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A Comparison of the Beetle (Coleoptera) Fauna Captured at Two Heights Above the Ground in a North American Temperate Deciduous Forest

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Abstract.—We compared the beetle fauna captured in 12 pairs of flight intercept traps suspended at two different heights above the ground (≥15 m and 0.5 m) in a temperate deciduous forest in the southeastern United States to better understand how the abundance, species richness, diversity and composition of insect communities differ among forest strata. A total of 15,012 beetle specimens were collected representing 73 families and 558 morphospecies. Shannon's diversity and evenness were both higher near the ground than in the canopy, but no differences in total abundance or species richness between the two layers were observed. There were many differences at the family level, however, and species composition differed considerably between the two layers. About 29% and 31% of species were captured exclusively in the canopy or near the ground, respectively. The canopy traps were more similar to one another than they were to those near the ground and vice-versa based on both Sorensen's quotient of similarity and Raabe's percentage of similarity. The canopy and ground trap locations were quite distinct based on nonmetric multidimensional scaling. The degree to which species composition was similar (*i.e.*, Sorensen's quotient of similarity) between pairs of traps decreased significantly with inter-trap distance for the traps in the canopy, but not for those near the ground, suggesting a more uniform community near the ground. Of the 41 families or subfamilies represented by more than 40 individuals, 12 were more abundant in the canopy and 14 were more abundant near the ground. Similarly, of the 16 families or subfamilies represented by more than 10 species, five were more species rich in the canopy and four were more species rich near the ground. Three families (Cerambycidae, Cleridae and Coccinellidae) were both more abundant and species rich in the canopy, whereas four other groups (Carabidae, Pselaphinae (Staphylinidae), Scolytinae (Curculionidae) and other Staphylinidae) were both more abundant and species rich near the ground. In addition to differing considerably among families, the vertical distribution patterns varied within many families as well. The distribution patterns for several groups are discussed in some detail with respect to known life history information.

Introduction

Naturalists have long been drawn to forest canopies and have, in recent years (Basset *et al.*, 2003b; Lowman and Rinker, 2004), become even more infatuated with this poorly understood and highly inaccessible ''biotic frontier'' (Erwin, 1983). Canopy research contributes to a more holistic view of forest processes which can then be directly applied toward a variety of issues including conservation biology (Winchester, 1997; Gering *et al.*, 2003), forest management (Su and Woods, 2001), epidemiology (Darbro and Harrington, 2006) and pest control (Hull and Grimm, 1983; Hanula *et al.*, 1984; Meagher and Hull, 1987; De Groot and DeBarr, 1998; Trout *et al.*, 2006).

Despite the recent surge in interest, the upper reaches of temperate deciduous forests remain mostly unexplored, and few attempts have been made to characterize the insect communities residing there. Some of the most basic questions regarding the spatial and temporal dynamics of these populations await investigation. Although numerous studies

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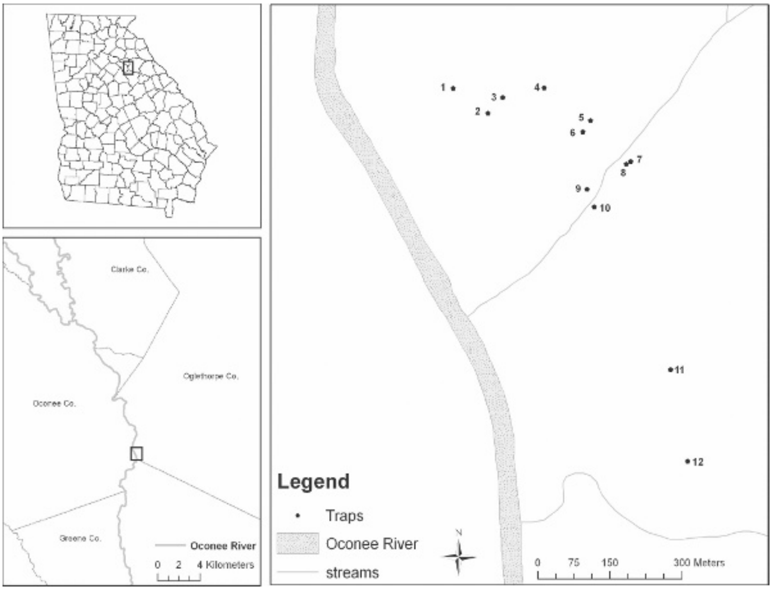

FIG. 1.—The project took place on the Oconee River flood plain, Oglethorpe County, Georgia USA. Sampling locations are indicated by the numbered dots (*Quercus phellos* (1,3,7), *Pinus taeda* (2,11,12), *Liquidambar styraciflua* (4–6), *Platanus occidentalis* (8–10))

show that temperate deciduous canopies support an impressive diversity of insects (Krinsky and Godwin, 1990; Krinsky and Godwin,1996; Gering and Crist, 2000; Vance *et al.*, 2003; Summerville *et al.*, 2003), how the abundance, species richness and composition of these insect communities differ among forest strata is not clear. Until we thoroughly investigate such patterns, our understanding of temperate forest systems will be incomplete, if not incorrect. The objective of this project was to compare the abundance, species richness, diversity, evenness and composition of the beetle fauna captured in the canopy and near the ground in a temperate deciduous forest in the southeastern United States.

METHODS

Study site.—This project took place in Scull Shoals Experimental Forest which is part of the Oconee National Forest in Oglethorpe County, Georgia. All of our sampling took place within a continuous mature bottomland hardwood forest bordering the Oconee River (Fig. 1). The upper canopy was dominated by willow oak (*Quercus phellos* L.), water oak (*Q. nigra* L.), sweetgum (*Liquidambar styraciflua* L.), sycamore (*Platanus occidentalis* L.), loblolly pine (*Pinus taeda* L.), river birch (*Betula nigra* L.) and several less common species. Hophornbeam (*Ostrya virginiana* (Mill.) K. Koch) was common in the lower canopy reaching heights of about 10 m. The understory was variable, but was completely dominated in places by Chinese privet (*Ligustrum sinense* Lour.), an introduced shrub from Asia, that grew to about 5 m in height.

Insect sampling.—We selected 12 dominant overstory trees (average height 31.67 ± 0.88 m, range 29–36 m) from the four most common tree species (*i.e.*, three trees per species) in our study area which were *Quercus phellos* L., *Liquidambar styraciflua* L., *Platanus occidentalis* L.

and *Pinus taeda* L. We chose trees with suitable limbs for hanging traps and that also offered unobstructed space through which to raise and lower traps. Each tree had one trap suspended in the canopy and one suspended near ground level for a total of 12 traps at each height. In Feb., before the trees put out leaves, a slingshot attached to a fishing reel was used to send a small lead weight over the highest limb possible in each tree. Heavier ropes were then pulled over the limbs and were later used to pull traps into the canopy. Considerable confusion surrounds the word ''canopy'' (Moffett, 2000), but in this paper we use the term to refer to the vegetative zone formed by the crowns of the tallest trees. Our goal was to suspend each trap above the lowest leaf-bearing branch in each tree. A light-weight rope was tied to the side of each trap and attached to a stake in the ground to ensure that the traps were raised to the same height each time and to aid in pulling them down. They were measured at the end of the study to determine trap heights (average height 18.83 ± 0.95 m, range 15–24 m). At each location, a second trap was suspended 0.5 m above the ground directly below the canopy trap from a metal pole driven into the ground.

The traps were made by cutting grooves halfway down the middle of two clear plastic vanes (20 × 30 cm) and sliding them together to create a + shaped barrier. The top of this barrier had a wire attached for hanging the trap and the bottom was wired to a white plastic bucket (diameter 16 cm, depth 15 cm). A hole (diameter 1.7 cm) in the side of the bucket covered with fine wire mesh (<1 mm) prevented the traps from overflowing during rain storms. Propylene glycol was added to the buckets to kill and preserve the catch.

The average horizontal distance between pairs of traps (calculated from GPS coordinates), was 290 m (range, 11–915 m). The traps were operated continuously from 5 Apr. to 28 Jun. and again from 12 Jul. to 4 Oct. 2005. Samples were collected every 2 wk during these periods. Insects were stored in 70% ethanol and beetles were later sorted to morphospecies. We followed the classification system of Arnett and Thomas (2001, 2002), but analyzed certain historically distinct families separately (*i.e.*, Scolytinae, Platypodinae, Pselaphinae and Scaphidiinae). Voucher specimens have been divided among the Louisana State Arthropod Museum (Pselaphinae), the research collection of MD Ulyshen (Colydiidae, Nitidulidae, Endomychidae and Scolytinae) and the Georgia Museum of Natural History (all other families).

Statistical analysis.—All analyses, unless otherwise stated, were performed using SAS (SAS Institute, 1990). Data from the different sampling periods were combined for all analyses except when investigating seasonal trends in which case we calculated the mean ± SE abundance and species richness for each two week sampling period separately. Paired *t*-tests were used to compare the overall abundance, species richness, Shannon's diversity and evenness of beetles captured in the canopy traps to those captured in the traps near the ground. Paired *t*-tests were also used to compare the abundance and species richness of the most abundant and species rich families between the two heights. We also used paired *t*-tests to compare the abundance of certain species, genera or taxonomic groups collected in the canopy and near the ground.

A one-way ANOVA and the Ryan-Einot-Gabriel-Welsch multiple range test (Day and Quinn, 1989) were used to compare mean abundance, species richness, diversity and evenness among the different tree species.

Two similarity indices were used to compare species composition: Raabe's percentage of similarity and Sorensen's quotient of similarity. Raabe's percentage of similarity places emphasis on the most abundant species whereas Sorensen's quotient of similarity measures only the number of species shared between two locations (Southwood, 1966). We used linear regression analysis to determine the correlation between Sorensen's quotient of similarity and horizontal between-trap distance as a way to compare patterns of species turnover between the two heights.

We used PC-Ord (McCune and Mefford, 2006) to create an ordination based on nonmetric multidimensional scaling (NMS). Only species captured at three or more locations (278 species) were used in this analysis. The habitat variables considered were height above the ground (*i.e.*, in the canopy or near the ground) and tree species.

RESULTS AND DISCUSSION

Overall abundance, species richness and diversity.—We collected 15,012 beetle specimens in 73 families and 558 morphospecies (Table 1). Abundance and species richness were similar between traps in the canopy and those near the ground, but Shannon's diversity index and evenness were greater near the ground (Table 2).

Only two previous studies have compared the overall numbers of beetles in the canopy and near the ground in temperate deciduous forests. Unfortunately, neither study was replicated and they produced somewhat conflicting results. Nielsen (1987) collected nearly seven times more beetles near the ground than in the canopy in Denmark, whereas in the northeastern United States, Preisser *et al.* (1998) reported no clear difference in abundance between the two heights. Our data are more similar to Preisser *et al.* (1998) in that we did not see a difference in overall beetle abundance between the two trapping locations.

Species composition.—The beetle fauna in the canopy and near the ground differed considerably with respect to species composition. Only about 40% of species were captured both in the canopy and near the ground (Table 1). According to both Raabe's percentage of similarity and Sorensen's quotient of similarity, the samples from the canopy traps were more similar to one another than to those near the ground (Fig. 2). Likewise, samples from the ground traps were more similar to one another than they were to those in the canopy. NMS ordination showed a strong correlation ($r^2 = 0.85$) existed between trap height (*i.e.*, in the canopy or near the ground) and axis 1, and the canopy and ground locations form obvious groupings along this axis (Fig. 3). The canopy locations form a tighter grouping than the ground locations.

That insect species composition differs among forest strata may not be surprising given that resources (*i.e.*, foliage, dead wood, fungi, carrion, etc.) differ considerably in both abundance and kind with height above the forest floor. However, some debate exists as to the degree to which the canopy fauna is distinct from that near the ground. In temperate zones, strict canopy specialization, or complete freedom from the ground, is probably quite rare because most insects are driven back to the forest floor following the seasonal loss of foliage and the onset of winter (Schaefer, 1991). In contrast, many insects in tropical rainforests are thought to spend their entire lives in the canopy and are sometimes morphologically adapted to that environment (Ober, 2003). The seasonally stable and structurally complex canopies of tropical rainforests likely encourage many insects to complete development in a variety of arboreal habitats including the organic material accumulated near mats of epiphytes (Nadkarni and Longino, 1990), water-filled plant structures (Kitching, 2000) and under bark (Arndt *et al.*, 2001). Therefore, the canopies of tropical forests are likely to contribute more to the total biodiversity of an area than are the canopies of temperate deciduous forests. Quantifying this contribution, though difficult, is essential for accurate biodiversity estimates. Recently, in an Australian rain forest, Stork and Grimbacher (2006) captured 39% and 20% of beetle species exclusively in the canopy or near the ground, respectively. In contrast, about an equal proportion of beetle species were captured exclusively in the canopy (29%) or near the ground (31%) in this study. These

TABLE 1.—List of families with the number of species and individuals captured in flight-intercept traps suspended in the canopy (≥15 m) and near the ground (0.5 m) in a temperate deciduous forest, Oglethorpe County, Georgia USA

Family	No. Species Canopy/Ground	Total No. Species	No. Individuals Canopy/Ground	Total No. Individuals
Aderidae	6/3	6	37/22	59
Anobiidae	9/8	12	82/44	126
Anthicidae	1/1	2	1/3	4
Anthribidae	5/3	7	7/4	11
Attelabidae	1/1	1	109/5	114
Biphyllidae	1/1	1	2/11	13
Bostrichidae	0/1	1	0/3	3
Brentidae	1/1	2	1/1	2
Bruchidae	1/0	1	1/0	1
Buprestidae	6/2	7	96/51	147
Byturidae	1/1	1	5/71	76
Cantharidae	12/7	13	57/45	102
Carabidae	19/25	33	45/129	174
Cerambycidae	36/22	43	471/77	548
Ceratocanthidae	1/1	1	32/7	39
Cerylonidae	1/2	2	2/10	12
Chrysomelidae	16/14	20	737/159	896
Ciidae	1/2	2	15/9	24
Clambidae	0/1	1	0/3	3
Cleridae	13/4	13	84/10	94
Coccinellidae	12/6	16	35/9	44
Colydiidae	6/8	9	54/50	104
Corylophidae	3/6	6	256/102	358
Cryptophagidae	1/4	5	1/28	29
Cupedidae	0/1	1	0/9	9
Curculionidae*	19/17	29	58/160	218
Scolytinae	20/21	26	96/344	440
Platypodinae	1/1	1	1/1	2
Dermestidae	7/2	7	375/31	406
Dytiscidae	1/1	2	1/1	2
Elateridae	22/23	28	328/287	615
Endomychidae	3/9	10	10/18	28
Erotylidae	4/4	6	4/14	18
Eucinetidae	0/1	1	0/10	10
Eucnemidae	4/2	4	31/105	136
Geotrupidae	0/1	1	0/1	1
Heteroceridae	0/1	1	0/1	1
Histeridae	3/7	7	25/109	134
Hydrophilidae	0/2	2	0/13	13
Laemophloeidae	4/4	6	7/16	23
Lampyridae	5/5	6	40/17	57
Latridiidae	4/3	5	1686/1033	2719
Leiodidae	2/6	6	9/185	194
Lycidae	3/2	5	6/3	9
Melandryidae	5/6	6	33/44	77
Meloidae	1/0	1	1/0	1
Melyridae	5/4	5	366/271	637

TABLE 1.—Continued

Family	No. Species Canopy/Ground	Total No. Species	No. Individuals Canopy/Ground	Total No. Individuals
Monommatidae	1/1	1	21/17	38
Monotomidae	1/1	1	371/32	403
Mordellidae	13/10	13	710/965	1675
Mycetophagidae	3/4	5	389/96	485
Nitidulidae	10/11	13	156/249	405
Oedemeridae	3/2	3	8/2	10
Passalidae	0/1	1	0/1	1
Passandridae	1/0	1	1/0	1
Phalacridae	2/2	2	176/41	217
Phengodidae	0/1	1	0/175	175
Ptiliidae	1/1	1	3/4	7
Ptilodactylidae	1/1	1	24/100	124
Pyrochroidae	1/1	1	1/2	3
Salpingidae	1/0	1	1/0	1
Scarabaeidae	13/16	21	151/129	280
Scirtidae	3/3	5	8/28	36
Scraptiidae	1/1	1	2/1	3
Scydmaenidae	2/2	3	39/31	70
Silphidae	2/3	4	3/468	471
Silvanidae	3/4	5	28/234	262
Sphindidae	0/2	2	0/114	114
Staphylinidae**	29/53	56	236/852	1088
Pselaphinae	4/15	15	8/109	117
Scaphidiinae	1/3	3	5/60	65
Synchroidae	0/1	1	0/19	19
Tenebrionidae	14/7	15	51/19	70
Throscidae	2/2	3	9/95	104
Trogidae	0/1	1	0/3	3
Trogossitidae	4/0	4	4/0	4
Zopheridae	0/2	2	0/27	27
undetermined	1/0	1	1/0	1
Total	383/398	558	7613/7399	15012

* Not including Platypodinae and Scolytinae

** Not including Pselaphinae and Scaphidiinae

TABLE 2.—The mean ± SE abundance, species richness, Shannon's diversity, and evenness of beetles captured in flight-intercept traps suspended in the canopy (≥15 m) and near the ground (0.5 m) in a temperate deciduous forest, Oglethorpe County, Georgia USA. Paired *t*-tests were used to compare canopy and ground traps

	Mean ± SE (n = 12)		
	Canopy	Ground	P value
Abundance	634.42 ± 61.42	616.58 ± 94.95	0.85
Species Richness	106.75 ± 4.87	118.58 ± 8.12	0.19
Diversity	3.40 ± 0.05	3.73 ± 0.07	<0.01
Evenness	0.73 ± 0.01	0.79 ± 0.02	0.01

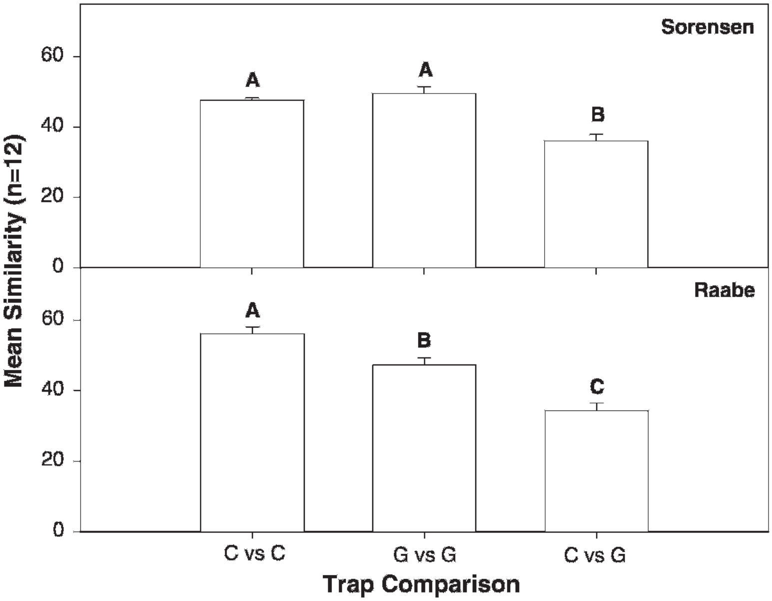

FIG. 2.—The mean ± SE Sorensen's quotient of similarity (top) and Raabe's percentage of similarity (bottom) of beetles captured by flight-intercept traps suspended in the canopy, C (≥15 m), or near the ground, G (0.5 m) of a temperate deciduous forest. Similarity was calculated for twelve randomly selected pairs of canopy traps (C vs C), twelve randomly selected pairs of ground traps (G vs G) and for twelve pairs of canopy and ground traps (C vs G). Bars with different letters above them are significantly different (Ryan-Einot-Gabriel-Welsch Multiple Range Test, $P < 0.05$)

results support the widely held assumption that the insect communities in the canopies of temperate deciduous forests are less distinctive and less stratified than are their tropical counterparts (Basset *et al.*, 2003a).

Beta diversity patterns.—One question central to biodiversity estimates is how β diversity patterns differ among forest strata (Basset *et al.*, 2003a). While certain features near the ground (bodies of water, soil type, herbaceous vegetation, rocks, logs, etc.) may affect the distribution and β diversity patterns of insects living on or near the forest floor, they may have little or no impact on those living high in the canopy. Similarly, in the canopy, the species of tree greatly influences the distribution patterns of herbivorous insects and other species, but may have little effect on those living on the ground (Schaefer, 1991). We found Sorensen's quotient of similarity to exhibit a significantly decreasing trend with horizontal between-trap distance for traps in the canopy ($P = 0.006$), but not for those near the ground ($P = 0.35$) (Fig. 4). These results suggest a more uniform beetle community, in terms of species composition, near the ground. Much more research is needed to clarify these patterns, however. Our traps were all less than 1 km (Figs. 1, 4) apart. How β diversity patterns and other measures of community change vary over larger distances remains to be investigated. We feel that plotting similarity against horizontal between-trap distance may be an easy and effective way to evaluate these patterns and to compare them among different forest types.

Tree specificity.—Because many insect species are thought to be closely associated with one or several tree species (Erwin, 1982), forests composed of many different tree species

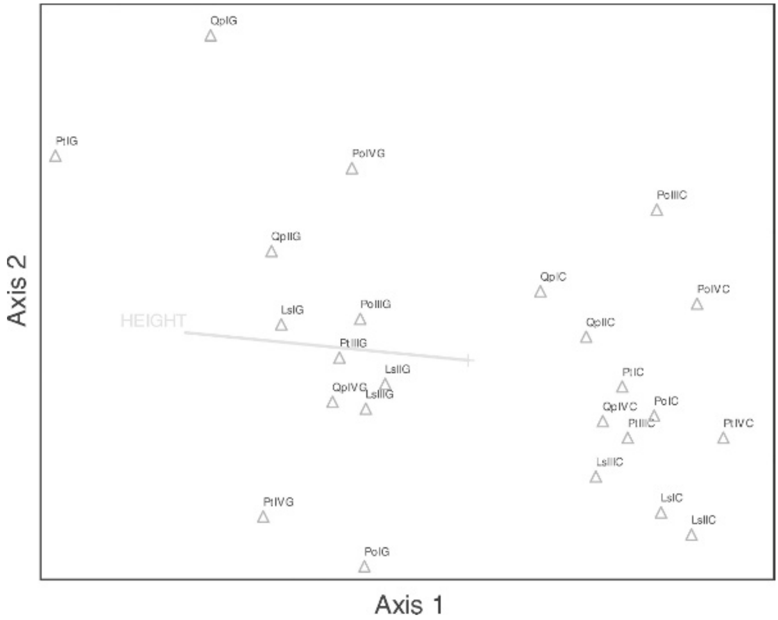

FIG. 3.—Nonmetric multidimensional scaling plot of the 24 locations used to sample the beetle community in a temperate deciduous forest. Labels above the location symbols refer to tree species (Qp = *Quercus phellos*, Pt = *Pinus taeda*, Po = *Platanus occidentalis* and Ls = *Liquidambar styraciflua*), tree number (roman numerals) and trap height (G = ground, C = canopy)

probably support more beetle species in the canopy than do less diverse forests. This might explain why Nielsen (1987) caught so many more beetles near the ground than in the canopy of a pure beech stand in Denmark, whereas no substantial differences were reported from a similar study conducted in a mixed hardwood forest in North America (Preisser *et al.*, 1998). We found few differences in abundance or species richness of beetles captured in the canopies of different tree species (Table 3). The NMS plot also suggests uniformity in beetle fauna among the different tree species because the two axes were only weakly correlated with tree species ($r^2 = 0.04$ and 0.03) (Fig. 3). Interestingly, traps suspended in the crowns of sycamore (*Platanus occidentalis*) had the fewest individuals and species and had significantly fewer individuals than traps in sweetgum (*Liquidambar styraciflua*) (Table 3). Some chrysopid (lacewing) larvae have been shown to build defensive trash packets from the trichomes of *Platanus*, and these structures may serve to protect the plants as well (Eisner *et al.*, 2002). Perhaps this explains why we captured fewer beetles near *P. occidentalis* than near other tree species. Because flight intercept traps are not designed for localized sampling, other collecting techniques, such as fogging with insecticides, are probably more appropriate for comparing canopy insect communities among tree species. For example, Gering and Crist (2000) fogged a forest canopy in southwestern Ohio with insecticides and found considerable differences in the species richness and abundance of beetles in the crowns of different tree species. More research is needed to clarify relationships between species richness of insects in canopies and the number of tree species present.

Seasonality.—The abundance and species richness of beetles decreased steadily throughout the season in the canopy and near the ground (Fig 5). These results agree

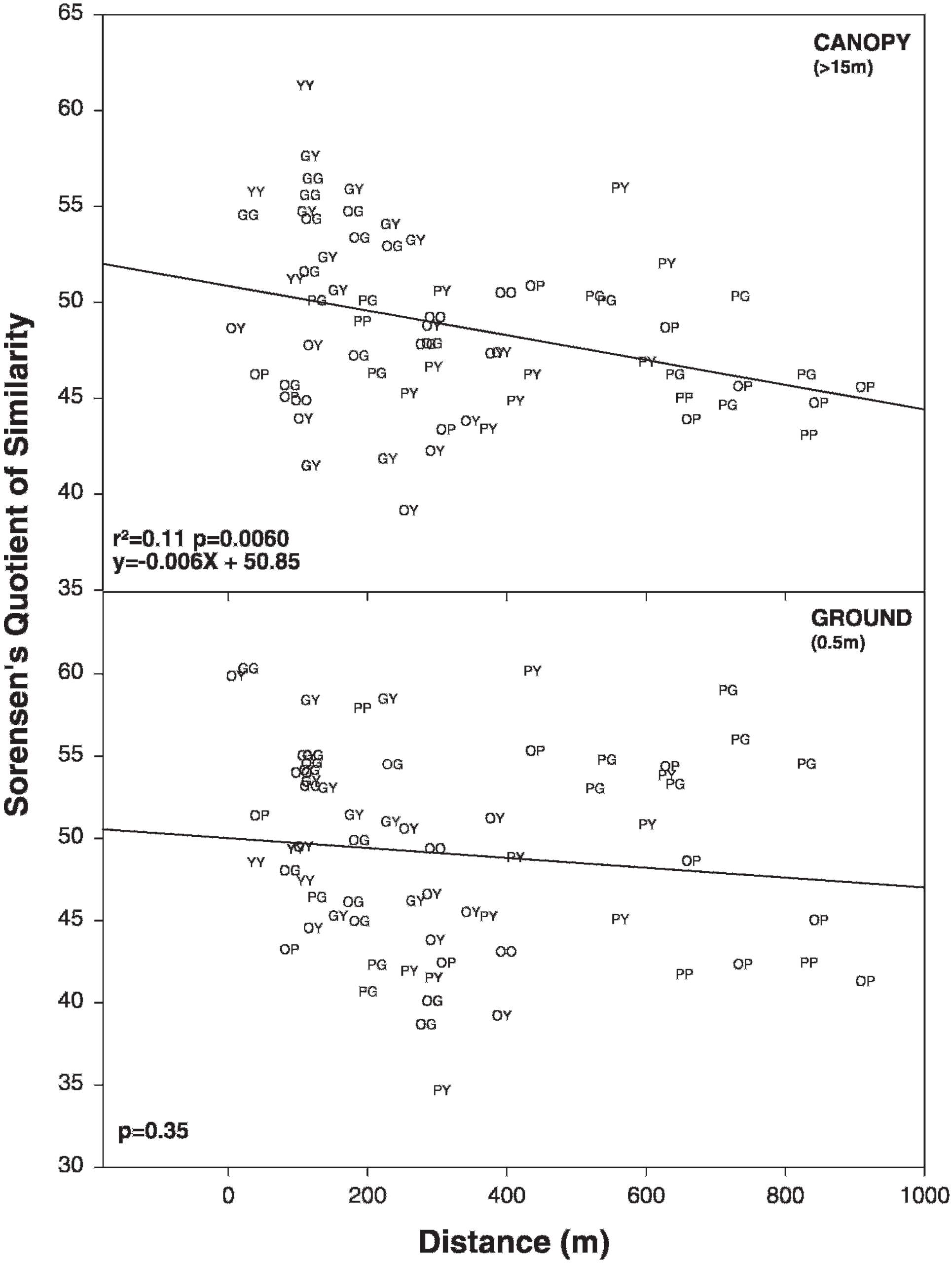

FIG. 4.—Sorensen's quotient of similarity vs. distance between traps for all possible pair-combinations of flight-intercept traps suspended at two different heights (≥15 m and 0.5 m) above the ground in a temperate deciduous forest. Letters indicate tree species (O = *Quercus phellos*, P = *Pinus taeda*, G = *Liquidambar styraciflua*, Y = *Platanus occidentalis*)

TABLE 3.—Mean ± SE abundance, species richness, Shannon's diversity, and evenness of the beetle fauna sampled by flight intercept traps suspended in the canopy (≥15 m) and near the ground (0.5 m) of four different tree species in a temperate deciduous forest, Oglethorpe County, Georgia USA. Means in rows with different letters next to them are significantly different (Ryan-Einot-Gabriel-Welsch Multiple Range Test, P < 0.05)

		Quercus phellos	*Pinus taeda*	*Liquidambar styraciflua*	*Platanus occidentalis*
Abundance	Canopy traps (n = 3)	585.00 ± 72.67 ab	647.67 ± 54.78 ab	874.33 ± 115.87 a	430.67 ± 102.14 b
	Ground traps (n = 3)	412.33 ± 128.65 a	708.67 ± 311.10 a	678.00 ± 51.29 a	667.33 ± 241.43 a
Species Richness	Canopy traps (n = 3)	110.33 ± 14.89 a	111.67 ± 4.70 a	113.00 ± 9.71 a	92.00 ± 6.11 a
	Ground traps (n = 3)	95.00 ± 11.53 a	123.67 ± 26.83 a	133.67 ± 3.84 a	122.00 ± 13.08 a
Diversity	Canopy traps (n = 3)	3.47 ± 0.14 a	3.45 ± 0.07 a	3.32 ± 0.12 a	3.37 ± 0.03 a
	Ground traps (n = 3)	3.68 ± 0.17 a	3.78 ± 0.21 a	3.86 ± 0.12 a	3.60 ± 0.11 a
Evenness	Canopy traps (n = 3)	0.74 ± 0.01 a	0.73 ± 0.01 a	0.70 ± 0.01 a	0.75 ± 0.01 a
	Ground traps (n = 3)	0.81 ± 0.04 a	0.80 ± 0.06 a	0.79 ± 0.03 a	0.75 ± 0.03 a

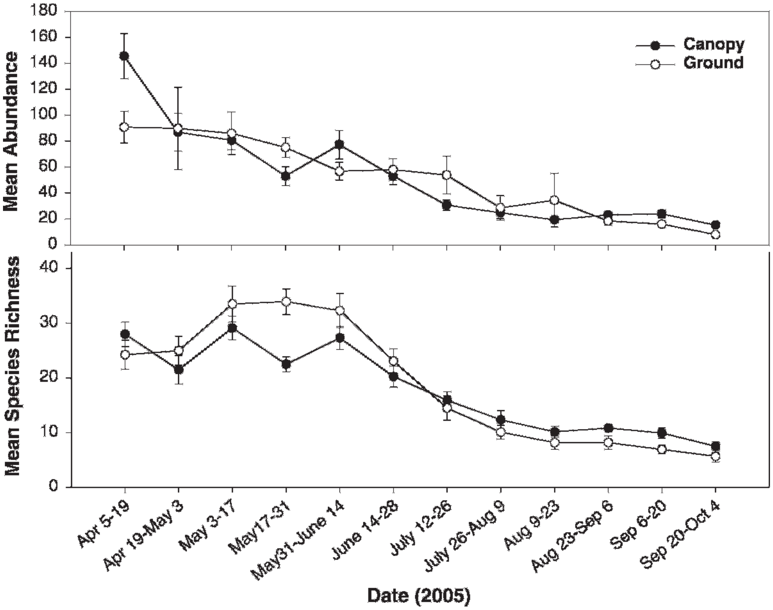

FIG. 5.—The mean ± SE abundance and species richness of beetles captured in flight-intercept traps suspended in the canopy (≥15 m) and near the ground (0.5 m) in a temperate deciduous forest (n = 12)

closely with those of Gering and Crist (2000) who attribute the high springtime diversity to the presence of both univoltine and bivoltine species. Many phytophagous insects, for example, are thought to be univoltine and feed mostly or entirely on the more palatable young plant growth in the early spring (Schaefer, 1991). As these resources decline in quality throughout the year, so does the number of herbivorous insect species. We captured very high numbers of beetles in the canopy before or during bud-break, suggesting that movement into the canopy begins very early in the year.

Variability among and within families.—There was considerable variation in the vertical distribution patterns among and within families. Of the 41 families or subfamilies represented by more than 40 individuals, 12 were more abundant in the canopy and 14 were more abundant near the ground (Table 4). Similarly, of the 16 families or subfamilies represented by more than 10 species, five were more species rich in the canopy and four were more species rich near the ground (Table 5). Three families (Cerambycidae, Cleridae and Coccinellidae) were both more abundant and species rich in the canopy than near the ground, and four other groups (Carabidae, Pselaphinae (Staphylinidae), Scolytinae (Curculionidae) and other Staphylinidae) were both more abundant and species rich near the ground than in the canopy (Tables 4, 5).

A number of abiotic and biotic factors influence the vertical distribution patterns of insects (Basset *et al.*, 2003a), but resource availability is perhaps the most important. For example, the abundance of plant material in the canopy likely explains why we captured Chrysomelidae in greater numbers there than near the ground (Table 4). Likewise, the concentration of decomposing material near the forest floor may explain why some saproxylic and scavenging groups (*e.g.*, Scolytinae, Silvanidae, Eucnemidae, Staphylinidae, Leiodidae, Silphidae, etc.) were captured in higher numbers near the ground than in the canopy (Tables 4, 5). One important, but often under-appreciated resource to beetles and many other insects in the forest canopy is honeydew, the sugary waste product of aphids and other sap-sucking insects (Elton, 1966). While some insects, notably the ants as well as certain wasps and beetles (Douglas, 2006), collect honeydew directly from insects that produce it, representatives of about 50 different insect families have been observed collecting honeydew residue from foliage as well (Elton, 1966, and references therein). Many flower-visiting species may supplement their diet with honeydew at times when floral nectar is scarce (Elton, 1966) and this may explain why we caught so many more ground-dwelling bees (Halictidae) in canopy traps than near the ground in mid-summer (M. Ulyshen, pers. obs.). Honeydew may be a very important resource to these bees, and to beetles with similar tastes, and may help explain the abundance of these groups in the forest canopy at certain times of the year.

In addition, sooty molds commonly grow on leaves covered with honeydew and these molds likely attract a number of insects including certain mycophagous beetle species (Elton, 1966). We found four predominantly mycophagous families (Corylophidae, Latridiidae, Monotomidae and Mycetophagidae) to be significantly more abundant in the canopy than near the ground (Table 4). Latridiidae was in fact the most abundant beetle family in the canopy (Table 1). Sooty molds and other fungal resources may be an important food source for these and other beetles in forest canopies. Wagner (2000) also captured large numbers of Latridiidae, Corylophidae and other mycophagous groups in the canopy of a tropical forest in Uganda, suggesting that molds and other fungi may be an important resource in the canopies of many forests.

The attractiveness of sooty molds to fungus-feeding beetles is thought to have been one of the first steps in the evolutionary process leading to predation on Hemiptera (Leschen,

TABLE 4.—The mean ± SE number of beetles (families represented by >40 individuals) captured in flight-intercept traps suspended in the canopy (≥15 m) and near the ground (0.5 m) in a temperate deciduous forest, Oglethorpe County, Georgia USA. Paired *t*-tests were used to compare canopy and ground traps for each family

		Mean ± SE (n = 12)		
	Family	Canopy	Ground	P value
Canopy	Coccinellidae	2.92 ± 0.51	0.75 ± 0.33	0.01
	Cerambycidae	39.25 ± 4.32	6.42 ± 1.47	<0.01
	Chrysomelidae	61.42 ± 21.00	13.25 ± 2.28	0.03
	Cleridae	7.00 ± 1.52	0.83 ± 0.34	<0.01
	Corylophidae	21.33 ± 5.62	8.5 ± 1.30	0.04
	Dermestidae	31.25 ± 6.64	2.58 ± 1.66	<0.01
	Lampyridae	3.33 ± 0.78	1.42 ± 0.58	0.04
	Latridiidae	140.5 ± 10.12	86.08 ± 13.33	<0.01
	Monotomidae	30.92 ± 3.77	2.67 ± 0.58	<0.01
	Mycetophagidae	32.42 ± 6.50	8.00 ± 2.03	<0.01
	Phalacridae	14.67 ± 1.39	3.42 ± 0.82	<0.01
	Tenebrionidae	4.25 ± 1.00	1.58 ± 0.45	0.02
Ground	Byturidae	0.42 ± 0.15	5.92 ± 1.87	0.01
	Carabidae	3.75 ± 0.60	10.75 ± 1.30	<0.01
	Eucnemidae	2.58 ± 0.47	8.75 ± 2.16	0.02
	Histeridae	2.08 ± 0.54	9.08 ± 2.27	0.01
	Leiodidae	0.75 ± 0.35	15.42 ± 4.13	<0.01
	Phengodidae	0 ± 0	14.58 ± 2.87	<0.01
	Pselaphinae (Staphylinidae)	0.67 ± 0.28	9.08 ± 1.92	<0.01
	Ptilodactylidae	2.00 ± 0.39	8.33 ± 1.63	<0.01
	Scaphidiinae (Staphylinidae)	0.42 ± 0.15	5.00 ± 0.73	<0.01
	Scolytinae (Curculionidae)	8.00 ± 1.30	28.67 ± 4.96	<0.01
	Silvanidae	2.33 ± 0.48	19.50 ± 3.05	<0.01
	Sphindidae	0 ± 0	9.5 ± 1.76	<0.01
	Staphylinidae*	19.67 ± 3.51	71.00 ± 10.68	<0.01
	Throscidae	0.75 ± 0.28	7.92 ± 2.46	0.01
No difference	Aderidae	3.08 ± 0.72	1.83 ± 0.77	0.28
	Anobiidae	6.83 ± 1.70	3.67 ± 0.99	0.19
	Attelabidae	9.08 ± 5.86	0.42 ± 0.19	0.16
	Buprestidae	8.00 ± 2.85	4.25 ± 1.87	0.18
	Cantharidae	4.75 ± 1.34	3.75 ± 1.31	0.59
	Colydiidae	4.50 ± 1.20	4.17 ± 1.07	0.83
	Curculionidae**	4.83 ± 0.82	13.33 ± 4.09	0.07
	Elateridae	27.33 ± 4.60	23.92 ± 4.53	0.64
	Melandryidae	2.75 ± 0.91	3.67 ± 0.79	0.47
	Melyridae	30.50 ± 7.27	22.58 ± 20.69	0.68
	Mordellidae	59.17 ± 11.07	80.42 ± 14.04	0.24
	Nitidulidae	13.00 ± 3.50	20.75 ± 3.72	0.15
	Scarabaeidae	12.58 ± 1.32	10.75 ± 4.55	0.72
	Scydmaenidae	3.25 ± 0.62	2.58 ± 0.56	0.46
	Silphidae	0.25 ± 0.18	39.00 ± 28.96	0.21

* Not including Pselaphinae and Scaphidiinae

** Not including Platypodinae and Scolytinae

TABLE 5.—The mean ± SE number of beetles species for the most species rich families (>10 species) captured in flight-intercept traps suspended in the canopy (≥15 m) and near the ground (0.5 m) in a temperate deciduous forest, Oglethorpe County, Georgia USA. Paired *t*-tests were used to compare canopy and ground traps for each family

		Mean ± SE (n = 12)		
	Family	Canopy	Ground	P value
Canopy	Cantharidae	3.17 ± 0.52	1.25 ± 0.33	<0.01
	Cerambycidae	10.50 ± 0.57	4.08 ± 0.73	<0.01
	Cleridae	3.50 ± 0.44	0.67 ± 0.22	<0.01
	Coccinellidae	2.17 ± 0.34	0.58 ± 0.23	<0.01
	Mordellidae	6.42 ± 0.45	4.42 ± 0.53	<0.01
Ground	Carabidae	3.00 ± 0.48	5.67 ± 0.54	<0.01
	Pselaphinae (Staphylinidae)	0.50 ± 0.19	4.83 ± 0.63	<0.01
	Scolytinae (Curculionidae)	4.50 ± 0.56	8.0 ± 0.56	<0.01
	Staphylinidae*	6.00 ± 0.63	17.92 ± 0.90	<0.01
No difference	Anobiidae	2.58 ± 0.45	2.00 ± 0.39	0.40
	Chrysomelidae	5.00 ± 0.44	3.75 ± 0.46	0.07
	Curculionidae**	3.42 ± 0.53	4.58 ± 0.70	0.13
	Elateridae	6.50 ± 0.61	6.42 ± 0.70	0.93
	Nitidulidae	4.50 ± 0.51	4.67 ± 0.40	0.77
	Scarabaeidae	4.42 ± 0.34	4.00 ± 0.60	0.55
	Tenebrionidae	2.33 ± 0.38	1.25 ± 0.28	0.05

* Not including Pselaphinae and Scaphidiinae

** Not including Platypodinae and Scolytinae

2000, and references therein). This predatory behavior is most widespread among the Coccinellidae, a diverse family of beetles that feed predominantly on aphids, scale insects and whiteflies (Leschen, 2000). The abundance of aphids and other sap-sucking Hemiptera in the forest canopy (Elton, 1966; Moran and Southwood, 1982), likely explains why we captured so many more coccinellids there than near the ground (Tables 4, 5).

Scarabaeidae fall into two groups based on adult feeding behavior. These are the lamellicorn scavengers which feed on dung, carrion or fungus (*i.e.*, Aphodiinae, Scarabaeinae, etc.) and the lamellicorn leaf chafers which are phytophagous (*i.e.*, Melolonthinae, Rutelinae, Cetoniinae, etc.) (Ritcher, 1957). Although we found no overall differences in the abundance or species richness of Scarabaeidae between the two layers (Tables 4, 5), substantial differences occurred in the vertical distribution patterns of these main feeding groups. The lamellicorn leaf chafers were captured in much higher numbers in the canopy than near the ground (11.33 ± 1.21 and 3.00 ± 0.49 individuals/trap, respectively; P = 0.0001) due in large part to the subfamily Cetoniinae which was almost exclusively captured in canopy traps (6.75 ± 1.19 and 0.08 ± 0.08 individuals/trap in the canopy and near the ground, respectively; P = 0.0002). The most numerous species, *Euphoria fulgida* (Fabricius) was captured exclusively in the canopy (59 specimens). As adults, Cetoniinae are mainly liquid feeders, feeding above ground on nectar or sap (Ritcher, 1957). Perhaps sap flows are more abundant in the canopy than near the ground. In contrast to the lamellicorn leaf chafers, the lamellicorn scavengers were captured exclusively near the ground (6.42 ± 4.46, P = 0.18). This group was composed mainly (79% of specimens) of *Deltochilum gibbosum* (Fabricius), a carrion feeding species that came in large numbers to several traps that had become slightly putrid. Clearly the two groups of

TABLE 6.—The ''Colorful Foliage Ground Beetles'' (Carabidae, Lebiini) captured in flight-intercept traps suspended in the canopy (≥15 m) and near the ground (0.5 m) in a temperate deciduous forest, Oglethorpe County, Georgia USA

Species	Canopy	Ground	Total
Calleida viridipennis (Say)	2	0	2
Coptodera aerata Dejean	0	2	2
Cymindis limbatus Dejean	8	4	12
Lebia ornata Say	1	8	9
Lebia tricolor Say	1	3	4
Lebia viridis Say	3	1	4
Phloeoxina signata (Dejean)	0	7	7
Plochionus timidus Haldeman	2	0	2
Total (Individuals/Species)	17/6	25/6	42/8

scarabs occupy different forest strata as adults whereas as larvae, both groups generally feed on or under the ground (Ritcher, 1957).

Because carrion beetles (Silphidae) rely on carcasses for food and breeding material, one might expect them to be concentrated near the ground where carrion is most readily available. This was the case (Table 1), but most were captured in only a few traps that had become putrid. Consequently, differences were not significant based on paired *t*-tests (Table 4). The same difficulty applied to the leaf-rolling weevils (Attelabidae) (Table 4) and *Deltochilum gibbosum* mentioned above. Interestingly, although silphids are generally much more abundant near the ground, one species, *Nicrophorus pustulatus* Herschel, appears to be more common in the canopy (Ulyshen *et al.*, 2007).

Ground beetles (Carabidae) were much more abundant and species rich near the ground than in the canopy (Tables 4, 5), but we caught similar numbers of the tribe Lebiini (Table 6) at the two heights (2.08 ± 0.72 and 1.42 ± 0.36 individuals/trap near the ground and in the canopy, respectively; P = 0.42). Unlike many ''ground beetles,'' Lebiini are primarily found on vegetation, and are common in canopies of both temperate and tropical forests. For example, the three most common carabid species collected by canopy fogging in the northeastern United States belonged to this tribe (Krinsky and Godwin, 1990). They are particularly numerous in the canopies of many tropical forests (Lucky *et al.*, 2002), where up to two-thirds of carabid species (belonging mostly to Lebiini and related tribes) live in and are often morphologically adapted to this habitat (Ober, 2003). Many of the Lebiini species we captured are known to feed on caterpillars or on immature leaf beetles (Chrysomelidae) as adults (*i.e.*, *Calleida viridipennis* (Say), *Cymindis limbatus* Dejean, *Lebia viridis* Say and *Plochionus timidis* Haldeman) (Larochelle and Larivière, 2003). Furthermore larvae of certain species, such as *Lebia viridis* Say, are ectoparasites of leaf beetle pupae (Larochelle and Larivière, 2003).

Bark beetles (Curculionidae: Scolytinae) were more abundant and species rich near the ground than in the canopy (Tables 4, 5), but members of the genus *Pityophthorus* were significantly more abundant in the canopy (1.92 ± 0.63 and 0.50 ± 0.19 individuals/trap in the canopy and near the ground, respectively, P = 0.04). Members of this genus attack small branches and twigs (Wood, 1982) which may be found more readily in the canopy. In addition to small twigs, forest canopies often contain large amounts of dead wood in the form of standing snags, dead branches and rotting heartwood (Fonte and Schowalter, 2004). Because many fungal species are sensitive to moisture availability, and many saproxylic arthropods are dependent on certain fungi (Jonsell *et al.*, 2005) and have specific moisture requirements themselves, differences in water content between snags and dead limbs in the canopy and logs lying on the ground are likely to result in compositionally distinct fungal and insect communities (Jonsell and Weslien, 2003; Lindhe *et al.*, 2004).

As adults, long-horned beetles (Cerambycidae) feed variously on flowers, the thin bark of twigs and branches, foliage, pine needles and cones, sap, fruit, roots and fungus (Linsley, 1961). A number of these resources are found in the canopy which might explain why we caught more individuals and species in the canopy than near the ground (Tables 4, 5). Of the 43 species we collected, 31 were more common in the canopy, and 21 were caught only in canopy traps (Table 7). These results differ from past work on this family in temperate deciduous forests. Leksono *et al.* (2006) found little variation in cerambycid abundance among three (0.5, 10, and 20 m) canopy layers in Japan. In Canada, Vance *et al.* (2003) captured similar numbers of species in the canopy and near the ground and caught more individuals near the ground. Although these studies did not find cerambycids to be significantly more numerous in the canopy than near the ground, they support the notion that forest canopies contain very species rich assemblages of long-horned beetles. Leksono *et al.* (2006), for example, captured 11 species in traps placed ten meters or more above the ground in Japan. Similarly, Vance *et al.* (2003) captured 18 species in traps suspended an average of 20.5 m above the ground in a Canadian maple forest and Krinsky and Godwin (1996) collected 52 species of cerambycids by canopy fogging in the northeastern United States.

Although we captured most cerambycid species more commonly in the canopy, 11 species were more common near the ground, and seven were captured there exclusively (Table 7). One species, *Orthosoma brunneum* (Prioninae), was frequently captured near the ground, but never in the canopy (1.08 ± 0.40 and 0.0 ± 0.0, respectively, $P = 0.02$). This species breeds in logs close to the ground (Linsley, 1962). Prionines often do not feed as adults and members of this subfamily rarely disperse long distances (Hanks, 1999). Therefore, *O. brunneum* may rarely, if ever, venture into the canopy.

Male glowworms belonging to the family Phengodidae were captured exclusively and quite commonly near the ground (Table 4). This is not surprising given the fact that both the larviform females and the larvae are confined to the forest floor where they prey upon millipedes (as reviewed in Arnett and Thomas, 2001).

The majority of the dermestid beetles (Dermestidae) we collected were *Cryptorhopalum ruficorne*, which was almost exclusively (271 vs. 9 indivuduals) captured in the canopy. Larvae of this species were collected from egg masses of gypsy moths found on tree boles in Pennsylvania (Mason and Ticehurst, 1984). Perhaps the species targets other Lepidopteran egg masses in the canopy as well. Mason and Ticehurst (1984) report collecting an adult from a dogwood (Cornus florida L.) bloom, so they may also fly high above the ground in search of flowers. One of the most unusual species of dermestids collected in this study was an unidentified species of *Thaumaglossa*, whose members are found only in the oothecae of mantids (Beal, 2003).

Endomychidae were captured more commonly near the ground than in the canopy (Table 1). However, *Micropsephodes lundgreni* Leschen and Carlton, was only captured in the canopy. This species was described in 2000 from specimens collected in flight intercept traps and under the bark of both live and dead trees, but little else is known about its biology (Leschen and Carlton, 2000). Based on this study, and from unpublished data from ongoing work in South Carolina (M. Ulyshen, pers. obs.), the species appears to be much more common in the canopy than near the ground.

The high degree of variability we observed among and within beetle families underscores the importance of fine-scale taxonomic analyses when trying to characterize spatial

Table 7.—List of longhorned beetles (Cerambycidae) captured in flight-intercept traps suspended in the canopy ($\geq$15 m) and near the ground (0.5 m) in a temperate deciduous forest, Oglethorpe County, Georgia USA

Species	Canopy	Ground	Total
Aegomorphus modestus (Gyllenhal)	2	3	5
Analeptura lineola (Say)	5	5	10
Anelaphus parallelus (Newman)	10	1	11
Anelaphus pumilus (Newman)	2	0	2
Astylopsis macula (Say)	0	2	2
Brachyleptura circumdata (Olivier)	2	0	2
Brachyleptura vegans (Olivier)	1	0	1
Callimoxys sanguinicollis sanguinicollis (Olivier)	1	0	1
Clytus marginicollis Castelneau & Gory	1	2	3
Clytus ruricola (Olivier)	22	7	29
Curius dentatus Newman	0	3	3
Cyrtinus pygmaeus (Haldeman)	0	1	1
Cyrtophorus verrucosus (Olivier)	20	0	20
Ecyrus dasycerus dasycerus (Say)	2	0	2
Enaphalodes rufulus (Haldeman)	1	0	1
Euderces picipes (Fabricius)	12	0	12
Euderces reichei reichei LeConte	1	2	3
Gaurotes cyanipennis (Say)	0	1	1
Grammoptera haematites (Newman)	165	6	171
Leptostylus asperatus (Haldeman)	2	3	5
Lepturges confluens (Haldeman)	2	0	2
Lycochoriolaus lateralis (Olivier)	2	0	2
Metacmaeops vittata (Swederus)	3	0	3
Molorchus bimaculatus bimaculatus Say	78	3	81
Monochamus titillator (Fabricius)	2	0	2
Neoclytus acuminatus acuminatus (Fabricius)	0	2	2
Orthosoma brunneum (Forster)	0	13	13
Rhagium inquisitor (Linnaeus)	1	0	1
Saperda lateralis Fabricius	0	1	1
Stenocorus cinnamopterus (Randall)	1	0	1
Stenocorus cylindricollis (Say)	2	0	2
Stenosphenus notatus (Olivier)	1	0	1
Strangalia acuminata (Olivier)	1	0	1
Strangalia famelica famelica Newman	3	0	3
Strangalia luteicornis (Fabricius)	44	8	52
Styloleptus biustus (LeConte)	4	3	7
Tilloclytus geminatus (Haldeman)	12	1	13
Trachysida mutabilis (Newman)	8	0	8
Trigonarthris minnesotana (Casey)	1	0	1
Typocerus acuticauda acuticauda Casey	34	4	38
Typocerus zebra (Olivier)	17	5	22
Urographus fasciatus (DeGeer)	4	0	4
Xylotrechus colonus (Fabricius)	2	1	3
Total (Individuals/Species)	471/36	77/22	548/43

distribution patterns of insects. Studies that limit their analyses to higher taxonomic groups (*i.e.*, orders) are of limited value. Catching an insect at a given height above the forest floor does not necessarily mean it feeds or reproduces at that level. Many insects may instead be captured as they disperse or migrate at preferred or random heights above the ground. Therefore, interpreting our results and those of similar studies is difficult, but only through such efforts can we hope to gain a better understanding of how insects are distributed in forests.

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