003a). Studies examining insect distribution and patterns in forest canopies show some differences in insect assemblages between the forest understory and

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canopy (Basset et al. 2003b, Schowalter and Zhang 2005). However, not all studies report consistent patterns in richness and composition (Le Corf and Marquis 1999).

Most of the work comparing canopy and understory insects in northeastern temperate forests has used branch pruning or tree climbing techniques to study herbivore assemblages (Le Corf and Marquis 1999). Because tree canopies are difficult to access, community patterns of insects actively flying in the canopy, such as dipterans, hymenopterans, and some coleopterans, have been more rarely reported. With recent improvements in sampling methodology for canopy work (Vance et al. 2003), our ability to sample actively flying insects has been greatly improved.

One order of flying insects that is especially important because of its diversity and range of functional roles in terrestrial ecosystems is the Hymenoptera. While this order is considered one of the richest in tropical forest canopies (Basset 2001), its diversity is thought to peak at mid-latitudes (Skillen et al. 2000), suggesting that some families (e.g., Ichneumonidae) will have a greater number of species in temperate than in tropical regions (Janzen 1981, Skillen et al. 2000). In Canada, the order includes >7,000 named species (~25% of the total known) and, like other parts of the world, is disproportionately represented by undescribed species (Mason and Huber 1993). Forest canopies have rarely been sampled for members of this order, particularly in northern forests, and thus one of the richest groups in the canopy, which is comprised of predators and parasitoids, is being seriously underrepresented (Schowalter 1989, Winchester and Ring 1996, Progar and Schowalter 2002). Lack of knowledge about hymenopteran taxonomy and biology is a serious conservation issue because many of the parasitic members of this order (which represent ≈50% of described Hymenoptera) are thought to occur at low densities in isolated populations (because of variation in their hosts' abundances). This upper trophic level and high degree of specialization flags them as particularly vulnerable to extinction (LaSalle and Gauld 1993, Shaw and Hochberg 2001).

In our study, we compare richness, relative abundance, and composition of hymenoteran families and mymarid genera between white pine (*Pinus strobus* L.) and sugar maple (*Acer saccharum* Marsh.) forests and between the canopy and understory in northeastern temperate forests. Because of the difficulty of cataloging all species in such a taxonomically complex and relatively poorly known group as the Hymenoptera, we focused on family (high-taxa level) and generic (low-taxa level) richness, both of which have been shown to be strong predictors of species richness in angiosperms, birds, and mammals (Balmford et al. 1996a). The efficiency of using this higher taxonomic level classification, as an alternative to species identification, is of special importance to conservation planning and biomonitoring in forest environments (Williams and Gaston 1994, Balmford et al. 1996a, b). We chose the Mymaridae for more detailed study because of their abundance in our samples and availability of taxonomic expertise.

Materials and Methods

Study Area. Research was conducted in Haliburton Forest and Wildlife Reserve (45°15′ N, 78°35′ W) in the Great Lakes–St. Lawrence region of southcentral Ontario. The region is primarily upland, on moderately rolling rocky Precambrian shield covered by shallow to moderately deep stony, silty sand (Hills 1959), and characterized by temperate-mixed (coniferous-deciduous) forests. Sugar maple and American beech (*Fagus grandifolia* Ehrh) dominate upland sites; also notable are numerous hemlock (*Tsuga canadensis* L. Carr.) stands. White pine is characteristic of the Great Lakes forest region and grows best in open areas; however, because of past logging activities, only sparse remnant stands occupy the landscape today.

Study Design. We used a split-split block design with three forested areas as blocks: forest type (maple and pine) was the main design factor; forest stratum (canopy and understory) was the first split factor; and collection bottle location (top or bottom of the malaise trap) was the second split factor. In each forested area, insects were sampled in one sugar maple and one white pine stand for a total of six stands. In addition to being chosen based on their overstory composition, stands also had to be easily accessible and not logged in the preceding 60 yr. In each stand, three sampling stations were set at least 50 m from each other and were considered independent samples. At each station, a pair of insect traps was suspended: one in the canopy and the other below it in the understory, just above ground level, to provide a total of 36 traps. Canopy traps were set using a bow and arrow and a pulley system (Vance et al. 2003) and were set at heights of 18–23 m in maple stands (average, 20.0 m) and at 21–27.5 m in pine stands (average, 24.5 m). Understory traps were suspended from a low branch 30–45 cm above ground.

Insect Sampling and Identification. Insects were sampled using modified malaise traps recommended by the Environmental Monitoring and Assessment Network to sample forest canopies (Finnamore et al. 1998, Vance et al. 2003). The main body of the trap consisted of two intersecting, rectangular panels of black netting (mesh width of 0.5 mm). As viewed from the side, the collecting surface was 1.2 by 1.4 m (hence, 6.7 m^2 of collecting surface per trap). Each trap had two collecting bottles. One bottle was located at the top and the other at the bottom of the trap, attached by mesh funnels above and below the main body to funnel captures into either bottle. Ethanol (70%) was used as both a collecting fluid in bottles and a preservative for storage before identification.

Insects were sampled during the first week of June, July, and August 2001 for a total of three sampling periods. Because of the vagaries of sampling (principally wind disturbances and bear depredations), the duration of the monthly sampling period ranged from 5 to 8 consecutive days. All captured Hymenoptera

were identified to family using Goulet and Huber (1993). Voucher specimens were deposited at the Royal Ontario Museum (Toronto, Canada) and the Mymaridae at the Canadian National Collection of Insects (Ottawa, Canada).

Habitat Variables. As potential correlates of forest type and variation in hymenopteran composition, 16 habitat variables were measured at each site including topographic slope, canopy openness, leaf area index, basal area, percentage vegetation cover in the understory, leaf litter depth, and percentage cover of downed woody debris. A complete description of habitat variables is provided by Vance et al. (2003).

Data Analysis. Abundance and richness of hymenopteran families and mymarid genera were used as response variables and compared between forest types, forest strata, and location of collection bottle. Abundances were standardized for capture effort by correcting monthly abundances for trap effort and calculating the mean across the 3 months of sampling. Thus, all analyses of hymenopteran abundance were performed on the average number of insects captured per trap per day, averaged over the three sampling periods.

A large number of methods to quantify species richness of communities have been described (Magurran 1988, Colwell and Coddington 1994). We selected the Jacknife estimator for species richness and calculated sample-based rarefaction curves of asymptotic richness using the EstimateS program (version 6.0; Colwell 1997). In rarefaction curves, the number of individuals was plotted as the independent variable and the number of genera or families as the dependant variable (Gotelli and Colwell 2001). The calculations used 100 multiple random orderings of the samples. We examined differences in community composition by estimating the percentage overlap or similarity, based on counting the number of taxa exclusively caught in a given forest type, forest stratum, or bottle location.

Abundances of common hymenopteran families (those with >65 individuals collected in >61% of the sampling stations) and mymarid genera (those collected in >50% of the sampling stations) were tested for treatment differences using a split-split plot analysis of variance (ANOVA) with forested areas as the blocking factor (SAS Institute 2000). Other families, and genera with six or more individuals captured, were tested for differences in abundance by forest type with a two-sample *t*-test and by forest stratum and bottle location with paired *t*-tests. Differences between treatments in the mean richness of hymenopteran families and mymarid genera were tested on the raw data using a split-split ANOVA and also using a split-split ANOVA with the number of individuals as a covariate (analysis of covariance [ANCOVA]). To satisfy assumptions of the ANOVA, abundances were square-root transformed before analysis. If data did not meet the assumptions even after transformation, they were tested using nonparametric equivalents (SAS Institute 2000). Because of low numbers of Symphyta, all seven families (Orussidae, Diprionidae, Argidae, Tenthredinidae, Xiphydriidae, Xyelidae, and Pamphiliidae) were grouped into this suborder for analyses.

To explore community patterns, multivariate techniques were undertaken using CANOCO (1998). First, a detrended correspondance analysis (DCA) was done on each of the family-level and genus-level data sets to determine gradient lengths. A unimodal model seemed appropriate for both data sets (gradient lengths of axis one were 2.07 and 4.3 for families and genera, respectively); therefore, correspondence analysis (CA) was used. The usual negative effects of CA were observed (arching and data compression); therefore, DCA was used. Data were square-root transformed before analysis, and rare families or genera were down-weighted (ter Braak and Scaron;milauer 1998). After constraining the hymenopteran families with habitat variables, gradient lengths were shortened to 0.91 and 0.69 for axes 1 and 2, respectively, so a linear response model was used. Similarly, gradient lengths for Mymaridae were shortened to 1.4 and 0.96 for axes 1 and 2, respectively. Therefore, two redundancy analyses (RDAs) on the correlation matrix were used: one to examine the relationships between the family composition of Hymenoptera and environmental variables and another to examine the relationships between generic composition of the Mymaridae and environmental variables. Because of high abundances in two families (Encyrtidae and Aphelinidae) and one genus (*Alaptus*), analysis was undertaken on the correlation matrix (Jongman et al. 1995). The first axis and all canonical axes were tested for significance using a Monte Carlo permutations test with 9,999 iterations (ter Braak and Scaron;milauer 1998). Habitat variables were tested using forward selection (CANOCO 1998).

Results

Overall Richness and Abundance. A total of 7,634 hymenopterans were captured from 35 families. Encyrtidae was the most abundant family, encompassing 60% (4,547 individuals) of the total Hymenoptera, followed by Aphelinidae (916 individuals), Braconidae (401 individuals), and Ichneumonidae (388 individuals). The following families were rare (less than six individuals each): Apidae, Cynipidae, Dryinidae, Eucoilidae, Eurytomidae, Halictidae, Ibaliidae, Mymarommatidae, Pompilidae, Proctotrupidae, and Torymidae. The total abundance of Hymenoptera (corrected for trap effort) was similar between forest types, forest strata, and bottle locations (Table 1). However, there was a significant interaction between vegetation stratum and bottle location because bottom bottles collected more individuals than top bottles in the canopy, whereas the opposite was true in the understory.

The 400 Mymaridae collected represented 15 genera. The most abundant genus was *Alaptus* (63% of the total), followed by *Anagrus* (10%), *Dicopus* (10%), and *Anaphes* (8%). All other genera represented 3.5% or less of the total number caught. The following genera

Table 1. Abundance of hymenopteran families in the canopy and understory of maple and pine forests

	Maple				Pine				Significance (P^a)			
	Canopy		Understory		Canopy		Understory					
	B	T	B	T	B	T	B	T	Tree	Stratum	Bottle	Interaction
Aphelinidae	1.55 ± 0.33	0.11 ± 0.05	1.05 ± 0.38	0.16 ± 0.06	1.66 ± 0.49	0.21 ± 0.09	0.34 ± 0.11	0.07 ± 0.03	0.550	0.160	**0.005**	NS
Braconidae	0.12 ± 0.03	0.37 ± 0.06	0.12 ± 0.03	0.76 ± 0.23	0.14 ± 0.06	0.16 ± 0.03	0.11 ± 0.02	0.48 ± 0.12	0.330	0.130	**0.048**	NS
Ceraphronidae	0.04 ± 0.02	0.03 ± 0.01	0.18 ± 0.03	0.04 ± 0.02	0.06 ± 0.03	0.03 ± 0.01	0.31 ± 0.02	0.02 ± 0.01	0.300	0.110	**0.017**	**S × B 0.022**
Chrysididae	4.0E−4 ± 4.0E−4	0.03 ± 0.01	5.3E−3 ± 5.3E−3	0	9.6E−4 ± 5.2E−4	6.7E−3 ± 5.1E−3	0	5.6E−3 ± 5.4E−3	0.450	**0.004**	**0.010**	
Diapriidae	0.04 ± 0.02	0.03 ± 0.01	0.16 ± 0.04	0.35 ± 0.13	0.03 ± 0.01	0.04 ± 0.01	0.12 ± 0.03	0.43 ± 0.26	0.750	**0.003**	0.079	**S × B <0.001**
Encyrtidae	7.03 ± 1.31	2.24 ± 0.44	3.21 ± 0.42	8.82 ± 1.91	2.96 ± 1.14	1.02 ± 0.29	0.39 ± 0.06	0.26 ± 0.10	0.066	0.460	0.320	**S × B 0.002**
Eulophidae	0.12 ± 0.08	0.04 ± 0.02	0	0.02 ± 0.01	0.08 ± 0.03	0.04 ± 0.01	0.05 ± 0.02	0.03 ± 0.01	0.090	0.056	0.200	
Figitidae	7.0E−4 ± 7.0E−4	0.02 ± 0.01	5.3E− ± 5.3E−3	5.3E−3 ± 5.3E−3	1.7E−3 ± 9.2E−4	0.03 ± 0.02	0.02 ± 7.9E−3	0.01 ± 6.5E−3	0.060	0.520	0.083	
Formicidae	0.01 ± 6.9E−3	0.02 ± 7.9E−3	0.01 ± 7.0E−03	0	0.02 ± 0.01	0.01 ± 5.9E−3	0.04 ± 0.02	0.02 ± 0.01	0.130	0.780	0.290	
Ichneumonidae	0.04 ± 0.01	0.39 ± 0.06	0.07 ± 0.02	1.09 ± 0.34	0.06 ± 0.01	0.20 ± 0.06	0.04 ± 0.01	0.35 ± 0.10	0.230	0.150	**0.012**	NS
Megaspilidae	0.03 ± 0.01	1.4E−4 ± 1.4E−4	0.05 ± 0.03	0.01 ± 8.5E−3	6.4E−3 ± 5.2E−3	3.5E−3 ± 1.5E−3	0.01 ± 7.0E−3	1.7E−3 ± 1.1E−3	0.090	0.280	**0.033**	
Mymaridae	0.15 ± 0.05	0.11 ± 0.04	0.22 ± 0.07	0.73 ± 0.21	0.20 ± 0.03	0.17 ± 0.03	0.48 ± 0.09	0.26 ± 0.06	0.770	0.069	0.135	
Platygastridae	0.02 ± 0.01	0.02 ± 0.01	0.07 ± 0.02	0.10 ± 0.03	0.05 ± 0.03	0.04 ± 0.01	0.08 ± 0.02	0.08 ± 0.06				
Pteromalidae	0.11 ± 0.02	0.02 ± 0.02	0.08 ± 0.03	0.08 ± 0.03	0.06 ± 0.03	0.06 ± 0.02	0.09 ± 0.03	0.08 ± 0.06	0.936	0.350	0.280	
Scelionidae	0.04 ± 7.5E−3	0.02 ± 9.1E−3	0.07 ± 0.03	0.12 ± 0.05	0.04 ± 0.02	0.02 ± 7.7E−3	0.05 ± 0.02	0.06 ± 0.02	0.700	0.320	0.900	
Sphecidae	0.01 ± 6.9E−3	0.01 ± 0.01	5.3E−3 ± 5.3E−3	0	8.8E−4 ± 4.5E−4	0.01 ± 0.01	0	4.7E−4 ± 3.1E−4	0.550	**0.014**	0.740	
Symphyta	0.07 ± 0.02	0.01 ± 6.5E−3	0.01 ± 0.01	0.03 ± 0.02	0.02 ± 0.01	6.5E−3 ± 3.0E−3	0.04 ± 0.03	0.03 ± 8.3E−3	0.730	0.970	0.170	
Trichogrammatidae	0.06 ± 0.02	0.15 ± 0.07	0.14 ± 0.07	0.15 ± 0.06	0.03 ± 0.02	0.04 ± 9.4E−3	5.3E−3 ± 5.3E−3	0.03 ± 0.02	0.220	0.510	0.073	
Vespidae	0.01 ± 8.5E−3	0.03 ± 0.01	0.04 ± 0.02	0.11 ± 0.05	0.02 ± 8.7E−3	7.6E−3 ± 3.2E−3	0	2.8E−3 ± 1.9E−3	**0.002**	0.170	0.180	**S × B**
Total ind./tran/days	9.45 ± 1.43	3.77 ± 0.51	5.51 ± 0.20	12.61 ± 1.89	5.56 ± 1.79	2.12 ± 0.40	2.17 ± 0.23	2.23 ± 0.12	0.110	0.860	0.260	0.004

Mean no. of individuals per trap-day (±SE) of relatively common hymenopteran families collected in modified malaise traps from temperate forests in the Great Lakes region during 2001. Abundances are summarized by treatment variable (forest type, forest stratum, and collection bottle [B = bottom and T = top]).

[a] *P* values significant at 0.05 are shown in bold. Interaction was only tested for taxa tested using ANOVA and only significant results are reported. S, stratum; B, bottle.

NS, not significant.

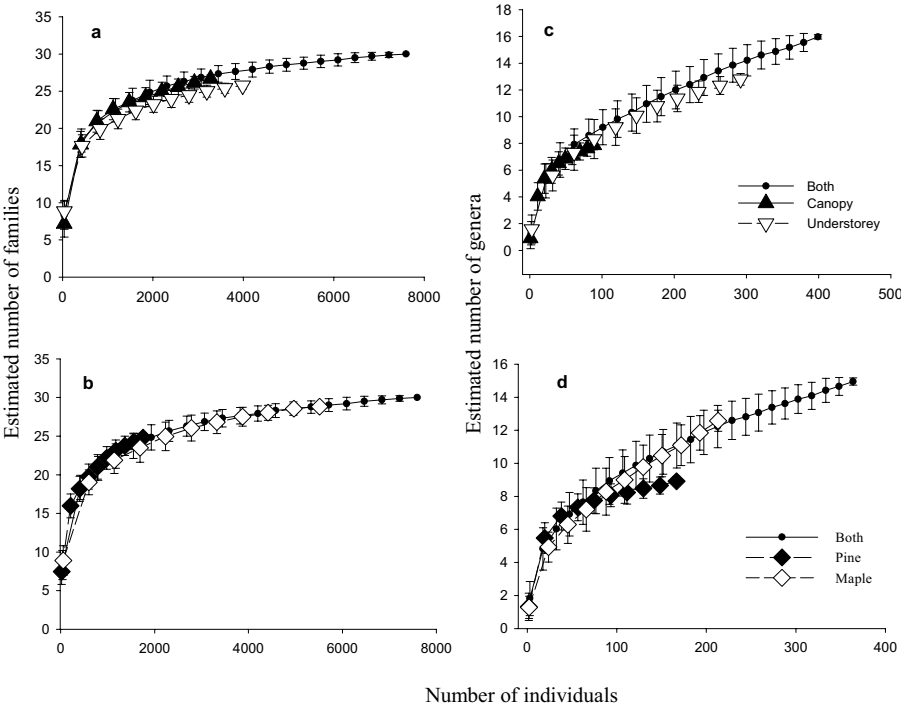

Fig. 1. Rarefaction accumulation curves of hymenopteran families (a and b) and mymarid genera (c and d) in different forest types and vegetation strata collected with modified malaise traps in mixed-temperate forest of southcentral Ontario, Canada.

were uncommon (≤10 individuals): *Acmopolynema*, *Camptoptera*, *Dicopomorpha*, *Erythmelus*, *Eustochus*, *Gonatocerus*, *Litus*, *Macrocamptoptera*, *Neomymar*, *Ooctonus*, and *Polynema.* Although the total abundance of mymarids did not differ between treatments (Table 1), at the generic level, some differences were detected (Table 2).

Differences by Forest Type. Vespidae was the only hymenopteran family showing significant differences by forest type, occurring more frequently in maple than pine stands (Table 1). Estimated hymenopteran family richness was higher in maple than in pine stands (Table 3). Although both raw richness and richness with abundance as a covariate did not differ significantly between forest types (ANOVA: $F_{1,2} = 11.15$, $P = 0.079$; ANCOVA: $F_{1,2} = 5.41$, $P = 0.14$), the trend was fairly strong with higher richness in maple than in pine sites. A view at the community composition corroborated this trend because there was 77% overlap or similarity between the two forest types, with six hymenopteran families occurring exclusively in the maple stands and only one exclusively in pine stands (Table 3). However, rarefaction curves showed that hymenopteran families accumulated at similar rates in both tree species (Fig. 1b).

The mymarids *Polynema* and *Ooctonus* were more abundant in pine than in maple forests ($U = -3.25$, $P = 0.0012$ and $U = -3.17$, $P = 0.0015$, respectively; Table 2). As with hymenopteran family richness, the estimated richness of mymarid genera was higher in maple than in pine forests (Table 3); however, differences between raw richness was not significant with or without abundance as a covariate (ANOVA: $F_{1,2} = 0.19$, $P = 0.71$; ANCOVA: $F_{1,2} = 0.02$, $P = 0.90$, respectively). Rarefaction curves showed that pine forests achieved slightly more of an asymptote than maple forests, indicating that most of the genera had been sampled in this forest type (Fig. 1d). This curve also plateaued beneath the maple accumulation curve, indicating lower overall generic richness in pine than in maple forests. Mymarid genera always showed less evidence of an asymptote in the rarefaction curves than hymenopteran families (Fig. 1), suggesting that more genera were present in these habitats than what was sampled, particularly in the maple stands. Composition of the mymarid assemblage showed 47% overlap between the two forest types; i.e., of the 15 genera, two were sampled exclusively in pine forests, whereas six were sampled only in maple forests (Table 3).

Differences by Forest Strata. Sphecidae was significantly more abundant in the canopy than in the understory, whereas Diapriidae and Chrysididae showed the opposite pattern (Table 1). A few significant interactions occurred between forest stratum and bottle location (Ceraphronidae, Diapriidae, and Encyrtidae) because the pattern of capture in collection bottles was inconsistent between strata. Raw family richness was almost significantly greater in the canopy than in the understory (ANOVA; $F_{1,2} = 13.56$, $P = 0.066$), but was not significant when the number of individuals

Table 2. Abundance of mymarid genera collected in the canopy and understory of maple and pine forests

	Maple				Pine				Significance (P^a)			
	Canopy		Understory		Canopy		Understory					
	B	T	B	T	B	T	B	T	Tree	Stratum	Bottle	Interaction
Alaptus	0.10 ± 0.03	0.04 ± 0.02	0.16 ± 0.06	0.49 ± 0.15	0.09 ± 0.03	0.09 ± 0.023	0.32 ± 0.07	0.15 ± 0.05	0.73	0.5	**0.065**	
Anagrus	0.02 ± 0.01	0.03 ± 0.01	0.01 ± 0.01	0.06 ± 0.04	0.03 ± 0.01	0.03 ± 0.01	0.03 ± 0.01	0.02 ± 0.01	0.32	0.18	0.11	
Anaphes	0.02 ± 0.01	0.01 ± 0.01	0.01 ± 0.01	0.09 ± 0.04	0.03 ± 0.02	0.01 ± 2.7E−3	0.01 ± 0.01	0.03 ± 0.01	0.30	0.68	0.16	
Dicopus	0	0.01 ± 0.01	0.03 ± 0.02	0.07 ± 0.05	0.01 ± 0.01	0.02 ± 0.01	0.08 ± 0.03	4.5E−3 ± 3.0E−3	0.12	**0.015**	0.56	
Ooctonus	0	0	0	0	4.7E−4 ± 4.7E−4	9.5E−4 ± 6.3E−4	0.02 ± 0.02	0.01 ± 0.01	**0.0015**	0.24	0.33	
Polynema	0.01 ± 0.01	0	0	0	0.03 ± 0.02	0.01 ± 7.2E−3	0	0.03 ± 0.03	**0.0012**	0.13	0.16	
Total individuals/trap-day	0.15 ± 0.05	0.11 ± 0.04	0.22 ± 0.07	0.73 ± 0.21	0.20 ± 0.03	0.17 ± 0.03	0.48 ± 0.09	0.26 ± 0.06	0.770	0.069	0.135	**S × B 0.004**

Mean no. of individuals per trap-day (±SE) collected using modified malaise traps from temperate forests in the Great Lakes region of south-central Canada during 2001. Data are summarized by forest type, vegetation stratum, and collection bottle (B = bottom; T = top).

[a] *P* values significant at 0.05 are shown in bold. Interaction was only tested for taxa tested using ANOVA and only significant results are reported. S, stratum; B, bottle.

Table 3. Richness and diversity of hymenopteran families and mymarid genera in pine and maple forests

	Forest type		Forest stratum		Bottle location[a]		Total
	Pine	Maple	Understory	Canopy	Top	Bottom	
Hymenoptera families							
Estimated richness[b]	28.0 ± 2.2	33.0 ± 1.9	30.0 ± 1.9	31.9 ± 2.2	33.0 ± 1.9	27.0 ± 1.7	34.0 ± 2.0
No. samples used	96	106	106	96	98	104	202
No. families	24	29	25	27	29	24	30
No. exclusive families	1	6	3	5	6	1	
No. individuals	1,848	5,786	4,179	3,455	3,527	4,107	7,634
Mymaridae genera							
Estimated richness[b]	11.0 ± 1.4	19.9 ± 2.5	17.0 ± 1.9	10.0 ± 1.4	12.0 ± 1.4	17.9 ± 2.4	21.0 ± 0.18
No. samples used	96	106	106	96	98	104	202
No. genera	9	13	13	8	9	12	15
No. exclusive genera	2	6	7	2	3	6	
No. individuals	176	224	306	94	215	185	400

Richness and diversity estimates (mean ± SD) from the canopy and understory of temperate forests in the Great Lakes region of south-central Canada during 2001.

[a] Location of the collection bottle on the modified malaise traps.

[b] Jackknife estimator was used to derive rarefaction curves and estimate family and genus richness (EstimateS program, version 6.0, Colwell 1997).

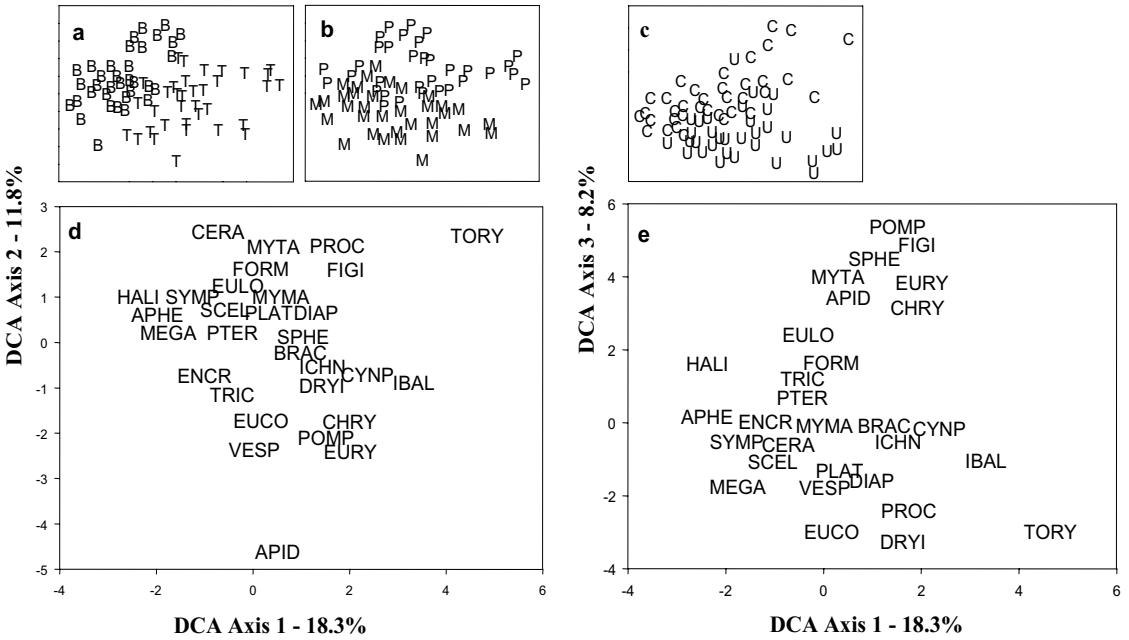

Fig. 2. First three axes from the DCA on hymenopteran families collected with modified malaise traps in mixed-temperate forests of southcentral Ontario, Canada. Treatments plotted are (A) bottle location in the trap (T: top, B: bottom), (B) forest type (M: maple, P: pine), (C) vegetation stratum (C: canopy, U: understory). Family scores are shown in D and E. Four-letter codes are first four letters in family names except MYTA = Mymarommatidae.

was used as a covariate (ANCOVA; $F_{1,2} = 4.16$, $P = 0.18$). As with forest type, estimates of family richness from the understory and canopy rarefaction curves were very similar to their combined curve (Fig. 1a), although they showed that canopy traps accumulated families at a slightly higher rate than did understory traps and a higher total number of families could be expected. This is consistent with the number of families actually collected by forest stratum; i.e., 5 families were found exclusively in the canopy and 3 exclusively in the understory (22 families occurred in both strata), resulting in 73% similarity.

The mymarid *Dicopus* was found more in the understory than in the canopy (paired *t*-test; $t_{35} = -2.56$, $P = 0.015$; Table 2). As opposed to the pattern observed for hymenopteran family richness, the richness of mymarid genera was significantly higher in the understory than in the canopy, with or without abundance as a covariate (respectively, ANOVA: $F_{1,2} = 25.0$, $P = 0.038$; ANCOVA: $F_{1,2} = 22.02$, $P = 0.042$). Canopy samples accumulated genera more slowly than did understory samples, and canopy traps also accumulated fewer individuals (Fig. 1c). Composition of the mymarid assemblage showed vertical stratification. Seven genera (*Camptoptera*, *Dicopomorpha*, *Erythmelus*, *Eustochus*, *Litus*, *Macrcamptoptera*, and *Ooctonus*) were captured exclusively in understory traps, two (*Acmopolynema*, *Neomymar*) in canopy traps alone, and only six genera at both forest strata (Table 3), indicating relatively high β-diversity (40% overlap).

Differences by Bottle Location. Differences in abundances between bottle locations were significant for six families; Aphelinidae, Ceraphronidae, and Megaspilidae were collected more often in bottom bottles, whereas Chrysididae, Braconidae, and Ichneumonidae were collected more often in top bottles. Estimated hymenopteran family richness was higher in top than in bottom collecting bottles, but the results were not significant for either raw richness or richness corrected for abundance (respectively, ANOVA: $F_{1,2} = 1.49$, $P = 0.346$; ANCOVA: $F_{1,2} = 1.25$, $P = 0.38$).

The mymarid genus *Alaptus* tended to be collected in bottom rather than top bottles (Table 2) but showed no significant relationship with forest type or stratum (forest type: $F_{1,2} = 0.15$, $P = 0.73$; forest stratum: $F_{1,2} = 0.66$, $P = 0.50$; bottle location: $F_{1,2} = 13.9$, $P = 0.065$). Estimated mymarid generic richness showed the opposite pattern to the analysis of hymenopteran families, being higher in bottom than in top bottles. However, raw abundance differences were again not statistically significant with and without the number of individuals as a covariate (ANOVA: $F_{1,2} = 7.0$, $P = 0.12$; ANCOVA: $F_{1,2} = 8.0$, $P = 0.11$).

Multivariate Analysis. The first axis of the DCA on hymenopteran family abundances separated bottle locations and represented 18.3% of the total variance (Fig. 2A). The two forest types separated strongly on the second axis (11.8% of variance), with pine on the positive side and maple on the negative side (Fig. 2B). Forest stratum was slightly less well resolved on the third axis (8.2% of the variance), with canopy traps on

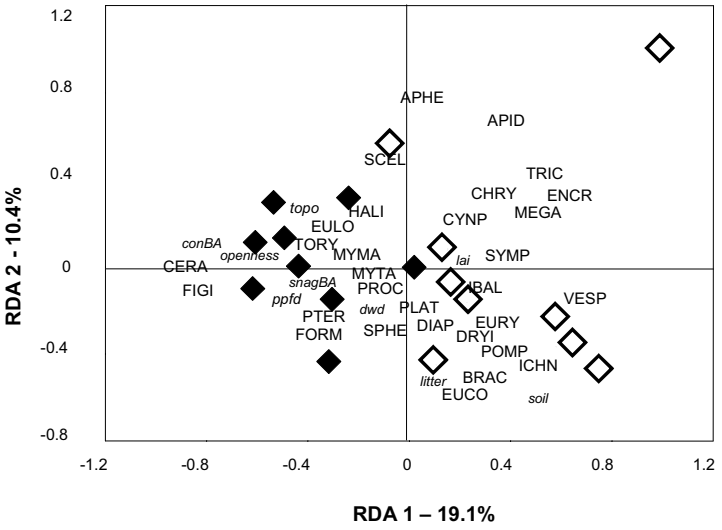

Fig. 3. RDA on the correlation matrix of hymenopteran families collected with modified malaise traps in mixed-temperate forest of southcentral Ontario, Canada. Families (4-letter capital codes), station scores (maple, ◇; pine, [daif]), and environmental variables are shown. Soil, moisture regimen; litter, leaf litter depth; snagBA, basal area of snags; conBA, basal area of coniferous trees; dwd, downed woody debris (decomp class 1–5); topo, topography.

the positive side and understory traps on the negative side of this axis (Fig. 2C). Torymidae and Ibaliidae were associated with top bottles, and Halictidae, Aphelinidae, Megaspilidae, and Ceraphronidae were associated with bottom bottles (Fig. 2D). Apidae, Vespidae, Eurytomidae, and Pompilidae were more closely associated with maple sites than pine sites, whereas Figitidae, Ceraphronidae, Torymidae, and Proctotrupidae were closer to the pine side of the ordination (Fig. 2D). Sphecidae, Pompilidae, and Figitidae were associated more with canopy traps, whereas Dryinidae, Eucoilidae, Torymidae, and Proctotrupidae were associated more with understory traps (Fig. 2E). A strong degree of separation between maple and pine stands along the first axis of the RDA on hymenopteran families was evident (Fig. 3); however, neither of the first two canonical axes was significant (respectively, Monte Carlo: $F = 1.89$, $P = 0.22$; and $F = 1.2$, $P = 0.16$). Using forward selection, the basal area of coniferous trees (conBA) was significant ($F = 2.45$, $P = 0.004$). Families associated with pine stands included Figitidae, Ceraphronidae, and Torymidae, whereas families associated with maple stands were Megaspilidae, Vespidae, and Encyrtidae. There were corresponding significant results for only the latter two families in univariate statistics.

Mymarid genera were not well separated by treatment type in the DCA (data not shown). None of the three factors was significant along any of the first three axes, but on the fourth axis, forest type was significant (two-sample t-test; $t = 4.43$, $P = 0.04$). Constraining the genera by environmental variables did not separate forest type on the first axis of the RDA, and this axis was not significant (Monte Carlo: $F = 1.13$, $P = 0.89$). Using forward selection, none of the environmental variables significantly explained variance in data, but the basal area of conifers had the strongest relationship ($F = 1.3$, $P = 0.18$).

Discussion

Forest Type. Many studies have shown differences in insect assemblages associated with tree species in tropical (Storke et al. 1997) and temperate forests (Le Corf and Marquis 1999, Schowalter and Zhang 2005), but the majority of these have focused on either coleopteran, formicid, or herbivorous groups. Few have addressed the response of flying insect assemblages to forest type. In New Zealand temperate rainforests, Didham (1997) found that dipterans varied with tree species. Similarly, we have shown here, in northern temperate forests of eastern North America, that hymenopteran families and mymarid genera differ between maple and pine stands. Although Vance et al. (2003) found the opposite pattern with cerambycids in the same study area, in general it seems that insect community composition has low similarity between different forest types, at least at low taxon levels (e.g., genus or species),

Unconstrained ordinations indicated a relatively strong relationship between hymenopteran families and the forest types sampled; however, the relationship was not mirrored in univariate statistics. The fewest significant differences in family abundances were found between the different forest types in comparison to the other design factors (forest stratum and collecting bottle location); only two families (Encyrtidae and Vespidae) were more likely to be collected in maple than in pine forests. Encyrtidae was abundant likely because of an outbreak of a soft scale, a primary host for encyrtids, on maple and beech saplings that occurred in the sampling year. High species richness

and abundance of Encyrtidae and Aphelinidae have also been observed in Borneon forests (Stork 1991). The high numbers of Vespidae in our maple forests is difficult to explain. Although many species are solitary, others are social and live in paper nests in trees or in pre-existing holes in the ground (Milne and Milne 1997). A deeper leaf litter in maple sites than the pine sites may have provided better conditions for paper-nest building species. Alternatively, traps may have been close to nests and captured disproportionately more individuals than normal.

Although a small turnover of families compared with genera occurred between forest types (77% of families and only 47% of the genera were common to both forest types), family ordinations more strongly separated forest type than genera ordinations. The large sample size of Encyrtidae may be causing the strong separation for families. Rates of genus accumulation and estimated richness for families and genera were higher in maple than in pine stands. As expected, we found greater richness in maple than in pine stands because of the higher structural complexity, understory herbaceous cover, and leaf area in the maple than in the pine stands (Vance et al. 2003). However, because our rarefaction curves suggest that not all genera of mymarids were sampled, their relationship to habitat remains unconfirmed and requires further study to determine if such differences actually exist.

Vertical Stratifiation. While certain insect groups (e.g., some herbivores) can be twice as diverse in the canopy as on the ground (Basset et al. 2001) or differ in species composition, such as ceramycids in northeastern temperate forests (Vance et al. 2003), some canopies have revealed similar species richness as their understories (DeVries et al. 1997, Basset et al. 2001). The general pattern seems to be, for tropical forests at least, that sap-sucking insects and ants tend to be richer and more abundant in canopies than in understories, as opposed to the majority of flying insects (De Dijn 2003). In Surinam rainforests, De Dijn (2003) found that non-ant hymenopterans were more abundant in the understory than in the canopy, when sampling with yellow pot traps. In northeastern temperate forests, we found that total abundance of hymenopterans was similar between forest strata, but family richness was slightly higher in the canopy. Le Corf and Marquis (1999) found a similar herbivore community in the canopy and understory of oak trees.

We found that the canopy and understory of both tree species shared 73% of the hymenopteran families collected, but rare families were found more frequently in the canopy. However, ordinations revealed a weaker trend for forest strata than forest type, and only three families in univariate statistics showed significant effects (Diapriidae, Chrysididae, and Sphecidae, the former two being most common in understories and the latter in canopies). The abundance of diapriids in understories may be explained by their preference for damp, shaded habitats such as forests and marshes, near or in water, and in soil (Masner 1993). Unlike Winchester and Ring (1996), who found no sphecid wasps in the canopy of sitka spruce [*Picea sitchensis* (Bong.) Carr.] from British Columbia, we collected more sphecids in the canopy than in the understory. Sphecid wasps are highly mobile and hunt a variety of insects (e.g., aphids, leafhoppers, thrips, flies), and thus may seem more abundant in the canopy because they spend significant lengths of time foraging there rather than in the understory of these temperate forests.

At the generic level, we found greater abundance and richness of mymarids in the understory than in the canopy and a 60% turnover in composition. Lower-taxa identification to species will likely reveal an even higher β-diversity for mymarids. In the same study area, cerambycids were also more abundant in the understory, but equally rich in both forest strata (Vance et al. 2003); the turnover for cerambicid species was 74%. Some authors have reported strikingly high richness or abundance of parasitoids and predators in the canopy (Moran and Southwood 1982, Schowalter 1989, Winchester and Ring 1996, Winchester 1997), but our results suggest that the diversity and richness of parasitoids may sometimes be even higher in the understory.

Trap Performance. These newly designed flight-interception traps collected smaller hymenoptera (e.g., Aphelinidae and Megaspilidae) more often in bottom bottles and larger hymenoptera (e.g., Ichneumonoidea and Chrysididae) more often in top bottles. This result is similar to traditional malaise traps that generally capture large, active-flying insects in the top bottles and small, less mobile insects in bottom-collecting units, such as pan traps (Darling and Packer 1988). Only 73% of families and 47% of genera overlapped between the two bottle locations. In some families, canopy-dwelling species behaved differently than understory species. For example, diapriids were collected more in bottom bottles in the canopy and top bottles in the understory. The rules of "positively phototropic, negatively geotropic" that apply to the majority of insects seem to be different for certain hymenopteran families, and moreover, may vary with height. Thus, we found that top- and bottom-collecting bottles of flight-interception traps catch different families and genera and both are important to sample community diversity.

Implications for Conservation and Management. Even within the relatively small guild range that hymenopterans and mymarids compose, contradictory results occur for these two taxa (with the exception of higher estimated richness in maple stands than pine). We found hymenopteran family richness higher in the canopy and the opposite for mymarid genera richness, which was higher in the understory. The ambiguity could be caused by the high species richness and low population density, which is typical of Hymenoptera and is supported by our sampling results: 11 of the 35 hymenopteran families we captured had fewer than six individuals. When Stork (1988) fogged a tropical tree, he found 739 species of chalcid wasps (Chalcidoidea), 437 of which were singletons and only 8 of which were collected >10 times. Rarely collected taxonomic groups make up a significant component in

the order Hymenoptera, perhaps because many are highly specialized (e.g., parasitoids with narrow host ranges). It would seem that taxonomic minimalism is not appropriate for this Order because family-level identification of hymenoptera did not accurately predict what occurred within the mymarid genera.

Our study showed separation of hymenopteran families by forest types in multivariate analyses. Because current resources make it impossible to identify and monitor all species of Hymenoptera, insect families may provide a more realistic approach, at least at this time, for management and conservation planning (Andersen 1995). Family, genus, and even order richness have correlated with species richness of woody plants and vertebrates, yet this correlation tends to decrease as the speciosity of higher taxa increases (Balmford et al. 1996a). Because parasitic Hymenoptera are a speciose group, it might limit the potential for a higher-taxa approach. However, because rare families are so numerous in Hymenoptera, family-level analysis may approach species-level analysis. Given the current lack of taxonomic expertise and available resources for conservation planning, family identification is an attractive starting point for forest biodiversity monitoring programs. Although higher-taxonomic level monitoring programs for Hymenoptera have the potential to reflect changes in overall richness of the order, more study is required to determine if this is indeed the case.

It is apparent that the order Hymenoptera does show variation with respect to forest type and forest strata, even in relatively simple forest systems such as we have in the temperate regions of eastern North America. Major differences were seen in the composition of assemblages for both factors. Based on our work, as well as other studies cited above, it seems that the composition of insect assemblages (especially at low-taxa levels), rather than relative abundance and richness, is the community attribute showing the greatest differences between tree species and vertical strata for various combinations of forest types and insect groups. Undoubtedly, the range of this variation will become more apparent as more studies are completed.

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