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Arboreal Invertebrates

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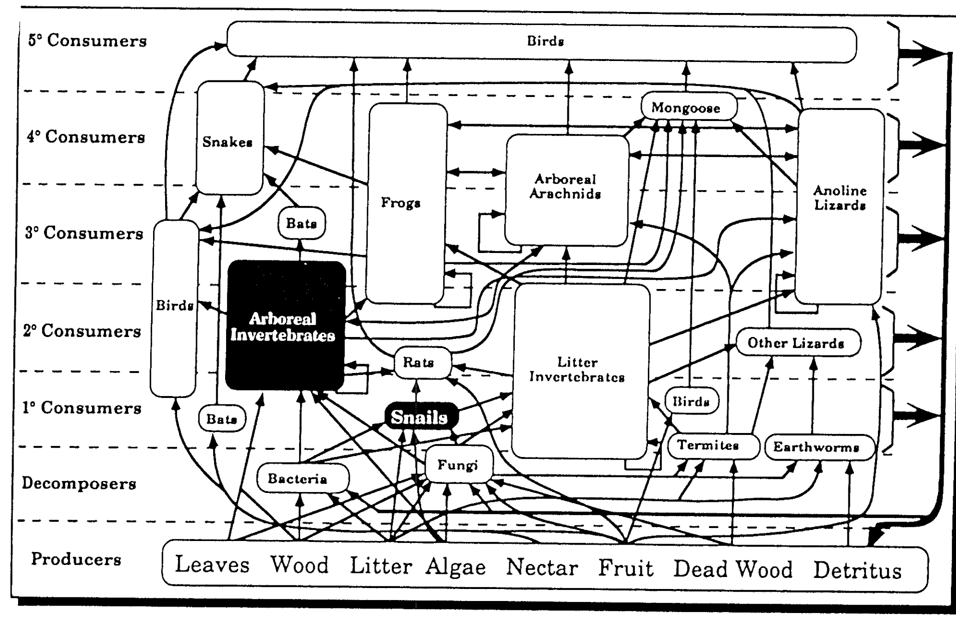

INVERTEBRATES make critical contributions to the structure and function of most ecosystems. Their dominance among consumers is derived from their high diversities, densities, and reproductive rates, as well as from their occupation of most consumer trophic categories within communities. Indeed, invertebrate size spans several orders of magnitude, with feeding specializations that include herbivore (folivore, granivore, frugivore, nectarivore), carnivore (predators, parasites, and parasitoids), and detritivore (including macrosaprophagic, necrophagic, and scatophagic) components. The contribution of invertebrates to tropical food web structure and function may be even more significant than that made by invertebrates in more temperate areas because species diversity, trophic diversity, and population densities of insects are frequently much greater in the tropics than elsewhere. However, these very attributes, along with the paucity of trained taxonomists in Latin America, obviate the delineation of most tropical food webs and result in poor understanding of how increased diversity affects food web structure and function (see Wolda 1983b for review).

Tropical islands such as Puerto Rico may enjoy high species diversity compared to temperate sites but are considerably simpler than their tropical mainland counterparts. The long tradition of ecosystem research at El Verde has resulted in a fortunate situation in which the taxonomic understanding of the invertebrate fauna is more advanced than that in almost any other site on the mainland of Latin America. As a result, delineation of the contribution of invertebrates to food web structure and function is a reasonable goal at El Verde, where many tropical attributes are reflected in the invertebrate fauna, though in a more tractable fashion.

Despite the obvious importance of invertebrates to unraveling the complexity of the food web at El Verde, comprehensive understanding of the relationships of most species with their environment is elusive. The ecology of even the more abundant species is poorly known compared to that of other consumer groups in the forest. Although Drewry (1970b) recorded over 1,200 species of insects from El Verde, few of them are seen by casual observers. Many species are rare or infrequent, and most are known from few specimens. The true number of species of invertebrates at El Verde must be considerably higher than the number reported in the literature (Owen 1983).

The most readily seen invertebrates at El Verde are the large camaenid snails (*Caracolus caracolla*), walking sticks (*Lamponius portoricensis*), cockroaches, arboreal crickets, various fulgoroid plant hoppers, and the pierid butterfly, *Dismorphia spio* (fig. 6.1).

The complexity of tropical food webs may be underestimated because species remain undetected or unnamed, or two or more taxa masquerade under

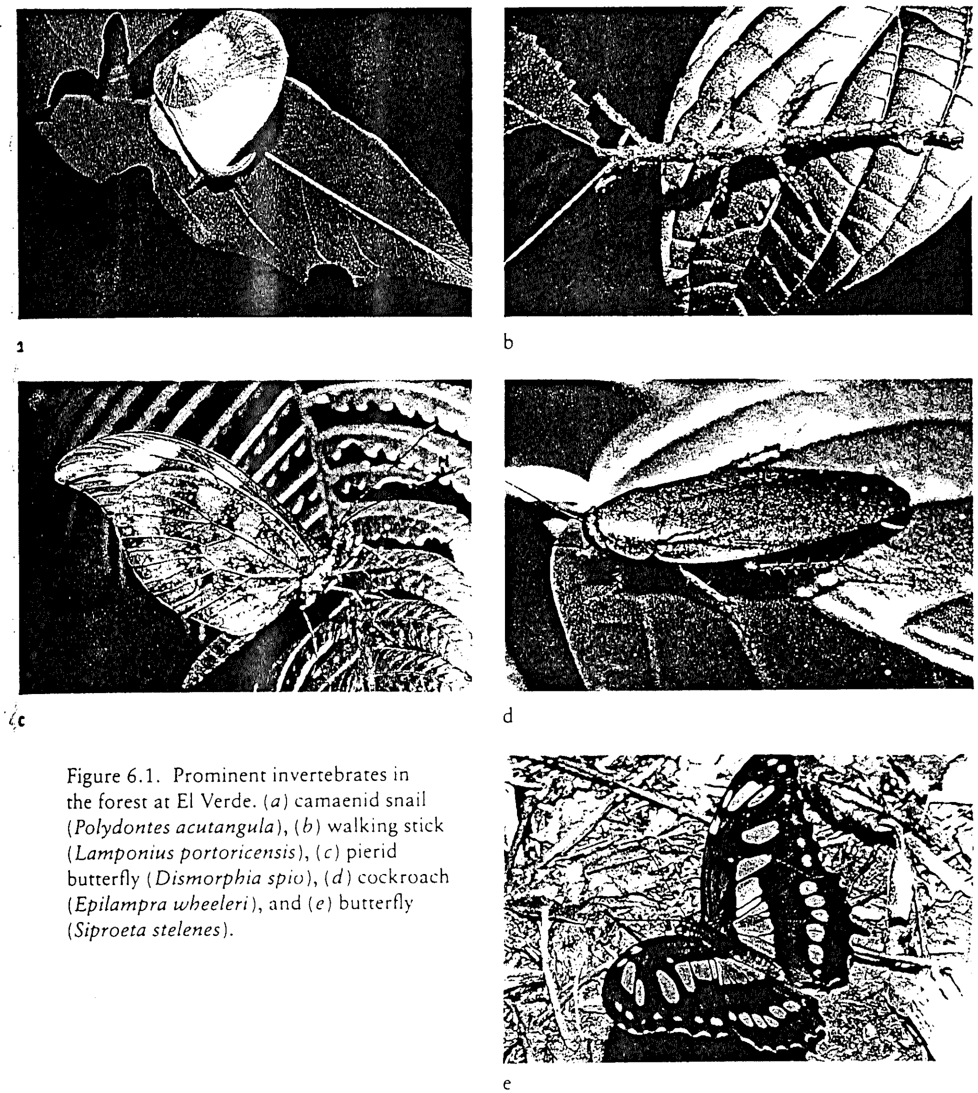

Figure 6.1. Prominent invertebrates in the forest at El Verde. (*a*) camaenid snail (*Polydontes acutangula*), (*b*) walking stick (*Lamponius portoricensis*), (*c*) pierid butterfly (*Dismorphia spio*), (*d*) cockroach (*Epilampra wheeleri*), and (*e*) butterfly (*Siproeta stelenes*).

a single name. Biased sampling procedures also compromise ecological and taxonomic studies of invertebrates, resulting in lower values for species richness, simplified views of taxonomic composition, and lower estimates of population densities. This bias is often habitat- or microhabitat-specific. Near ground sites are more adequately sampled (e.g., Beebe 1916; Williams 1941; Schubart and Beck 1968; Beck 1971; Willis 1976; Pfeiffer, chap. 5, this volume) than are canopy sites (e.g., Wolda 1979; Erwin and Scott 1980; Erwin 1983a, 1983b; Shelly 1988). Preliminary data suggest that the canopy harbors greater numbers of invertebrate species (e.g., Erwin 1983a, 1983b) and individuals (Rees 1983; Sutton 1983; Shelly 1988) than near ground-level sites, but great difficulties characterize sampling such locations. Erwin (1983b) described the difficulties of sampling arboreal insects.

In discussing arboreal invertebrates, we include in this chapter those that are aerial or occur in the canopy, understory, or shrubbery above the forest litter. Some invertebrates (e.g., springtails) have life stages which occur in the litter as well as in the understory. Others, such as millipedes, centipedes, and certain ants, occur in both litter and understory. Because most of these animals are primarily inhabitants of litter, they are dealt with in chapter 5. Termites (Isoptera) are considered in chapter 4 and arboreal arachnids in chapter 7.

HISTORY

Most biological data on invertebrates at El Verde are qualitative. Martorell (1975) listed plant-insect relationships gleaned from literature referring to insects in Puerto Rico, and Velez (1979) provided a bibliography of the entire literature dealing with the invertebrate fauna of the island.

The first field studies on the invertebrate fauna of El Verde are probably those of McMahan and Sollins (1970), who assessed species diversity of soil microarthropods within and outside of the Radiation Center. They concluded that low-level irradiation did not result in lower diversity of organisms compared with control (non-irradiated) areas. Drewry (1970b) provides a list of over 1,200 insect species known from El Verde. The list was the result of several years of work by George Drewry and Robert Lavigne, who collected or reared thousands of specimens, many of which were sent to specialists for identification. Voucher specimens were deposited at the El Verde Field Station insect collection, which continues to be a resource for other entomologists. Appendix 6 is an expansion of their work, based on more recent collections and identifications of several groups by specialists.

Some common groups have received attention because of their conspicuousness or abundance. Heatwole and Heatwole (1978) described the biology of the large camaenid snail, *Caracolus caracolla*. Lavigne (1970b, 1977) provided information on ant ecology and diversity at El Verde. The foraging

activities of some Puerto Rican ants (not from El Verde) are discussed by Torres and Canals (1983) and Torres (1984a, 1984b); Willig et al. (1986) detailed the population dynamics of the common walking stick, *Lamponius portoricensis*. Lister (1981), in an analysis of niche relationships among three species of *Anolis* lizards in the tabonuco forest near El Verde, used sticky traps and collections by sweep net to measure arthropod diversity, abundance, and biomass. He found no significant differences among arthropod diversity, numbers, and biomass between wet and dry seasons. Araneida (spiders), Orthoptera (crickets, etc.), Coleoptera (beetles), and Diptera (flies) were dominant components, both in numbers and biomass during wet and dry seasons. However, Lister's analysis was focused at the ordinal level and most likely would underestimate differences in these categories, compared to analyses to familial, generic, or specific levels. Liebherr (1988) edited a volume on the zoogeography of insects of the Caribbean, in which ten authors reviewed the biogeographic history of various insect groups. Willig and Camilo (1991) documented declines of six invertebrate species at El Verde and Torres (1992) described outbreaks of various lepidopteran species (especially *Spodoptera eridana*) following Hurricane Hugo.

TAXONOMIC STATUS OF INVERTEBRATES AT EL VERDE

The systematics of many insect groups are well known for Puerto Rico compared to other islands of the Greater Antilles (Cuba, Hispaniola, Jamaica). Principal works on systematics of Puerto Rican invertebrates that are of importance to the El Verde fauna are given in table 6.1. This list, although not exhaustive, gives an idea of the uneven taxonomic coverage for invertebrate groups. For example, taxonomic treatment of auchenorrhynchous Homoptera is considered reasonably complete (Ramos 1988), but virtually nothing has been published on the microlepidoptera.

An updated and expanded list of known invertebrate taxa from El Verde appears in appendix 6, and incorporates the data in Drewry (1970b). The update incorporates nomenclatural changes, where possible, and comprises over 1,560 species, an increase of approximately 30%, compared to the over 1,200 species listed by Drewry (1970b).

The higher classification of some insect groups is in dispute. For example, the order Orthoptera (grasshoppers) is considered by some (e.g., Borror et al. 1989) to include walking sticks, cockroaches, mantids, and others, whereas we generally follow the classification of the Insects of Australia (CSIRO 1991). Unfortunately, the systematics of many holometabolous insects (e.g., Coleoptera, Lepidoptera, Diptera, Hymenoptera) has lagged far behind that of the hemimetabolous forms (e.g., Odonata, Hemiptera, Homoptera, Orthoptera). Dissimilar morphology, and differences in habits, habitat use, and species richness of these groups render a more complete knowledge of the

Table 6.1. Taxonomic references to invertebrate fauna of the El Verde Field Station and surroundings

Taxon	Reference	Comments
General	Martorell 1945a,b	Thorough account of insect pests of forests
General	Wolcott 1948	Anecdotal account of insects of Puerto Rico, mostly out of date
General	Martorell 1975	Listing of food plants of insects recorded in literature
General	Velez 1979	Bibliography of taxonomic works for Puerto Rico
Aquatic biota	Hurlbert and Villa-Figueroa 1982	Compilation of taxonomic references by many specialists
Mollusca	van der Schalie 1948	Keys, descriptions
	Aguayo 1961	Puerto Rican snails
	Enrique de Jesus 1987	Taxonomy of land snails of Caribbean National Forest
Araneae	Petrunkevitch 1929, 1930a,b	Descriptive treatment of the spiders of Puerto Rico, with keys
	Archer 1965; Banks 1896, 1914; Bryant 1940, 1942, 1943, 1945, 1947a,b, 1948; Chickering 1945, 1964, 1968a,b,c,d, 1969a,b, 1970, 1972a,b,c; Coddington 1986; Exline & Levi 1962; Lehtinen 1967; Levi 1955a,b, 1957, 1959, 1962, 1963a,b,c, 1971, 1977, 1978, 1980, 1981, 1986a,b; Levi & Randolph 1975; Opell 1979, 1981, 1984; Platnick 1974; Roewer 1951; Shear 1978	Descriptions of spiders
Acarina	Cromroy 1958	Plant mites
Collembola	Wray 1953	New species described
	Mari Mutt 1976, 1987	Keys to genera, descriptions
Ephemeroptera	Travers 1938	Keys
	Peters 1971	Revision of West Indian Leptophlebiidae
Odonata	Klots 1932	Keys to adults, larvae
	García-Diaz 1938	Ecology of adults, larvae
	Garrison 1986	Updates Puerto Rican Odonata
Blattodea	Rehn & Hebard 1927	Keys, descriptions
Orthoptera	Otte 1981	Monograph of North American Orthoptera
Thysanoptera	Medina-Gaud 1961, 1963	Keys, descriptions
Hemiptera	Barber 1939	Keys
	Drake & Maldonado 1954	Waterstriders
	Martorell 1955	Describes new Tingid
	Maldonado-Capriles 1969	Keys to Puerto Rican Miridae
Homoptera	Davis 1928	Cicadas of Puerto Rico
	Osborn 1935	Keys, descriptions
	Caldwell & Martorell 1950a	Keys, descriptions of Cicadellidae
	Caldwell & Martorell 1950b	Keys, descriptions of Fulgoroidea
	Caldwell & Martorell 1951b	Descriptions of new leafhoppers
	Young 1953	Descriptions of *Empoasca* leafhoppers
	Ramos 1957	Keys, descriptions of Membracidae, Cercopidae, Kinnaridae
	Smith 1960, 1970	Describes new aphids
	Smith et al. 1963, 1971	Keys, descriptions of Aphididae
	Caldwell 1942	Describes psyllids
	Caldwell & Martorell 1951a	Review Psyllidae of Puerto Rico
	Nakahara & Miller 1981	Lists Coccoidea of Puerto Rico
Coleoptera	Hlavac 1969	Treatment of genus *Scarites*
	Peck 1970, 1972	Leiodidae
	Matthews 1965, 1966	Keys, descriptions, biogeography of Scarabaeinae
	Chalumeau 1978, 1982, 1985	Descriptions, notes of Antillean Scarabaeidae
	Chalumeau & Gruner 1976	Descriptions of melolothines and rutelines of Antilles
	Chapin 1940	Revision of West Indian Aphodiinae
	Ratcliffe 1976	Revision of West Indian *Strategus*
	Blake 1941, 1943, 1948, 1950, 1951, 1952, 1953, 1964, 1970	Descriptive treatment of various Chrysomelidae
	Bright 1985	Descriptions of new Scolytidae
	Equihua-Martínez & Atkinson 1987	Catalog of North and Central American Platypodidae
Trichoptera	Flint 1964, 1992	Keys, descriptions
Lepidoptera	Forbes 1930	Microlepidoptera
	Schaus 1940a,b	Macromoths
	Comstock 1944	Butterflies
	Riley 1975	Butterflies
	Ramos 1982	Checklist of Puerto Rican butterflies
Diptera	Curran 1928, 1931	Flies, keys, and descriptions
	Alexander 1932	Descriptions of Tipulidae
	Fox 1946	Culicidae
	Snyder 1957	Keys, descriptions of *Neodexioopsis*
	Wheeler & Takoda 1963	Revision of *Mycodrosophila*
	Drewry 1969b,c	Keys to Dolichopodidae and Muscidae of El Verde
	Borgmeier 1969	Phoridae
	Romero & Ruppel 1973	New species of Lonchaeidae
	Telford 1973	Syrphidae, keys
	Thompson 1981	Syrphidae of the West Indies
Hymenoptera	Wheeler 1908	Formicidae of Puerto Rico
	Smith 1936	Formicidae of Puerto Rico
	Smith & Lavigne 1973	New species of ants
	Lavigne 1970b, 1977	Key, Formicidae of El Verde
	Bohart & Strange 1965	Revision of *Zethus*

Note: This list is not intended to be exhaustive.

immature stages of the holometabolous forms almost impossible. A more thorough knowledge will be acquired only by careful rearing of immature stages to adult (see Janzen 1988).

DIVERSITY

The arboreal invertebrate fauna of El Verde in particular, and of Puerto Rico in general, can be considered depauperate compared to mainland tropical forests (Martorell 1945a; Allan et al. 1973; Waide 1987). Examples from four insect groups illustrate this statement.

Odonata

Dragonflies and damselflies are large, predaceous insects which are most speciose in the tropics. Their taxonomy in the Antilles is well known, and few species likely remain to be discovered in Puerto Rico. Garrison (1986) cited forty-nine species for the island, but only ten species (app. 6) occur at El Verde. In contrast, Paulson (1982) listed 228 species from Costa Rica, and the probability of finding new records and species there seems high. Infrequent collecting at one site in Rondônia State, Brazil, has revealed over 130 species (pers. observation). As with the Lepidoptera, Puerto Rico and the other Antilles lack characteristically Neotropical families. No calopterygids of the genus *Hetaerina* (ruby spots) are known from the Antilles, although thirty-seven species are known from the United States south through South America (Garrison 1989). Other families known from the mainland tropics include Polythoridae, Platystictidae, and Perilestidae, all unknown from the Antilles. A dominant genus of the American mainland tropics is *Argia* (Coenagrionidae). Over 110 species are known, with at least forty to fifty new taxa to be described. However, only one endemic Lesser Antillean species, *A. concinna,* is known from the Caribbean.

Homoptera

Another relatively well known insect group at El Verde is the flying auchenorrhynchous Homoptera, including cicadas (Cicadidae), tree hoppers (Membracidae), leaf hoppers (Cicadellidae), and plant hoppers (Fulgoroidea). We have recorded only sixty-four species for El Verde, compared with at least 120 species from a site in central Sulawesi (Rees 1983).

Puerto Rico has an even lower diversity of sternorrhynchous forms (Aphididae, Coccidae, Diaspididae). The aphids (Aphididae) comprise only one species at El Verde, although Smith et al. (1963) cite several records from El Yunque. Dixon et al. (1987) addressed the problem of low species diversity of this family in the tropics. They attributed nonuse of most rare host plants to constraints in aphid biology (i.e., short life cycles, inability to live long without food, high degree of host specificity, and low efficiency in locating proper host plants). Aphids are not favored in tropical communities, they argue, because high plant diversity and low numbers of plants per species are generally the rule.

The same reasoning may apply to coccids and diaspidids. Adult females in these families are completely sessile. The only coccid thus far found at El Verde is *Ceroplastes rubens,* a widespread species which is highly polyphagous (Gimpel et al. 1974). Similarly, only one diaspidid has been found at El Verde: a heavy infestation of the black thread scale, *Ischnaspis longirostris* on *Guarea guidonia* during March 1942 (Martorell 1945a).

Coleoptera: Cerambycidae

Longhorned beetles are attractive insects and favorites with collectors. The family is speciose; all species are phytophagous. Hovore (1989a,b) provided a list of all species of the family from the Monteverde Cloud Forest, Costa Rica, collected from 1974 to 1989, and from the Turrialba region of Costa Rica. The Monteverde region contains at least 225 species, and Hovore speculates that perhaps 25 to 50% more will be found at the site. A total of 348 species has been recorded from Turrialba, and Giesbert and Hovore (pers. comm.) record about 400 species from eight years of collecting 10 to 15 km north of El Llano, Pana Province, Panama. In stark contrast, there are thus far only nineteen species of cerambycids known from El Verde.

Lepidoptera

About 1,560 species of invertebrates are recorded from El Verde (app. 6), yet Janzen (1988) records 3,142 species of Lepidoptera alone from an approximately 100 km^2 area within Santa Rosa National Park, Costa Rica. Even a continental temperate site such as Ithaca, New York, is credited with 1,577 species of Lepidoptera (Janzen 1988), yet we found only 234 species of Lepidoptera at El Verde. Admittedly, our investigation was not as thorough as those for Costa Rica or New York, but our fauna is only about 7% as rich as that of Costa Rica, and about 15% as rich as that of New York. Perhaps a more accurate comparison can be made when comparing the butterflies, including skippers (Hesperiidae). These showy diurnal insects are well known, and estimates of species numbers are probably more accurate. We have found only twenty-six species at El Verde, compared with 345 in Costa Rica and 105 in New York (Janzen 1988). Again, species richness at El Verde is only 8% that of Costa Rica and 25% that of New York. Only 106 species of butterflies occur in Puerto Rico (Ramos 1982), and only about 300 species occur throughout the Antilles (Riley 1975), compared with over 600 species in Trinidad alone (Barcant 1970) and 1,500 to 1,600 species from a 750 ha tract in Rondônia, Brazil (Emmel and Austin 1990). The unusually high number of butterfly species recorded from Trinidad is probably due to its proximity to Venezuela.

Puerto Rico also contains no unusual elements in its lepidopteran fauna, and some characteristic, predominantly New World taxa are lacking. Owl butterflies (Brassolinae), morphos (Morphinae), and ithomiid butterflies (Ithomiinae) are absent, and the island has only one species of satyr (Satyrinae). Similarly, only one species of saturniid moth (Saturniidae) is found in Hispaniola (Ferguson 1971), compared with thirty-five species in Santa Rosa National Park, Costa Rica, and eleven species in Ithaca, New York (Janzen 1988).

DENSITY

Data on the density of arboreal invertebrates at El Verde are known for only two groups, snails and the large walking stick, *Lamponius portoricencis.*

Snails

Recent work (Alvarez 1991; Cary 1992; Alvarez and Willig 1993; Alvarez and Willig unpublished; Willig et al. unpublished) focuses on the population and community ecology of common snails (*C. caracolla, Nenia tridens, Austroselenites alticola, Megalomastoma croceum,* and *Subulina octana*) and the community ecology of all terrestrial snails at El Verde. Alvarez (1991) and Alvarez and Willig (1993) identified seven species of snails at El Verde that were not previously recorded for the tabonuco forest (*Lamellaxis micra, Opeas pumilum, Nesovitrea subhyalina, Guppya gundlachi, Habroconus ernsti, Striatura meridionalis,* and *Chondropoma riisei*). These taxa may have been absent from earlier inventories at El Verde in part because of their small size (diameter or length less that 5 mm) and in part because of their soil or litter microhabitat associations during the day. In the tabonuco forest at Bisley, the densities of the common snails *Nenia tridens, Gaeotis nigrolineata,* and *C. caracolla* were 6.2, 0.7, and 3.8 individuals 100 m^{-2}, respectively; moreover, each species is significantly hyperdispersed (Willig and Camilo 1991).

Based on quadrats arranged along transects that bisected thirteen light gaps at El Verde, Alvarez (1991) and Alvarez and Willig (1993) could evaluate the density response of the five common snail species to changes in cover. Three species (*A. alticola, M. croceum,* and *S. octana*) did not significantly differ in density between light gaps and the surrounding forest matrix. In contrast, two species did respond to light gaps created by treefalls. The abundance of *N. tridens* was significantly higher in gaps, whereas that of *C. caracolla* was significantly higher in the surrounding forest. Differences in microhabitat distribution may be attributable to factors related to diet and body water loss rates.

Substrate selection by each of the five common snail species was compared separately in the wet and dry seasons by Alvarez (1991) and Alvarez and Willig (1993). Substrate was classified into four categories: litter or topsoil, rock, live plant material, and dead plant material. Differences among species in substrate selection were identical in both seasons in that two statistically distinguishable groups of snails were produced. The first group comprised *A. alticola, M. croceum,* and *S. octana:* these snails may be considered forest floor specialists because they were collected in litter or topsoil over 85% of the time in each season. The second group comprised *C. caracolla* and *N. tridens:* these snails were captured more frequently in plant material above the forest floor. In particular, *N. tridens* was highly associated with dead plant material, and was collected from this substrate more than 70% of the time in either season. *Caracolus caracolla* exhibits a seasonal change in substrate associations: 53% of individuals were collected from the litter or topsoil in the dry season, whereas 45% were collected from live plant material in the wet season.

Two levels of community analysis were undertaken by Alvarez (1991) and Alvarez and Willig (unpublished). The first focused on the five common species and the second examined the entire assemblage of snail species. In the former case, they were able to distinguish between quadrats occurring in gaps and those occurring in the undisturbed forest based upon the joint densities of the common taxa. This suggests that these habitats harbor different assemblages of snails and may represent different spatial compartments within the detrital food web. Nonetheless, distinctions between gaps and undisturbed forest were not obtained when the entire snail fauna was considered in community-level analyses, in part because many rare species overwhelmed any pattern based upon the common taxa. It may also have been related to variation among gaps in microhabitat attributes which change during secondary succession. Such variation may obviate the production of distinct assemblages for such a diverse fauna.

Walking Sticks

Willig et al. (1986) examined the population structure of one deme of the only common walking stick, *Lamponius portoricensis,* in a small light gap (100 m^2) at El Verde. They found an average of 0.4 to 1.0 walking sticks m^{-2} during the wet season. Individuals moved an average of 0.5 m day^{-1} and were generally restricted to their host plants. In a nearby part of the tabonuco forest (Bisley), Willig and Camilo (1991) estimated the densities of *L. portoricensis* and *Agamemnon iphemedia,* based upon minimum numbers known alive in each of forty circular quadrats (78.54 m^2), to be 0.034 and <0.001 individuals m^{-2}, respectively. The lower density at Bisley than at El Verde for *L. portoricensis* is attributable to two methodological differences between the studies. First, the survey regime at Bisley predominantly sampled undisturbed forest with some light gaps, whereas at El Verde the entire grid was located in a single light gap. Second, the minimum number known alive technique used at Bisley is likely an underestimate of ecological density because it is based on a single survey; in contrast, the multiple mark and recapture rates used at El Verde adjust population estimates based on recapture rates during repeated surveys and is a more accurate measure of ecological density. Finally, each species of walking stick was significantly hyperdispersed at Bisley and El Verde (Willig et al. 1986; Willig and Camilo 1991).

POST-HURRICANE EFFECTS

On 18 September 1989, Hurricane Hugo with sustained winds of 166 km h^{-1} (Scatena and Larsen 1991) passed over the eastern end of Puerto Rico resulting in extensive damage to the rain forest at El Verde. This hurricane had a dramatic effect on the invertebrate fauna because mature forest was heavily damaged and there was, soon after, a luxuriant growth of secondary or early successional vegetation. Documentation of response to this disturbance is given by Willig and Camilo (1991) for five species of forest snails and two species of walking sticks, by Torres (1992) for larvae of various lepidopteran species, by Schowalter (1994) for canopy phytophagous insects, and by Perfecto and Camilo (in press), for ants.

Willig and Camilo (1991) noted significant decreases in population densities of two walking sticks (*Lamponius portoricensis* and *Agamemmon iphimedia*) and three of four species of snails in the season before Hurricane Hugo (July–August 1989) as compared to similar samplings ten to eleven months after the hurricane. All of these species suffered reductions of up to 75%. The large reductions were a consequence of direct effects of the hurricane (e.g. dislodging of snails and walking sticks by strong winds), as well as of indirect effects (substantial alteration of habitat manifested by reduction of food sources and increased insolation due to the destruction of forest canopy). The dramatic proliferation of low, early successional plant species can present extremely favorable conditions for rapidly reproducing phytophagous insects. Torres (1992) reported substantial increases in population densities of the noctuid moth, *Spodoptera eridania* by April 1990. Larvae of this moth are known to feed on at least fifty-six species of plants from thirty-one families (Torres 1992). Four plant species, *Phytolacca rivinoides, Impatiens wallerana, Ipomoea tiliacea,* and *Cestrum macrophyllum,* were especially abundant, and many sites with these plants suffered moderate to complete defoliation by *S. eridania.* After Hurricane Hugo, canopy lepidopterans, predaceous beetles, and decomposers were more abundant in standing trees than in gap areas, whereas sapsucking insects were more abundant in canopy gap areas (Schowalter 1994). One introduced species of ant, *Wasmania auropunctata,* became the dominant ant species representing 94% of the individual ants collected at transects at El Verde in March 1990, less than one year after the hurricane (Perfecto and Camilo in press). Pre-hurricane sampling in the summer of 1989 yielded eighteen species of ants from 120 sites. Two common species, the endemic *Linepithema mellea* (formerly *Iridomyrmex melleus*), an associate of the sierra palm, *Prestoea montana,* and the epigaeic *Pheidole moerens* were the most commonly found species before Hurricane Hugo. Stomach analysis of *E. coqui* collected in June 1990 revealed that *Wasmania* comprised a major component of the ant diet (pers. observation).

A comprehensive two-year study of the autecology of *C. caracolla* (Cary 1992; Willig and Cary unpublished) was conducted at El Verde on three grids (374.68 m^2), beginning two years after Hurricane Hugo. Grids were selected based on hurricane damage. In general, the grid less affected (based on tree damage and canopy openness immediately after the hurricane) consistently had higher snail densities (141 to 182 individuals per grid) than did either of the other two more disturbed sites (91 to 139 and 88 to 126 individuals per grid). Nonetheless, survivorship (between seasons) on the three small grids was indistinguishable during the course of the study (survivorship averaged 0.56). Snails grew more slowly on the less disturbed grid (mean growth rate, 2.38 mm y^{-1}) than on the disturbed grids (mean growth rate, 4.99 mm y^{-1}), in part as a consequence of increased resource levels derived from fallen trunks and limbs, as well as because of increased density of early successional shrubs in disturbed grids. Simulation analyses indicated that snails exhibited site fidelity and have home ranges (Minimum Convex Polygon Method; Cary 1992) that are significantly smaller than those expected by chance alone on all three grids. However, after controlling for the effects of season, snail size, and number of captures, analysis of covariance detected a significant difference between the two disturbed grids as a group (mean, 4.30 m^2) and the less disturbed grid (mean, 9.50 m^2), but no difference between the two disturbed grids (4.06 versus 4.53 m^2) The same statistical results were obtained when attention was restricted to foraging home range (day retreats were not included in calculations of home range). Hence, snails traverse a smaller range in search of forage and retreat sites in disturbed grids; if this translates to reduced energy costs, it likely contributes to the higher growth rates enjoyed in disturbed sites.

AGE STRUCTURE

Virtually no data on age structure of invertebrates exist for El Verde. Some species, such as ants, are undoubtedly continuously brooded, while others are synchronously brooded. We compared results gathered from the two-week sticky trap survey during 9–22 June 1981. Nineteen 5 oz. plastic cups were covered with Tanglefoot® sticky trap adhesive and suspended at 1 m intervals on a string parallel to the El Verde Tower. Samples were collected at 0900 and 1800 hrs. over a two-week period (ten days, eight nights), excluding weekends. Our results indicated that one taxon, phorid flies, is probably synchronously brooded. The data indicate a sudden mass emergence or mass flight over a short period of time. Only one specimen was collected on 9 June, one on 10 June, two on 11 June, six on 12 June, and 285 on 15 June (the next sampling period). Peak density of 913 was reached on 16 June, but numbers fell to eighty-four on 17 June. It is not known if several broods occur throughout the year, or whether mass emergence is restricted to the wet season.

Other invertebrates are long-lived. The large snail, *Caracolus caracolla,* apparently lives an average of three to six years (Heatwole and Heatwole 1978). One adult specimen was recaptured seven years and four months after initial marking. Because the individual was at least three years old when marked (minimum time to reach maturity), its total age was over ten years. As mentioned earlier, the life span of the Central American chrysomelid beetle, *Chelobasis perplexa,* is probably about two years (Strong 1983), and some species of adult *Heliconius* butterflies are known to live six months (Ehrlich and Gilbert 1973).

SEASONALITY

Several studies have stressed the differences in invertebrate abundance throughout the year in the tropics (e.g., Janzen and Schoener 1968; Allan et al. 1973; Janzen 1973a,b; Wolda 1978a,b, 1979, 1980a,b, 1983b; McElravy et al. 1981; Penny and Arias 1982; McElravy et al. 1982; Wolda and Flowers 1985), but fewer studies have been conducted on island faunas (Allan et al. 1973; Frith 1975; Janzen 1973a,b; Tanaka and Tanaka 1982; Snyder et al. 1987; Stewart and Woolbright, this volume). In general, these studies indicate seasonality in size of many invertebrate populations and corresponding increases in species diversity, abundance, and biomass during the rainy season. Studies reported by Snyder et al. (1987) and Stewart and Woolbright (this volume) have shown this to be true at El Verde. Janzen and Schoener (1968) report high habitat specificity in many insect species during the dry season, but with the onset of rains they leave moist riparian areas to repopulate previously dry areas (Janzen 1983b). However, not all insects follow a seasonal trend. The Panamanian cicadellid, *Polana scinna,* showed no detectable differences in numbers trapped throughout the year, whereas other species, even other congeners, did (Wolda 1980a).

In tropical areas where the dry season is not marked, fluctuations in invertebrate populations numbers may be less evident. This may be the case for certain mayflies (Wolda and Flowers 1985). In contrast, many dragonflies and damselflies are highly seasonal. Adult platystictids, *Palaemnema desiderata* and *P. paulitoyaca,* are present as adults only during the rainy season in Mexico (Garrison and Gonzalez pers. observation). The onset of rain can trigger emergences of various stream and lake species (pers. observation). Tanaka and Tanaka (1982), in their study of arthropod abundance in Grenada, found that most species increased in number about two weeks after rainfall. In the tabonuco forest at El Verde, increased insect abundance was detected in February in the middle of the dry season (Snyder et al. 1987). Stewart and Woolbright (this volume) provide further comparisons of availability of invertebrate prey between wet and dry seasons.

Species diversity may correspondingly be expected to increase during the rainy season. This has been shown for Hemiptera (Janzen 1973b) and Coleoptera in Costa Rica (Janzen 1973b; Buskirk and Buskirk 1976), but such was not the case for Coleoptera in Grenada (Tanaka and Tanaka 1982). Janzen (1973b) and Tanaka and Tanaka (1982) argue that tropical island faunas, being depauperate compared with mainland tropical ecosystems, comprise more generalist species, that is, species more polyphagous than their mainland counterparts. Such island generalists respond to the onset of the rainy season with an increase in numbers of individuals, whereas species previously not present at mainland sites appear during the rainy season.

FEEDING GUILDS

Herbivores

We categorize phytophagous invertebrates into two broad groups: polyphages and monophages. Some polyphagous species may be limited to only a few species of hosts and represent a special category, oligophages. Many, if not most, hemimetabolous insects can be considered polyphagous, as many do not seem to be host-specific and sample a wide variety of plant species. A detailed analysis of one common herbivore, *Lamponius portoricensis* (Willig et al. 1986; Sandlin-Smith 1989; Sandlin and Willig 1993; Willig et al. 1993), and host records gleaned from Martorell (1975) for various Orthoptera and Homoptera support this designation. Some Homoptera are extremely host specific, although we have no evidence for the common species recorded at El Verde.

Polyphagous Forms

SNAILS. Prior to 1990, the only substantive ecological work on snails at El Verde was that of Heatwole and Heatwole (1978), and they focused primarily on the large common camaenid, *Caracolus caracolla.* They report that

C. caracolla is quite polyphagous. It has been observed eating dead brown leaves (one leaf was identified as an introduced *Hibiscus*), unidentified green leaves, large seeds (one was *Ormosia krugi*), wet discarded paper, arum roots, and inflorescences of *Inga vera*. In the laboratory, these snails fed on carrots, paper, and *Hibiscus* leaves (Heatwole and Heatwole 1978). A macroscopic analysis of fecal material of snails at El Verde revealed that 54% was leaf material, 18% thin fibers, 14% wood, and 10% bark. A microscopic examination of fecal material showed that *C. caracolla* primarily ingested diatoms (42%), wood cells (34%), plant hairs (11%), and calcium oxalate crystals (5%). Ratios of these items differed in fecal samples collected at El Yunque, a site east of El Verde and at a higher elevation in the Luquillo Mountains. However, Lodge (this volume) reports that epiphyll composition on leaves adjacent to snail feeding trails was 77% fungi and 23% algae; fungi do not appear in fecal samples.

BLATTODEA. About twenty to twenty-five species of cockroaches occur at El Verde (Drewry 1970b, app. 6), some of which are common and reach high densities in the forest litter (Pfeiffer, chap. 5, this volume). One of these, *Epilampra wheeleri*, is large (25 mm), but nothing is known of its foraging ecology. A preliminary study of food habits of *Eleutherodactylus coqui* (Woolbright and Garrison unpublished) indicates that about 18% by volume of the diet comprises these insects.

ORTHOPTERA. Grasshoppers are considered to be generalized feeders (Mulkern 1967; but see Rowell et al. 1983 for exceptions). Orthoptera at El Verde are large (5–45 mm). A few species are common, and many are consumed regularly by frogs and *Anolis* lizards (Lister 1981; pers. observation). All species are probably important herbivores at El Verde. Two common katydids and nine gryllids (table 6.2) are the dominant forms at El Verde. *Orocharis* contains two small species (*O. vaginalis, O. terebrans;* about 15 mm) which occur from the understory to the canopy. Martorell (1975) records several host plants for *Cyrtoxipha* and *Orocharis,* but these plants are primarily monocultural crops. No definite host relationships have been recorded for any of these species at El Verde. Over 50% of the total volume of food consumed by *E. coqui* comprises these insects (Woolbright and Garrison unpublished), so they provide an important link in the food chain.

PHASMATODEA. Four species of walking sticks occur at El Verde, but only one, *Lamponius portoricensis,* is common. At El Verde, *Lamponius* commonly consumes leaves from four plant taxa (Willig unpublished; Sandlin and Willig 1993): *Piper treleaseanum* and *P. hispidum* (herbaceous shrubs in the Piperaceae), *Urera baccifera* (a woody shrub in the Urticaceae which grows from prostrate stems), and *Dendropanax arboreus* (a mid-successional canopy tree in the Araliaceae). In areas with appreciable human modification in the tabonuco forest, *Hibiscus rosa-sinensis* is a common ornamental and forage species for *Lamponius* as well.

Lamponius is the largest common insect at El Verde, and is the only one for which food consumption data have been quantified in any detail (Willig unpublished; Sandlin-Smith 1989; Sandlin and Willig 1993). In controlled experiments where five foods were offered for consumption in equal amounts by wet weight (Willig unpublished), *U. baccifera* was the most preferred food regardless of total availability; however, all other foods were consumed as well, even though the supply of *U. baccifera* was not exhausted during feeding trials. *Urera baccifera* had the lowest caloric content but the highest or second highest content of phosphorus, sulfur, zinc, manganese, potassium, calcium, and magnesium. Moreover, despite significant changes in consumption patterns which accompanied alterations in total abundance of foods offered, the ratio of nutrients (calories, ash, elements listed above, nitrogen, and sodium) remained constant in the diet of the experimental population of *Lamponius*.

Willig et al. (1993) subsequently evaluated microhabitat selection by multiple regression analysis. The percentage of all captures (618) during which *Lamponius* was found on or consuming its natural forage plants was 62% *P. treleaseanum,* 12% *D. arboreus,* 9% *P. hispidum,* 4% *U. baccifera,* and 13% other taxa (*Ruellia coccinea, Panicum adspersum, Hippocratea volubilus, Inga vera, Palicourea barvineira,* and *Prestoea montana*). Walking sticks were associated with areas characterized by high apparency (foliar development in the understory) of *P. treleaseanum* and *Symplocos martinicensis,* and low apparency of *Dryopteris deltoides*. The total development of the understory, regardless of taxonomic composition, at 2.5 feet and 3.5 feet above the ground also contributed to high density of walking sticks. In addition, *Lamponius* occurred twice as often on *P. treleaseanum* as expected based on its total contribution to the understory flora. The authors hypothesized that the disproportionate occurrence on *P. treleaseanum* was related to the production by *Piper* of aromatic attractants that act as proximate cues in patch selection.

To understand why *Lamponius* disproportionately occurs on its least preferred forage plant, a number of experiments were conducted that evaluated the manner in which forage attributes (e.g., nutrient content) or herbivore characteristics (age, sex, or previous foraging experience of walking sticks) interact to affect food preference. Multivariate repeated measures analysis of variance revealed that at different ages, males and females exhibit different patterns of food consumption when offered *P. treleaseanum, P. hispidum, U. baccifera,* and *D. arboreus*. Likewise, preexposure to only one food influences subsequent diet composition differently, depending on walking stick sex and which of the four plants were preexposure foods during a particular

Table 6.2. Common phytophagous insects at El Verde

Taxon	Foraging Time	Food Plants (if known)
POLYPHAGOUS FORMS:		
Blattodea: Blattellidae		
Aglaopteryx facies	Night	—
Cariblatta hebardi	Night	—
Cariblatta suave	Night	—
Plectoptera infulata	Night	—
Epilampra wheeleri	Night	—
Neoblattela vomer	Night	—
Orthoptera: Tettigoniidae		
Anaulocomera laticauda	Night	*Inga vera*[a]
Turpilia rugosa[a]	Night	Probably *Inga vera*[b]
Orthoptera: Gryllidae		
Anaxipha sp.	Night	—
Cyrtoxipha gundlachi	Night	*Citrus* spp., *Musa sapientum, Saccharum officinarum, Solanum melongena, Zea mays*[a]
Laurepa krugii	Night	*Coffea arabica, Rhizophora mangle*[a]
Orocharis terebrans	Night	*Citrus* spp., *Coffea arabica*[a]
Orocharis vaginalis	Night	*Citrus* spp., *Saccharum officinarum, Coffea arabica, Dracaena fragrans, Gossypium hirsutum*[a]
Orocharis spp. (4 undescribed)	Night	—
Phasmatodea: Phasmatidae		
Lamponius portoricensis	Night	*Dendropanax arboreus*[c], *Hibiscus rosa-sinensis*[c], *Piper hispidum*[c], *Piper treleaseanum*[c], *Urera baccifera*[c], probably *Lobelia portoricensis*[a]
Psocoptera (13 spp.)	?	Fungal spores, lichen[d]
Homoptera: Cicadidae		
Borencona aguadilla	Day, Dusk?	*Coffea arabica*[a]
Homoptera: Cicadellidae		
Sibovea coffeacola	Day	*Castilla elastica, Coffea arabica, Inga fagifolia, Manilkara bidentata, Pothomorphe peltata, Rubus rosifolius, Solanus* spp.[a]
Homoptera: Cixiidae		
Bothriocera undata	Day, Night?	22 plants listed by Martorell (1975)
Homoptera: Delphacidae		
Ugyops occidentalis	Day, Night	*Coffea arabica, Inga fagifolia*[a]
Homoptera: Derbidae		
Dawnaria sordidulum	Day, Night	*Musa sapientum*[a]
Dysmia maculata	Day, Night	—
Homoptera: Achilidae		
Catonia cinera	Day, Night	*Dendropanax arboreus, Guarea guidonia, Hibiscus rosa-sinensis, Inga vera, Montezuma speciosissima*[a]
Catonia dorsovittata	Day, Night	—
Catonia arida	Day, Night	—
Homoptera: Tropiduchidae		
Ladellodes stali	Day, Night	*Panicum muticum*[a]
Homoptera: Flatidae		
Melormenis magna	Day, Night	—
MONOPHAGOUS FORMS:		
Lepidoptera (larvae): Papilionidae		
Papilio pelaus	Night?	*Zanthoxylum martinicense*[a]
Lepidoptera: Pieridae		
Dismorphia spio	Night?	*Ruellia coccinea*
Lepidoptera: Nymphalidae		
Siproita stelenes	Night?	*Ruellia coccinea*[a]

Sources and notes: [a]Martorell (1975). Food plants gleaned from Martorell (1975): does not indicate that those plants occur at El Verde.

[b]Martorell (1975: 144) records a similar tettigoniid, *Anaulacomera laticauda*, as feeding on *Inga vera;* thus this tree is probably used by other orthopterans at El Verde.

[c]From Willig (1989)

[d]Feeding habits for this order summarized by Broadhead (1983).

experiment. In addition, preferences were shown for different qualities of leaves within single forage species (old, intermediate-aged, or young leaves). In particular, older leaves of *P. treleaseanum* were preferred, whereas intraspecific differences in consumption based on leaf age or position did not occur for *D. arboreus* or *U. baccifera.* In summary, walking sticks distinguish among plant species, recognize differences in plant quality associated with age or position for some taxa, and modify diet content to reflect past experience.

Studies of insect consumption by birds, anoles, and frogs at El Verde indicate that walking sticks constitute only a minor part of their diet. However, their large size, abundance, and ability to defoliate forage plants indicate that *Lamponius* may be important in returning nutrients to the soil during early successional stages.

PSOCOPTERA. The thirteen species of Psocoptera from El Verde are common elements in the understory. We have no data regarding their feeding habits, but Broadhead (1983) characterizes the group as microepiphyte feeders, of which some species are primarily bark inhabitants and others are foliage inhabitants. Broadhead classifies species as fungal spore and lichen feeders. However, the two groups are not obligatory in their feeding habits: both can switch to the alternate food source when their preferred host is scarce or absent. Our fauna (thirteen species) is depauperate compared with that of the Canal Zone, Panama, from which Broadhead (1983) cites 219 species.

HOMOPTERA. About eighty species occur at El Verde, of which at least sixteen (table 6.2) are common there. These species, according to records (Martorell 1975), sample a wide array of food plants. As with the Orthoptera, many of the food plants are primarily of agricultural importance. However, many species of Homoptera are known to be extremely host specific, and several less frequently encountered species at El Verde may be monophagous or oligophagous. Measurements of herbivory rates by this group are scarce, because damage to plant tissues is difficult to assess. Laboratory experiments have been conducted to measure the feeding rate of few sucking insects. Most subjects involved relatively sessile aphids (e.g., Auclair 1958, 1959; Mittler 1958, 1970; Van Hook et al. 1980); we know of no studies conducted for more vagile tropical Homoptera. Their feeding habits may cause reduced viability in certain plants, and several homopterans are economically important pests. Another deleterious and far-reaching consequence of homopteran herbivory is the ability of some species to transmit plant viruses and other diseases. Homoptera are an important food source for arboreal *Anolis* lizards (*A. evermanni, A. stratulus,* Garrison and Reagan unpublished).

Monophagous Forms

We include here members of the large orders Coleoptera and Lepidoptera, which are more speciose than the more primitive Orthoptera and Homoptera. The Lepidoptera generally are considered to have a narrow foodplant range (Gilbert 1984), and evidence suggests that Coleoptera follow this trend also. For example, Linsley (1961), in discussing host selection of the North American Cerambycidae, indicated that the more primitive tribes tend to be more polyphagous than are more advanced tribes. Linsley (1959) noted that nearly seventy-five species of the cerambycid genus *Plagithmysis* (confined to the Hawaiian Islands), are highly host specific. Abundance of ecological niches and diversity of hosts have probably contributed to the abundance of species in this genus. Exceptions occur, and many species of both orders are important pests, feeding on a wide array of plant species. Examples include the sugar cane weevil, *Diaprepes abbreviatus,* and the Melolonthine scarab, *Phyllophaga portoricensis.* Many species of these orders are known from El Verde, but virtually nothing is known of their food habits or importance in the food web.

COLEOPTERA. The most common beetles encountered in our sampling program have been bark beetles (Scolytidae). These insects are injurious to stressed or unhealthy trees in the temperate zone, but little is known of their feeding habits at El Verde, though some species are polyphagous and probably play an important role in the food web. At least three pantropical species collected at El Verde (app. 6) are introduced: *Xyleborus ferrugineus, X. affinus,* and *Coccotrypes carpophagus.* Both species of *Xyleborus* are among the most important tropical tree pests in the world. Wood (1982) cites records of over 150 hosts for *X. ferrugineus* and over 250 for *X. affinus. Xyleborus ferrugineus* is known to be a principal vector of *Ceratoeystis fimbriata,* which causes wilt disease in cacao trees (Saunders 1965). *Coccotrypes carpophagus,* as its specific name indicates, breeds in large seeds, especially those of palms, on the ground.

Some bark beetles have been reared from decaying seed pods of *Inga vera.* Larvae of the common Middle American bark beetle, *Scolytodes atratus panamensis* (Cecropia Petiole Borer) feed only on petioles of recently fallen *Cecropia* leaves (Wood 1983). Wolcott (1948) lists thirty species from Puerto Rico, but there must certainly be more than that. Wolcott (1948) lists *Xyleborus affinus* as attacking healthy *Inga vera. Xyleborus* (*Ambrosiodmus*) *lecontei* has been collected from dying terminals of *Cedrela mexicana,* and a species of *Pterocyclon* has been found attacking *Dacryodos excelsa.*

Only three species of chrysomelid beetles have been listed for El Verde, but a more realistic number is probably eighty-five to ninety species (E. Sleeper pers. comm.). Strong (1983) describes the biology of rolled-leaf hispines of the tribes Cephaloliini and Arescini. Members of the genus *Cephaloleia,* of which there are 182 species, are specific to families of plants of the order Zingiberales.

LEPIDOPTERA. Little is known of the host plant range for the 234 species of Lepidoptera at El Verde. The larval forms of almost all Lepidoptera are phytophagous. The adults are nectar feeders, but some species (e.g., *Gonodonta* spp., Noctuidae, Todd 1959) have short tongues for piercing fruit and imbibing fruit juices. Two butterflies at El Verde, the green and white *Siproeta stelenes* and the pierid *Dismorphia spio,* are known to feed on *Ruellia coccinea* (Wolcott 1948 pers. observation). The large swallowtail butterfly, *Papilio pelaus,* feeds on *Zanthoxylum martinicense* Wolcott (1948).

Janzen (1988) documented the host range of most of the Lepidoptera at Santa Rosa National Park in Costa Rica. He provided good evidence of the narrow host range for larvae of the order. At least half of the caterpillar species studied are monophagous; and he speculated that at least 80% of the remainder are oligophagous. He believed that about twenty of 3,142, or less than 1%, of the fauna are polyphagous.

Total defoliation of various plant species in mature ecosystems by caterpillars or by other insects is apparently rare in the Neotropics. Janzen (1988) records forty such episodes over nine years at Santa Rosa National Park, and Wolda and Foster (1978) document an outbreak of the dioptid moth, *Zunacetha annulata.*

Carnivores

Two broad classes are defined here, predators and parasitoids/parasites. Predators, which attack and consume other invertebrates, are usually indiscriminate in prey acquisition and therefore sample a wide array of organisms. Parasitoids are usually specific to one kind of organism; their larvae feed on and destroy the host. In contrast, parasites may be host specific but do not usually kill the host. The holometabolous orders Diptera and Hymenoptera (table 6.3) represent this feeding guild.

Predators

The only common group of predators appears to be the beetle family, Lampyridae (table 6.3). Seven species occur at El Verde. The sickle-shaped mandibles of the larvae are used to stab and suck dry their prey. Females of some lampyrids are predatory on other similar species (Lloyd 1965), but it is not known if this phenomenon occurs at El Verde. Lampyrids are occasionally found in the stomachs of frogs (*Eleutherodactylus*) and lizards (*Anolis*), and

Table 6.3. Common carnivorous insects of El Verde

Taxon	Foraging Time	Feeding Guild	Host (Parasitoids)
Coleoptera			
Lampyridae (about 6 spp.)	Night	Predator	
Diptera (adults)			
Culicidae (9 spp.)	Day, Night	Parasite	
Ceratopogonidae (about 34 spp.)	Day, Night	Parasite	
Dolichopodidae	Day	Predator	
Diptera (larvae)			
Phoridae (about 65 spp.)	Day, Night	Predator[a]	
Muscidae			
Philornis spp.	Day, Night	Parasite	Aves[b]
Hymenoptera			
Mymaridae (about 13 spp.)	Day, Night	Parasitoid	Eggs of Lepidoptera, Coleoptera, and other insects depending on species
Eulophidae (about 14 spp.)	Day, Night	Parasitoid	Homoptera, Lepidoptera, and other insect larvae
Scelionidae (about 17 spp.)	Day, Night	Parasitoid	Eggs of insects, spiders, depending on species
Formicidae			
Linepithema mellea	Day	Predator[c]	
Myrmelachista ramulorum	Day	Predator[b]	
Vespidae			
Mischocyttarus phthisicus	Day	Predator	
Polistes crinitus	Day	Predator	

Notes: These data are based on general knowledge of the biology of various insect groups. Primary hosts are included for host specific forms.

[a] Larvae of one species have been observed eating eggs of *E. coqui* (Woolbright pers. observation).

[b] Snyder et al. (1987).

[c] Are also scavengers.

one was found in the stomach of a juvenile Puerto Rican boa, *Epicrates inornatus* (Reagan 1984).

Curiously, members of the large coleopterous family Carabidae appear to be absent from El Verde. A few species are found at higher elevations near El Yunque, but none has been collected at El Verde.

Parasites and Parasitoids

The Hymenoptera and Diptera compose these groups. Generally, they are small to very small insects and, according to preliminary sticky trap sampling, are represented abundantly at El Verde. Their precise role as potential regulators of other insect and vertebrate groups is largely unknown, although the general biology of the groups indicates that most species are extremely host specific. Janzen (1988) reports over 300 species of tachinid, ichneumonid, and brachonid parasitoids from Santa Rosa National Park, Costa Rica. Many of these are monophagous, and others limit their host selection to clusters of closely related species.

Many nematocerous Diptera (Culicidae, Ceratopogonidae) adults suck the blood of vertebrate and invertebrate hosts, but no quantitative data have been gathered for these insects. Snyder et al. (1987) provide data on avian parasitism by larvae of the warble fly, *Philornis* spp. They observed a 26% to almost 47% death rate of nestling pearly eyed thrashers due to infestations of these flies.

The ectoparasite fauna of bats is reported by Willig and Gannon (this volume). Levels of parasitism based on the age and sex of both bat host and invertebrate parasite species are documented elsewhere (Gannon 1991; Gannon and Willig 1994b, in press). The level of infestation by *P. iheringi* on *S. rufum* depends upon the age and sex of the host, but not upon season of capture (wet versus dry season). In particular, subadult bats harbored significantly higher numbers of this wing mite than did adult males or adult females. The same pattern obtains for *P. iheringi* on *A. jamaicensis*. In contrast, levels of infestation by the other ectoparasites (*M. aranea, Aspidoptera* sp., *Trichobius* sp., and *Spelaeorhynchus* sp.) of *A. jamaicensis* are not influenced by the age or sex of the host. For the other bat taxa, the number of captured hosts was too small to conduct powerful tests for differences in ectoparasite infestation levels.

Two species of ectoparasite (*P. iheringi* and *Trichobius* sp.) occurred on all three common bat taxa; differences in infestation by each of these ectoparasites, as well as by all ectoparasites, could be compared among host taxa and between seasons. In all three cases, season-independent, host-specific differences in ectoparasite infestation were detected in statistical analyses. In particular, infestation levels by *Trichobius* sp. were the same on *S. rufum* and *A. jamaicensis,* but levels of infestation on *M. redmani* differed from that on each of the other bats. In contrast, levels of infestation by *P. iheringi* and all ectoparasites were the same on *S. rufum* and *M. redmani,* but each of these bat taxa differed from *A. jamaicensis*.

The distribution of ectoparasites on hosts differs among host age-sex groups and may be related to behavioral attributes of each bat species. The number of ectoparasites per host was randomly distributed in *A. jamaicensis* and *M. redmani,* whereas the distribution of ectoparasites on *S. rufum* was significantly hyperdispersed (even). Both *A. jamaicensis* and *M. redmani* roost in colonies where ectoparasite transmission among bats may be facilitated. In the case of bats which roost in a solitary fashion, such as *S. rufum,* barriers to interhost transmission may give rise to the clumped distribution of ectoparasites.

Comparisons of ectoparasite community composition can be evaluated based upon the proportional representation of ectoparasite species. Because the sample size of hosts was large, the effect of host age and sex on community composition was determined for *A. jamaicensis*. Differences in ectoparasite community composition were detected among adult males, adult females, and subadults. Less powerful *a posteriori* tests were unable to identify pairwise differences. Nonetheless, the contrast between adult females and subadults approached significance ($p = .052$) and most likely contributed to overall differences.

FORAGING ACTIVITY

Most foraging probably occurs at night, because most invertebrate activity is observed during that time. Data pertinent to the day-night comparison and vertical stratification of flying insects were accumulated from the 9 to 22 June 1981 study mentioned above. After we identified all invertebrates, we tabulated mean numbers and subjected the data to a one-way analysis of variance (ANOVA) and sum of squares simultaneous testing procedure (SS-SSTP) (Sokal and Rohlf 1969). Stewart and Woolbright (this volume) provide further data on day-night activity and abundance of forest dwelling arthropods at El Verde. Data on seasonal abundance of flying insects were gleaned from unpublished data accumulated by Kepler and summarized by Snyder et al. (1987) and by Lister's (1981) work with *Anolis* lizards.

Table 6.4 lists invertebrates collected over ten days and eight nights, and table 6.5 gives the percentage contribution of each order. No significant differences in mean numbers of invertebrates were detected between day and night, but Blattodea, Orthoptera, and Lepidoptera showed a nocturnal preference (table 6.5). The dipteran suborders Brachycera and Cyclorrhapha (except Phoridae) were strongly diurnal (table 6.4). Willig (unpublished) has found that *Lamponius* feeds only at night. During the day, Orthoptera and Blattodea remain hidden, while *Lamponius* remains quiescent. The sticky trap survey and personal observation indicate that Homoptera are active day and night, but it is not known if they feed during both times. Heatwole and Heatwole (1978) have observed *Caracolus caracolla* feeding only at night; however, these snails become active when humidity is high or during frequent showers throughout the year (Cary 1992; Willig pers. observation).

Evidence of diel cycles among ants comes from gut analysis of nocturnal frogs and diurnal *Anolis* lizards. The major ant eaten by *E. coqui* appears to be *Paratrachina* spp., but these species seldom appear in diets of *Anolis* lizards. The most common ant components of the diet of these animals are *Pheidole moerens, Linepithema mellea* (formerly *Iridomyrmex melleus*), and *Myrmelachista ramulorum*.

Table 6.4. Flying or wind-drifting arthropods trapped 9–22 June 1981

Taxon	Day [a]	Night [b]
Class ARACHNIDA		
Order ARANEAE		
unidentifiable to family	1	2
Pholcidae		
unidentifiable to species	1	
Modisimus sp.	2	
Linyphiidae	1	
Clubionidae	1	5
Araneidae		
unidentifiable to species	1	1
Leucauge regnyi	1	2
Thomisidae		
Epicaudus mutchleri	1	
Salticidae	3	1
Order ACARINA		
Suborder Cryptostigmata	1	
Class ELLIPURA		
Order COLLEMBOLA		
Entomobryidae		
Lepidocyrtinus sp.?	1	
Class INSECTA		
Order EPHEMEROPTERA		
Leptophlebiidae?	1	
Order BLATTODEA		
Blattidae	1	
Blattellidae		
Cariblatta hebardi		2
undetermined species		4
Order ORTHOPTERA		
Gryllidae		
Cyrtoxipha gundlachi		3
undetermined Trigonidinae		1
Orocharis vaginalis or *terebrans*	4	
Order ISOPTERA		
Termitidae		
Nasutitermes sp.	1	
Kalotermitidae		
Glyptotermes ?pubescens (winged)	3	2
Order PSOCOPTERA		
Polypsocidae		2
Epipsocidae		2
Psocidae		3
Lepidopsocidae	12	7
Order THYSANOPTERA		
Phlaeothripidae	8	10
Thripidae	5	2
Order HEMIPTERA		
Dipsocoridae	1	
Miridae		
undetermined species	1	
Polymerus pallidus	1	
Lygaeidae		6
Cydnidae		
?*Amnestus* sp.	1	

Table 6.4. (*continued*)

Taxon	Day [a]	Night [b]
Order HOMOPTERA		
Membracidae		
Nessorchinus esbeltus	1	
Cicadellidae		
undetermined species	1	
undetermined species (larva)	1	
Sibovea coffeacola		1
Xestocephalus maculatus		2
Ponana insularis		3
Superfamily FULGOROIDEA		
Cixiidae (larva)	1	
Delphacidae		
Ugyops occidentalis		1
Derbidae		
undetermined species	1	
Dysimia maculata		1
Dawnaria sordidulum		9
Patara albida		1
Achilidae		
Amblycratus striatus? (larvae)	8	7
Catonia cinerea		1
Catonia dorsovittata (larvae)	3	5
Quadrana punctata? (larva)		1
undetermined species (larvae)	2	
Tropiduchidae		
Ladellodes stali	1	8
Issidae		
Thionia borinquensis	3	
Colpoptera maculifrons	6	
Colpoptera brunneus	9	5
Neocolpoptera monticolens	1	
Kinnaridae		
Quilessa fasciata	2	
Psyllidae	1	3
Superfamily COCCOIDEA	1	1
Order COLEOPTERA		
Ptiliidae		
Actinopteryx sp.	1	
Scaphidiidae		1
Staphylinidae		
undetermined species	4	3
Palaminus sp.		1
Pselaphidae	3	
Histeridae	4	1
Elateridae		1
Throscidae	4	2
Anobiidae		3
Trogositidae (Tribe Tenebroidini)	1	
Cucujidae		2
Coccinellidae	3	3
Tenebrionidae		1
Colydiidae		1
Melandryidae		1
Mordellidae	1	

Table 6.4. (*continued*)

Taxon	Day[a]	Night[b]
Euglenidae	3	3
Chrysomelidae	1	2
Scolytidae	7	7
Anthribidae	1	
Curculionidae		2
Order LEPIDOPTERA		
Gracillariidae?		1
Cosmopterygidae?		1
Gelechiidae?		1
Order DIPTERA		
Tipulidae	5	9
Mycetophilidae	18	4
Sciaridae	35	20
Cecidomyiidae	8	11
Psychodidae	9	11
Scatopsidae	7	1
Ceratopogonidae	102	80
Chironomidae	125	44
Asilidae		1
Empididae	14	4
Dolichopodidae	28	12
Phoridae	1,520	1,879
Pipunculidae	1	
Lonchaeidae	1	
Tephritidae	1	
Odiniidae	4	
Agromyzidae	1	
Lauxaniidae	2	
Chamaemyiidae?	1	
Heleomyzidae	3	2
Drosophilidae	3	3
Ephydridae	1	
Chloropidae	3	
Muscidae	7	
Calliphoridae	4	1
Sarcophagidae	1	
Tachinidae	39	5
Order HYMENOPTERA		
Braconidae	2	5
Ichneumonidae		1
Mymaridae	11	1
Trichogrammatidae	1	4
Eulophidae	6	2
Encyrtidae	54	18
Eupelmidae	8	
Agaonidae	2	
Torymidae	1	1
Pteromalidae		1
Cynipidae	1	
Ceraphronidae	3	
Diapriidae	4	
Scelionidae	29	14
Platygasteridae	5	

Table 6.4. (*continued*)

Taxon	Day[a]	Night[b]
Bethylidae	4	
Dryinidae	1	1
Formicidae		
Monomorium floricola	1	
Linepithema mellea (formerly *Iridomyrmex melleus*)	3	1
Myrmelachista ramulorum	1	4
Brachymyrmex heeri	1	
undetermined workers	7	3
winged males	6	5
Sphecidae (Cabroninae)	4	

[a]Ten days.

[b]Eight nights.

Table 6.5. Invertebrates collected by day and by night

Order	Day[a]	Night[b]	Total	% Overall Total
Acarina	0	1	1	0.02
Araneidae	9	14	23	0.51
Collembola	0	1	1	0.02
Ephemeroptera	1	0	1	0.02
Blattodea	0	7	7	0.16
Orthoptera	0	8	8	0.18
Isoptera	4	2	6	0.13
Psocoptera	12	14	26	0.58
Thysanoptera	13	12	25	0.55
Hemiptera	4	6	10	0.22
Homoptera	42	49	91	2.02
Coleoptera	33	28	61	1.35
Lepidoptera	0	3	3	0.07
Diptera	1,943	2,087	4,030	89.42
Hymenoptera	152	62	214	4.75
Totals	2,213	2,294	4,507	100%

[a]Ten days.

[b]Eight nights.

VERTICAL STRATIFICATION

Our brief trapping survey and data gleaned from the literature (e.g., Lister 1981) confirm that certain kinds of invertebrates are not equally distributed vertically at El Verde. A total of 4506 invertebrates representing fifteen orders and 105 families (table 6.4) was collected over the ten-day, eight-night sampling period. Diptera constituted the most abundant insect group (89%), followed by Hymenoptera (5%), Homoptera (2%), and Coleoptera (1%) (table 6.5). Phorid flies representing several species made up 75% of the en-

Height (m)	1	2	3	11	5	19	14	15	4	9	13	7	17	6	12	16	8	10	18
$\bar{X}$	839.5	340.5	177.5	70	69.5	69	61	60	59	55.5	55	53.5	52	52	51.5	50	50	49	40.5

Figure 6.2. Sum of Squares-Simultaneous Test Procedures (SS-STP) for differences of mean numbers of insects along 1 m height intervals. Horizontal lines indicate ranges over which differences are nonsignificant.

tire invertebrate fauna and were obviously the dominant group during the sampling period. Diptera comprised the most families (twenty-seven), followed by Coleoptera (twenty) and Hymenoptera (nineteen).

There were significant differences among the mean numbers of invertebrates collected at the nineteen heights ($F_{[0.01](18,19)} = 6.68$, $p < .001$). An SS-STP test (fig. 6.2) showed the first 2 m to contain a significantly greater number of invertebrates than did the upper 17 m. The Phoridae likewise showed significant differences in mean numbers collected along the 19 m ($F_{[0.01](18,19)} = 6.68$, $p < .001$) and were the major factor contributing to the differences observed among total invertebrate groups. An SS-STP test of phorids showed the same results as for all trapped invertebrates. When all invertebrates minus the Phoridae were compared no mean differences were detected.

Members of the superfamily Fulgoroidea (Delphacidae through Issidae, app. 6), or plant hoppers, are conspicuous herbivores in the rain forest. Though they are often seen and collected in sweep-net and D-Vac samples near the ground, more of these insects were found near the canopy than below. When the 19 m strata were divided into three equal samples of 6 m (the first meter sample was deleted because it had so few specimens, and to equalize sample sizes, i.e., numbers of cups), a significant difference was observed between the top 6 m and the lower 12 m (fig. 6.3).

The small, inconspicuous Diptera appear to be the most abundant insects on a regular basis. Studies reported by Drewry (1969a) and Snyder et al. (1987) showed Diptera to make up 91% and 63% of all insects collected in their mosquito light trap and sticky-trap samples at El Verde and El Yunque, respectively. Similarly, Penny and Arias (1981), after a year of light and trap sampling in the Amazonian rain forest, found 84 to 91% of the invertebrates to be Diptera, primarily *Luzomyia* spp. (Psychodidae). Phorid flies were the most abundant Diptera trapped at the tower. Phorids are a large group with varied habits. Adults and larvae probably feed on decaying organic matter, which explains their greater numbers near the ground. Phorids collected at 1 m above ground during separate twenty-four-hour periods ranged from zero to 913. Next to phorids, the nematoceran families (Tipulidae through Cecidomyiidae) were the most common insects trapped. Their numbers were relatively constant throughout the 19 m. Large invertebrates, such as drag-

Height (m)	2 - 7	8 - 13	14 -19
$\bar{X}$	4.5	4.5	28

Figure 6.3. Sum of Squares-Simultaneous Test Procedures (SS-STP) for differences of mean numbers of fulgoroids per 6 m height interval (above lowest 1 m). Horizontal lines indicate ranges over which differences are nonsignificant.

onflies and butterflies, were absent from our samples and may have avoided the traps or escaped.

Sutton (1983), in conducting a vertical census in a rain forest in Sulawesi, found higher numbers of Homoptera, Hemiptera, Lepidoptera, Diptera, Hymenoptera, and Coleoptera in the upper canopy than in the understory. Erwin (1982, 1983a) believes that tropical canopies, when adequately sampled, will yield dramatic increases in the number of species.

Erwin (1983b) found low degrees of vagility among canopy Coleoptera in the Amazonian rain forest. This resulted in each forest type harboring its own assemblage of species. Even if this is true for most Coleoptera, we suspect that more vagile insects, such as macrolepidoptera and Homoptera, are more widely distributed. Dispersion of such insects also may be influenced by wind and rugged terrain patterns such that neighboring tree crowns are not in close proximity to each other. Sutton (1983), for example, found intercrown diversity to be fairly uniform for Homoptera.

Among ants, *Pheidole moerens* appears to be primarily a litter species, as we have taken it commonly in litter traps. It is consumed most commonly by the ground-dwelling anole, *A. gundlachi*. *Myrmelachista ramulorum*, on the other hand, appears to be primarily an arboreal species. It constitutes the greatest number of Formicidae consumed by the arboreal anole, *A. stratulus*, but is rarely found in stomachs of *A. gundlachi* (see Reagan, this volume). Further, we have collected specimens of *M. ramulorum* from birds which use them to smear formic acid over their feathers to help ward off ectoparasites. The most common ant species, *Linepithema mellea* (formerly *Iridomyrmex melleus*), is found from litter to canopy. We have taken them in litter traps and in sticky traps in the canopy, and they are consumed by anoles that occur from ground to canopy.

ENERGY FLOW AND NUTRIENT CYCLING

Estimation of energy and nutrient flow in the forest canopy is hindered by the difficulty of sampling that assemblage. We are aware of no studies that provide nutrient cycling data for arboreal neotropical ecosystems. Schowalter et al. (1981), in assessing herbivore consumption in a temperate zone forest, used 2.5 ± 3.2 mg dry sap mg^{-1} dry insect d^{-1} as an average consumption rate for sucking herbivores. This figure was extrapolated from previous papers. They estimated that 100 to 200 kg ha^{-1} yr^{-1} of foliage biomass was consumed by sucking insects. This number is higher than the 60 to 70 kg ha^{-1} yr^{-1} measured for chewing herbivores and indicates that Homoptera can be important primary consumers.

SUMMARY

Aboveground invertebrates occupy many trophic roles in the El Verde food web. Their contribution to nutrient cycling roles within the forest is emphasized by their great diversity compared to vertebrates. Although over 1,500 invertebrate species have been recorded at El Verde, diversity is poor compared to comparable mainland ecosystems. For example, ten species of Odonata are found at El Verde compared to over 130 species recorded from a rain forest site in Brazil; sixty-four species of auchenorrhynchous Homoptera are found at El Verde compared to 120 from a site in Sulawesi; and 234 species of Lepidoptera are found at El Verde compared to 3,142 and 1,577 species from sites in Costa Rica and New York, respectively. Although the rain forest at El Verde is superficially similar to mainland tropical rain forests, Puerto Rico is lacking in characteristic families and subfamilies present in these mainland tropical ecosystems. Well-known Neotropical families such as Calopterygidae, Polythoridae, Platystictidae, and Perilestidae (all Odonata) and Brassolinae, Morphinae, Ithomiinae, and Saturniidae (all Lepidoptera) are lacking at El Verde. Intensive, long-term studies have been conducted for only two groups of invertebrates. Snails and the walking stick, *Lamponius portoricencis,* allow evaluation of the effects of disturbance on population dynamics. Three species of snails, *Austroselenites alticola, Megalomastoma croceum,* and *Subulina octana,* were found to be primarily ground dwellers that were equally suited to forest cover and light gaps. Two others, *Nenia tridens* and *Caracolus caracolla,* occurred primarily on plant material above the forest floor during the wet season but respond differently to light gaps. *Caracolus caracolla* was more common in the forest, but *N. tridens* was more likely to be associated with light gaps. The arboreal walking stick, *L. portoricencis,* was found distributed among their food plants where they moved little (0.5 m d^{-1}). Hurricane Hugo had a profound effect on the densities of these organisms. Most suffered population reductions of up to 75%.

Seasonal variation in invertebrate populations occurs at El Verde. Sticky-trap studies conducted over a two-week period at El Verde documented an abrupt increase and decrease of phorid flies indicating a synchronous emergence. Greater insect abundance was detected during the onset of the rainy season. Increases in numbers were detected from passive (sticky-trap) collections as well as from an assessment of *E. coqui* and *Anolis* stomach contents.

Trophic relationships for most of the invertebrate taxa at El Verde can only be generalized from comparison with known feeding habits of similar taxonomic categories. El Verde has a diversity of polyphagous herbivores (snails, cockroaches, crickets, katydids, walking sticks, bark lice, and various sucking insects), monophagous herbivores (many beetles, moths, and butterflies), generalized predators (Lampyrid beetles), and parasites and parasitoids (parasitic wasps and flies, blood sucking flies). Data gleaned primarily from sticky-trap samples, gut analyses of nocturnal frogs and diurnal *Anolis* lizards, and personal observations at El Verde indicate variation in diurnal activity patterns for some groups of invertebrates. Cockroaches, tree crickets, walking sticks, and Lepidoptera larvae appear to be more common at night, when they probably feed; other invertebrates, such as various flies, are more active during the day. Some species such as the snail, *C. caracolla,* and the walking stick, *L. portoricensis,* are usually inactive during the day and feed primarily at night, although they may feed during frequent showers during the day. Vertical stratification of invertebrates occurs for some groups of insects. Plant hoppers were more abundant in the upper story of the forest, whereas others, such as adult phorid flies, were most common in the understory. Of three abundant ants, one, *Myrmelachista ramulorum,* is arboreal, another, *Pheidole moerens,* occurs in the litter on the forest floor, and *Linepithema mellea* (formerly *Iridomyrmex melleus*) occurs from canopy to forest floor.

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Appendix 6 Foraging Status of Invertebrates at El Verde

Taxon	Foraging location (see notes on p. 245)			
Class ADENOPHOREA (Nematoda)				
(many species)*	S	L	U	C?
Class SECERNENTEA (Nematoda)				
(many species)*	S	L	U	C
Class GASTROPODA				
Order Archaeogastropoda				
Helicinidae				
Alcadia alta			U	
Alcadia n. sp. 1			U	
Alcadia striata			U	
Alcadia n. sp. 2			U	
Order Mesogastropoda				
Cyclophoridae				
*Megalomastoma croceum**	S	L		
Megalomastoma verruculosum		L		
Pomatiasidae				
Chondropoma riisei			U	
Chondropoma yunquei			U	
Order Systellommatophora				
Veronicellidae				
Vaginulus occidentalis		L	U	
Order Stylommatophora				
Camaenidae				
*Caracolus caracolla**		L	U	
Caracolus marginella		L	U	
Polydontes lima		L?	U	
Polydontes luquillensis		L	U	
*Polydontes acutangula**			U	
Cepolidae				
Cepolis squamosa		L	U	
Helicarionidae				
Habroconus ernsti		L	U	
Zonitidae				
Nesovitrea subhyalina		L	U	
Sagdidae				
Hyalosagda selenina		L	U	
Platysuccinea portoricensis		L	U	
Thysanophora plagioptycha		L		
Yunquea denselirata		L		
Bulimulidae				
*Gaeotis nigrolineata**			U	
Clausiliidae				
*Nenia tridens**		L	U	
Subulinidae				
Lamellaxis gracilis		L		
Lamellaxis micra		L		
Leptinaria unilamellata		L		
Obeliscus terebraster		L		
Obeliscus swiftianus		L		
Obeliscus hasta		L		
Opeas alabastrinum		L		

Taxon	Foraging location			
Opeas pumilum		L		
Subulina octana		L		
Haplotrematidae				
Austroselenites alticola		L		
Oleacinidae				
Oleacina glabra			U	
Oleacina playa			U	
Oleacina interrupta			U	
Zonitidae				
Glyphyalinia indentata		L		
Euconulidae				
Guppya gundlachi		L		
Gastrodontidae				
Striatura meridionalis			U	
Zonitoides arboreus		L		
Limacidae				
Deroceras laeve		L		
Pupillidae				
Pupisoma minus			U	
Pupisoma dioscoricola			U	
Vertigo hexodon		L	U	
Class OLIGOCHAETA				
Order Haplotaxida				
Megascolecidae				
Pheretina hawayana *	S			
Class ONYCHOPHORA				
Peripatidae				
Peripatus juanensis		L		
Class ARACHNIDA				
Order SCORPIONIDA				
Buthidae				
Tityus obtusus		L	U	
Order PSEUDOSCORPIONIDA				
Menthidae				
Menthus sp.*		L		
Ideoroncidae (1 sp.)*		L		
Order SCHIZOMIDA				
Schizomidae				
Schizomus portoricensis		in termite mounds		
Schizomus yunquensis		L		
Order AMBLYPYGIDA				
Charinidae				
Charinides sp.		L		
Phrynidae				
Phrynus longipes *	understory (tree trunks), rock substrate			
Order ARANEAE				
Dipluridae				
Masteria petrunkevitchi *			U	
Barychelidae				
Trichopelma corozali		L	U	
Theraphosidae				
Avicularia laeta				C
Ischnocolus culebrae		L	U	
Scariidae				
Loxosceles carribbaea			U	

Taxon	Foraging location		
Ochyroceratidae			
Ochyrocera sp.		U	
Theotima sp. (possibly *radiata*)*	L		
Pholcidae			
Micromerys dalei			C
Modisimus montanus *		U	C (rarel
Modisimus signatus *		U	
Caponiidae			
Caponina sp.		U	
Nops sp.	L		
Oonopidae			
Dysderina sp.	L		
Oonops spinimanus	L		
Triaeris stenopsis	L		
Mimetidae			
Mimetus portoricensis		U	
Uloboridae			
Miagrammopes animotus *			C
Theridiidae			
Achaearanea porteri		U	
Argyrodes caudatus		U	
Argyrodes exiguus		U	
Argyrodes nephilae		U	
Theridiosomatidae			
Ogulnius gloriae	L		
Theridiosoma nechdomae	L		
Wendilgarda clara	L		
Wendilgarda theridionina	L		
Linyphiidae			
Centromerus ovigerus	L	C	
Tetragnathidae			
Leucauge moerens		U	
Leucauge regnyi *		U	C
Tetragnatha tenuissima		U	
Araneidae			
Agryiognatha gloriae		U	
Alcimosphenus borinquenae		U	
Capichameta hamata		U	
Cyclosa caroli		U	
Cyclosa walckenaeri		U	
Edricus crassicauda		U	
Eriophora edax		U	
Eustala sp.	L		
Gasteracantha cancriformis		U	C
Micrathena militaris		U	
Nephila clavipes		U	
Verrucosa arenata		U	
Hahniidae			
Neohahnia ernesti	L		
Anyphaenidae			
Hibana tenuis		U	
Wulfila macropalpus	L	U	
Wulfila tropica		U	
Wulfila sp.	L		
Clubionidae			
Clubiona portoricensis	L		

Taxon	Foraging location			
?Liocranidae				
Phrurolithus sp.		L		
Corinnidae				
Corinna jayuyae		L		
Trachelas borinquensis		L		
Gnaphosidae				
Lygromma sp.		L		
Ctenidae				
Oligoctenus ottleyi *		L		
Selenopidae				
Selenops sp. (probably *lindborgi*)		L		
Heteropodidae				
Olios antiguensis			U	C
Pseudosparianthus jayuyae		L		
Stasina portoricensis *		L	U	
Thomisidae				
Epicaudus mutchleri			U	
Misumenops bulbulcus			U	
Salticidae				
Corythalia gloriae			U	
Emanthis portoricensis			U	
Emanthis tetuani			U	
Lyssomanes portoricensis			U	
Order OPILIONES				
Cosmetidae				
Neocynortoides obscura			U	
Cynorta v-album *			U	
Phalangoididae				
Stygnomma spinula			U	
Pseudomitraceras minutus			U	C
At least 4 other sp.			U	C
Order ACARINA				
Suborder Metastigmata				
Argasidae				
Ornithodoros sp.	on bat host: *Erophylla sezekorni*			
Suborder Mesostigmata				
Ameroeseiidae? (at least 1 sp.)		L	U	
Ologamasidae (at least 1 sp.)		L	U	
Phytoseiidae (at least 1 sp.)			U	
Podocinidae (at least 1 sp.)		L		
Spelaeorhynchidae				
Spelaeorhynchus monophylli	on bat host: *Monophyllus redmani*			
Spelaeorhynchus sp.	on bat hosts: *Artibeus jamaicensis, Monophyllus redmani*			
Spinturicidae				
Periglischrus iheringi	on bat hosts: *Artibeus jamaicensis, Stenoderma rufum*			
Periglischrus vargasi	on bat host: *Artibeus jamaicensis*			
Periglischrus sp.	on bat hosts: *Erophylla sezekorni, Monophyllus redmani*			
Spinturnix sp.	on bat host: *Eptesicus fuscus*			
Uropodidae		L		

Taxon	Foraging location			
Suborder Prostigmata				
Eupodidae (at least 1 sp.)		L		
Suborder Astigmata				
Labidocarpidae				
Paralabidocarpus artibei	on bat hosts: *Artibeus jamaicensis, Stenoderma rufum*			
Paralabidocarpus foxi	on bat host: *Stenoderma rufum*			
Paralabidocarpus stenodermi	on bat host: *Stenoderma rufum*			
Suborder Cryptostigmata				
Cymbaeremaidae				
Scapheremaeus sp.		L		
Dampfiellidae				
Beckiella sp.		L	U	
Eremulidae				
Eremulus sp.		L	U	
Galumnidae				
Acrogalumna/Allogalumna group		L	U	
Haplozetidae				
Haplozetes sp.		L	U	
Rostrozetes sp.		L	U	
Malaconothridae				
Trimalaconothrus sp.		L	U	
Oppiidae				
Oppia (*sensu latu*) sp.		L	U	
Phthiracaridae				
Hoplophorella sp.		L	U	
Plasmobatidae				
Orbiculobates sp.		L	U	
Scheloribatidae				
Scheloribates sp.		L	U	
Trhypochthoniidae				
Afronothrus sp.		L	U	
Allonothrus sp.		L	U	
Class CRUSTACEA				
Order ISOPODA				
Oniscidae				
Philoscia richmondi *		L	U	
Porcellionides sp. ? *		L	U	
Sphaeroniscus portoricensis		L		
Synuropus granulatus		L		
Order PODOCOPA (1 sp. ?) *	S	L		
Subclass COPEPODA (1 sp. ?) *	S	L		
Order DECAPODA				
Pomamonidae				
Epilobocera situatifrons		L		
Class CHILOPODA				
Order Scutigeromorpha				
Scutigeridae				
Antillora portoricensis		L		
Order Lithobiomorpha				
Henicopidae (1 sp.)		L		
Order Scholopendromorpha				
Cryptopidae				
Scolopocryptops ferrugineus		L		

Taxon	Foraging location			
Scolopendridae				
*Scolopendra alternans**		L	U	C
Class DIPLOPODA				
Order Polyxenida				
Lophoproctidae				
Lophoturus niveus		L		
Order Glomeridesmida				
Glomeridesmidae				
*Glomeridesmus marmoreus**		L		
Order Polydesmida				
Cryptodesmidae				
*Docodesmus maldonadoi**		L		
Liomus obscurus		L		
Liomus ramosus		L		
Stylodesmidae				
Styraxodesmus juliogarciai		L		
Chelodesmidae				
Ricodesmus stejneri		L		
Vanhoeffenidae		L		
Agenodesmus reticulatus				
Paradoxosomatidae				
Orthomorpha coarctata		L		
Order Spirobolida				
Spirobolellidae				
*Spirobelellus richmondi**		L		
Order Spirostreptida				
Epinannolenidae				
Epinannolina trinidadensis		L		
Order Stemmiulida				
Stemmiulidae				
*Prostemmiulus heatwoli**		L		
Order Siphonophorida				
Siphonophoridae				
Siphonophora portoricensis		L		
Class PAUROPODA (1 sp.)		L		
Class ELLIPURA				
Order COLLEMBOLA				
Sminthuridae				
Ptenothrix sp.	S	L		
Sphyrotheca sp.	S	L		
1 other sp.	S	L		
Entomobryidae				
Drepanocyrtus sp.		L		
Dicranocentropha sp.*	S	L		
Dicranocentruga sp.	S	L		
Entomobrya sp.		L		
Liepdocyrtinus sp.		L		
Salina sp.		L		C
Isotomidae				
Proisotoma sp.	S	L		
1 other sp.	S	L		
Poduridae				
Pseudachorutes sp.	S	L		
1 other sp.	S	L		

Taxon	Foraging location		
Class INSECTA			
Order ARCHAEOGNATHA			
Machilidae (1 sp.)		U	
Order EPHEMEROPTERA			
Leptophlebiidae (1 sp.)		U	C
Order ODONATA			
Coenagrionidae			
Enallagma coecum		U	C
Telebasis vulnerata		U	C
Aeshnidae			
Aeshna psilus		U	C
Coryphaeschna viriditas		U	C
Gynacantha nervosa		U	C
Triacanthagyna septima		U	C
Triacanthagyna ?trifida		U	C
Libellulidae			
Erythrodiplax umbrata		U	C
Macrothemis celeno		U	C
Micrathyria didyma		U	C
Orthemis ferruginea		U	C
Scapanea frontalis		U	C
Order BLATTODEA			
Blattidae			
Pelmatosilpha coriacea	L	U	
Periplaneta australasiae	L	U	C?
Blattellidae			
*Aglaopteryx facies**	L	U	C
Aglaopteryx sp.			C
Cariblatta craticulata	L	U	
*Cariblatta hebardi**	L	U	C
Cariblatta plagia	L	U	
*Cariblattoides suave**	L	U	
Cariblattoides sp.	L	U	
*Epilampra wheeleri**	L	U	
Eurycotis sp.	L	U	
Neoblattella borinquensis	L	U	
Neoblattella vomer	L	U	
Neoblattella sp. a	L	U	
Neoblattella sp. b	L	U	
Plectoptera dorsalis	L	U	
*Plectoptera infulata**	L	U	
Pseudosymploce personata	L	U	
Pseudosymploce sp.	L	U	
Blaberidae			
Panchlora sagax	L	U	
Order ISOPTERA			
Termitidae			
*Nasutitermes costalis**		U	C
Nasutitermes nigriceps		U	C
Parvitermes discolor	L		
Kalotermitidae			
Glyptotermes ?pubescens		U	C
Order MANTODEA			
Mantidae			
Gonatista grisea		U	C

Taxon	Foraging location			
Order DERMAPTERA				
Carcinophoridae (1 sp.)		L	U	C
Labiidae (1 sp.)		L	U	C
Order ORTHOPTERA				
Acrididae				
Schistocerca colombina			U	
Tettigoniidae				
Phaneropterinae				
Anaulocomera laticauda			U	C
Microcentrum triangulatum			U	C
Turpilia rugosa			U	C
Copiphorinae				
Erioloides sp.			U	
Neoconocephalus triops			U	
Agraecinae (1 sp.)			U	
Conocephalinae				
Conocephalus cinereus			U	
Gryllacrididae				
Gryllacridinae				
Abelona sp.		L	U	
Gryllidae				
Phalangopsinae				
Amphiacusta caraibea *		L		
Gryllinae				
Anurogryllus muticus *		L		
Gryllus assimilis		L		
Trigonidiinae				
Cyrtoxipha gundlachi *			U	C
Anaxipha sp.*			U	C
Eneopterinae				
Orocharis vaginalis			U	C
Orocharis terebrans *			U	C
Orocharis sp. a			U	C
Orocharis sp. b			U	C
Orocharis sp. c			U	C
Orocharis sp. d			U	C
Laurepa krugii *			U	C
Tafalisca lurida			U	C
Nemobiinae (1 sp.)	S	L		
Gryllotalpidae				
Scapteriscus vicinus	S	L		
Order PHASMATODEA				
Heteronemiidae				
Pseudobacteria yersiniana			U	
Phasmatidae				
Agamemnon iphimedeia			U	
Diapherodes achalus			U	
Lamponius portoricensis *			U	
Order EMBIOPTERA			U	
Teratembiidae (1 sp.)				
Order PSOCOPTERA			U	C
Polypsocidae (1 sp.)*		L	U	C
Epipsocidae (3 spp.)*		L	U	C
Psocidae (2 spp.)*		L	U	C

Taxon	Foraging location		
Pseudocaeciliidae			
Pseudocaecilius pretiosus	L	U	
1 other sp.	L	U	
Psyllopsocidae (1 sp.)	L	U	C
Lepidopsocidae (1 sp.)	L	U	C
Pachytroctidae (1 sp.)	L	U	C
Liposcelidae			
Liposcelis divinatorius *	L		
Myopsocidae (1 sp.)	L	U	C
Order HEMIPTERA			
Veliidae (2 spp.)	water surface		
Belostomatidae			
Belostoma subspinosum	in water		
Schizopteridae (3 spp.)	L		
Dipsocoridae (1 sp.)	L	U	C
Enicocephalidae (1 sp.)	L	U	
Phymatidae (1 sp.)		U	
Miridae			
Itacoris trimaculatus		U	
Itacoris nigroculus		U	
Antias miniscula		U	
Pycnoderes heidemanni		U	
Pycnoderes quadrimaculatus		U	
Fulvius anthocorides		U	
Dagbertus sp.		U	
Collaria oleosa		U	
Rhinacloa pusilla		U	
Rhinacloa pallida		U	
Diphleps unica		U	
Phytocoris ricardoi		U	
Polymerus pallidus		U	C
Cyrtopeltis modesta		U	
Parthenicus nigrosquamis		U	
1 other sp.		U	
Reduviidae			
?*Ploiaria* sp.*	L	U	
Oncerotrachelus sp.		U	
Empicoris sp.		U	
Nabidae			
Neogorpis neotropicalis		U	
Lygaeidae			
Ozophora atropicta		U	C
Ozophora subimpicta		U	C
Ozophora sp.	L		C
Pachybrachius sp.		U	
Coreidae			
Phthia rubropicta		U	
1 other sp.		U	
Aradidae (2 spp.)	L		
Saldidae (1 sp.)	shores of streams		
Cydnidae			
?*Amnestus* sp.	L	U	C
Scutelleridae			
Pachycoris fabricia		U	

Taxon	Foraging location		
Pentatomidae			
Piezosternum subulatum		U	
Loxa pilipes		U	
Acrosternum marginatum		U	
Edessa cornuta		U	
Edessa parvinula		U	
Fecelia minor		U	
Order HOMOPTERA			
Superfamily CICADOIDEA			
Cicadidae			
Borencona aguadilla *		U	C
Membracidae			
Nessorchinus esbeltus			C
Cicadellidae			
Sibovea coffeacola *		U	C
Xestocephalus maculatus *	L	U	C
Xestocephalus sp. a		U	
Xestocephalus sp. b		U	
Cicadulina tortilla		U	
Hortensia similis		U	
Krisna insularis		U	
Deltocephalus flavicosta		U	
Ponana insularis			C
Protalebrella braziliensis		U	
Macrosteles fascifrons		U	
Tylozygus fasciatus		U	
Protalebra sp.		U	
Empoasca sp.		U	
Balclutha sp.		U	
Osbornellus sp.		U	
Graminella sp.		U	
Idiocerus parvulus		U	
Hybla maculata		U	
Superfamily FULGOROIDEA			
Cixiidae			
Bothriocera undata *		U	C
Oliaris slossonae		U	C
Pintalia alta *		U	C
Pintalia supralta *		U	C
Pintalia nemaculata *		U	C
Pintalia sp. nr. *nemaculata*		U	C
Pintalia martorelli		U	C
Pintalia osborni *		U	C
Pintalia sp.		U	C
Cubana tortriciformis		U	C
Delphacidae			
Ugyops osborni		U	C
Ugyops occidentalis *		U	C
Neomalaxa flava		U	C
Nilaparvata sp.		U	C
Abbrosoga sp.		U	C
Euidella sp.		U	C
Punana sp.		U	C
Derbidae			
Dysimia maculata *		U	C

Taxon	Foraging location		
Dawnaria sordidulum *		U	C
Dawnaria sp.		U	C
Patara albida		U	C
Cedusa wolcotti		U	C
Cedusa sp.		U	C
Otiocerus schonherri		U	C
Achilidae			
?*Amblycratus striatus*		U	C
Catonia cinerea *		U	C
Catonia dorsovittata *		U	C
Catonia arida *		U	C
Martorella puertoricensis		U	
Quadrana punctata		U	C
Tropiduchidae			
Ladellodes stali *		U	C
Ladellodes nepallata		U	C
Ladellodes or *Neurotmeta* sp.		U	C
Flatidae			
Petrusa epilepsis		U	C
Petrusa pivota		U	C
Petrusa torus		U	C
Petrusa rocquensis		U	C
Flatormenis pseudomarginata		U	C
Ilesia nefuscata		U	C
Puertormenis virgina		U	C
Melormenis antillarum		U	C
Melormenis basalis		U	C
Melormenis magna *		U	C
Pseudoflatoides albus		U	C
Issidae			
Thionia borinquensis		U	C
Colpoptera maculifrons		U	C
Colpoptera brunneus		U	C
Neocolpoptera monticolens		U	C
Neocolpoptera puertoricensis		U	C
Acanalonidae			
Acanalonia agilis		U	C
Acanalonia vivida		U	C
Kinnaridae			
Quilessa fasciata		U	C
Superfamily PSYLLOIDEA			
Psyllidae (5 spp.)		U	C
Superfamily APHIDOIDEA			
Aphididae (1 sp.)		U	
Superfamily COCCOIDEA			
Coccidae			
Ceroplastes rubens		U	C
Ortheziidae (1 sp.)	L		
Diaspididae (1 sp.)	L		
Order THYSANOPTERA			
Phlaeothripidae			
At least 2 spp.*	L	U	C
Thripidae			
At least 8 spp.	L	U	C

Taxon	Foraging location			
Order NEUROPTERA				
Coniopterygidae (1 sp.)			U	
Mantispidae				
Mantispa sp.			U	
Climaciella cubana			U	
Hemerobiidae				
Nusalalia cubana			U	
Chrysopidae				
Chrysopa collaris			U	
Chrysopa nr. *cubana*			U	
Chrysopa sp. a			U	
Chrysopa sp. b			U	
Nodita sp.			U	
Ascalaphidae				
Ululodes opposita			U	
Order COLEOPTERA				
Suborder Adephaga				
Carabidae (5 spp.)		L		
Dytiscidae				
Copelatus posticatus	in water			
Suborder Polyphaga				
Hydrophilidae				
Enochrus debilis	in water			
Ptiliidae				
Actinopteryx sp.		L	U	C
Scydmaenidae (1 sp.)		L		
Silphidae (1 sp.)	S	L	U	
Scaphidiidae (1 sp.)				C
Staphylinidae				
Palaminus sp.				C
6 other spp.*	S	L		
Pselaphidae (4 spp.)*		L		
Histeridae				
Ormalodes ruficlavis			U	C
Opalides sp.			U	C
Passalidae (1 sp.)				
Paxillus crenatus		L	U	
Scarabaeidae				
Strategus oblongus		L	U	C
Phyllophaga portoricensis		L	U	C
Phyllophaga sp. a		L	U	C
Phyllophaga sp. b		L	U	C
Phyllophaga sp. c		L	U	C
Phyllophaga sp. d		L	U	C
Chalepides barbata		L	U	C
Canthonella parva		L	U	C
Canthochilum borinquensis		L	U	C
Canthochilum histeroides		L	U	C
Ataenius floridanus		L		
Dascillidae (3 spp.)			U	
Ptilodactylidae (at least 5 spp.)			U	
Chelonariidae (1 sp.)			U	
Limnichidae				
Limnichoderus insularis	in water			

Taxon	Foraging location		
Elmidae			
Neoelmis sp.	in water		
Phanocerus sp.	in water		
Elateridae			
Dicrepidius ramicornis		U	C
Pyrophorus luminosus	L	U	C
Platycrepidus sp.		U	C
2 other spp.		U	C
Throscidae (1 sp.)		U	C
Telegeusidae (1 sp.)		U	C
Lampyridae			
Callopisma borencona		U	C
Photinus triangularis		U	C
Photinus vittatus		U	C
Photinus dubiosus		U	C
Photinus sp.*	L	U	C
Cantharidae			
Tylocerus barberi		U	C
Lycidae (4 spp.)		U	
Dermestidae (1 sp.)		U	
Anobiidae (2 spp.)		U	C
Trogositidae (1 sp.)		U	C
Cleridae (2 spp.)		U	
Nitidulidae			
Europs maculata	L	U	
1 other sp.	L	U	
Rhizophagidae (1 sp.)		U	
Cucujidae (at least 3 spp.)	L	U	C
Cryptophagidae (1 sp.)		U	
Phalacridae (1 sp.)		U	
Coccinellidae			
Curinus sp.		U	
2 other spp.	L	U	C
Endomychidae (2 spp.)		U	
Tenebrionidae (at least 3 sp.)	L	U	
Colydiidae (1 sp.)	L	U	C
Oedemeridae (1 sp.)		U	
Melandryidae (1 sp.)		U	C
Mordellidae (1 sp.)		U	C
Euglenidae (at least 2 spp.)		U	C
Cerambycidae			
Parandrinae			
Parandra cribrata	L	U	C
Prioninae			
Callipogon proletarius	L	U	C
Derancistrus thomae	L	U	C
Stenodontes exsertus	L	U	C
Lepturinae			
Bellamira scalaris		U	C
Cerambycinae			
Brittonella chardoni		U	C
Chlorida festiva	L	U	C
Elaphidion tomentosus		U	C
Methia necydalea		U	C
Neoclytus araneiformis	L	U	C

Taxon	Foraging location		
Lamiinae			
Batocera rubis	L	U	C
Leptostylus antillarum		U	C
Leptostylus longicornis		U	C
Leptostylus oakleyi		U	C
Lagochirus araneiformis		U	C
Nanilla sp.		U	C
Oreodera prob. *glauca*		U	C
Proecha spinipennis		U	C
Typanidius nocturnus	L	U	C
Distenidae			
Distenia darlingtoni		U	C
Chrysomelidae			
Diabrotica sp.		U	
2 other spp.	L	U	C
Platypodidae (1 sp.)		U	C
Scolytidae			
Ambrosiodmus hagedorni		U	C
Coccotrypes carpophagus	L	U	C?
Corthylus papulans		U	C
Xyleborus affinis *	L	U	C
Xyleborus ferrugineus *	L	U	C
Xlyeborus sp.		U	
at least 2 other spp.	L	U	C
Brentidae			
Stereodermus sp. 1	probably U on tree trunks		
Belophorus maculatus	U, on tree trunks		
Belophorus sp.		U	
Brentus volvulus	U, on tree trunks and branches		
Anthribidae			
Homocloeus? conspersus?		U	
Ormiscus sp. 1		U	
Ormiscus sp. 2		U	
Phaenotheriopsis conciliatus		U	
Phaenotheriopsis sp.		U	
Euxenus? sp. 1	L	U	
Genus? (was *Neanthribus*)		U	C
Attelabidae			
Attelabinae			
Euscelus biguttatus		U	
Euscelus dentipes		U	
Euscelus sexmaculatus		U	
Rhynchitinae			
Auletobius sp. 1		U	C
Pselaphorhynchites sp. 1		U	C
Apionidae			
Cylas formicarius elegantulus		U	
Apion martinezi		U	
Apion oakleyi		U	
Apion salarium		U	
Apion subaeneum		U	
Apion sp. 1		U	
Apion sp. 2		U	
Curculionidae			
Apodrosus argentatus		U	C
Apodrosus wolcotti		U	C

Taxon	Foraging location		
Polydrosinae			
Polydacrys depressifrons		U	
Artipus sp. 1		U	
Menoetius coffeae montanus		U	
Menoetius curvipes		U	
Menoetius trilineatus		U	
Menoetius yaucona?		U	
Pachnaeus psittacus		U	
Compsus luquillo		U	C
Compsus mariacao		U	C
Diaprepes abbreviatus		U	
Diaprepes maugei		U	
Exophthalmus quindecimpunctatus		U	
Exophthalmus roseipes		U	C
Exophthalmus sphacelatus?		U	
Exophthalmus sp. 1		U	C
Molytinae			
Heilipus elegans		U	C
Conotrachelus seniculus		U	C
Conotrachelus sp. 1		U	
Conotrachelus sp. 2		U	
Conotrachelus sp. 3		U	
Anchonus sp. 1	L	U	
Anchonus sp. 2	L	U	
Smicronyx sp. 1		U	
Smicronyx sp. 2		U	
Pantoteloides sp. 1	L	U	
Derelomus? albidus?		U	
Notolomus sp. 1		U	
Phyllotrox? pallidus		U	
Nanus uniformis	L	U	
Micromyrmex pulicarius		U	
Sicoderus sp. 1		U	C
Anthronomus albocapitis		U	C
Anthonomus alboannulatus		U	C
Anthonomus annulipes		U	
Anthonomus convexifrons		U	C
Anthonomus costulatus		U	
Anthonomus dentipes		U	
Anthonomus flavus		U	
Anthonomus incanus		U	
Anthonomus nigrovarigatus?		U	
Anthonomus sp. 1		U	
Anthonomus sp. 2		U	
Pseudanthonomus sp. 1		U	
Tychiinae			
Lygnyodes sp. 1		U	
Sibinia aliguantula		U	
Sibinia pulcherrima		U	
Sibinia setosa		U	C
Sibinia sp. 1		U	
Pyropinae			
Pyropus sp. 1		U	
Cryptorhynchinae			
Pseudomus militaris		U	C
Pseudomus sp. 1		U	

Taxon	Foraging location		
	L	U	C
Tyloderma danforthi	L	U	
Euscepes porcellus		U	C
Euscepes postfasciatus		U	C
Neoulosomus sp. 1		U	
Neoulosomus sp. 2		U	
Cryptorhynchus? sp. 1		U	
Cryptorhynchus? sp. 2		U	
Pseudomopsis cucubano?		U	C
Pseudomopsis sp. 1		U	C
Pseudomopsis sp. 2		U	C
Pseudomopsis sp. 3		U	C
Pseudomopsis sp. 4		U	C
Pseudomopsis 4–5 more spp.	L	U	
Macromerus sp. 1		U	C
Sternocoelus armipes		U	C
Eubulus sp. 1		U	C
Zygopinae			
Lechriops psidii		U	C
Lechriops sp. 1		U	C
Ceutorhynchinae			
Hypurus bertrandi		U	
Auleutes insepersus		U	
Panophthalmus puertoricanus		U	
Baridinae			
Peridinetus concentricus		U	C
Peridinetus signatus		U	
Baris torquata		U	
Ampeloglypter cissi		U	
Geraeus? montanus		U	
Anacentrinus sp.		U	
Rhynchophorinae			
Sphenophorus sp.		U	
Metamasius hemipterus	? Taken on bananas in market in El Verde		
Cosmopolites sordidus	? Taken with *Metamisius* above		
Sitophilus granarius		U	
Stiophilus linearis	U, in grain at pet store		
Sitophilus oryzae	In grain and flour products		
Cossoninae			
Cossonus impressus	U, under bark		
Decuanellus pecki	L		
Decuanellus sp. 2	L		
Decuanellus sp. 3	L		
Caulophilus oryzae	L		C
Stenotrupis acicula	L		
Stenancylus sp. 1		U	C
Micromimus sp. 1	L	U	
Dryophthorinae			
Dryophthorus sp. 1	L		
Order TRICHOPTERA			
Philopotamidae			
Chimarra albomaculata		U	C
Chimarra maldonadoi		U	

Taxon	Foraging location		
	L	U	C
Psychomyiidae			
Antillopsyche tubicola		U	
Xiphocentron borinquensis		U	
Polycentropodidae			
Cernotina mastelleri		U	
Polycentropus zaneta		U	
Hydropsychidae			
Smicridea protera		U	
Rhyacophilidae			
Atopsyche trifida		U	
Glossosomatidae			
Cariboptila orophila		U	
Cariboptila trispinata		U	
Hydroptilidae			
Hydroptila martorelli		U	
Ochrotrichia juana		U	
Ochrotrichia marcia		U	
Ochrotrichia squamigera		U	
Ochrotrichia ceer		U	
Oxyethira janella		U	
Oxyethira puertoricensis		U	
Alisotrichia circinata		U	
Alisotrichia hirudopsis		U	
Alisotrichia setigera		U	
New genus, sp.		U	
Helicopsychidae			
Helicopsyche minima		U	
Helicopsyche ramosi		U	
Calamoceratidae			
Phyllocius pulchrus		U	
Leptoceridae			
Nectopsyche sp.		U	
Order LEPIDOPTERA			
Tineidae			
Tiquadra aeneonivella		U	
Acropholus sp. a*		U	
Acropholus sp. b*		U	
Acropholus sp. c*		U	
Acropholus sp. d*		U	
Acropholus sp. e*		U	
Acropholus sp. f*		U	
Acropholus sp. g*		U	
Acropholus sp. h*		U	
Acropholus sp. i*		U	
?Gracillariidae (at least 1 sp.)		U	C
Oecophoridae			
Ethmia zanthorrhoa		U	
Blastobasidae (1 sp.)		U	
?Cosmopterygidae (1 sp.)		U	C
Gelechiidae			
Dichomeris sp.	L	U	C
Alucitidae			
Orneodes sp.		U	
Cossidae			
*Psychonoctua personalis**		U	

Taxon	Foraging location	
Tortricidae		
Eulia sp. a	U	
Eulia sp. b	U	
Bactra sp.	U	
1 other sp.	U	
Hesperiidae		
Panoquina nero	U	
Perichares phocion	U	
Perichares philetes	U	
Choranthus vittellius	U	
Urbanus dorantes	U	
Proteides mercurius	U	
Epargyreus zestis	U	
Pyrgus syrichtus	U	
Wallengrenia otho druryi	U	
Papilionidae		
Papilio pelaus	U	C
Pieridae		
Dismorphia spio *	U	C
Phoebis sennae	U	C
Phoebis phileae	U	C
Phoebis trite	U	C
Phoebis argante	U	C
Eurema portoricensis	U	C
Nymphalidae		
Heliconiinae		
Heliconius charitonius	U	C
Dryas julia	U	C
Satyrinae		
Calisto nubila	U	C
Charaxinae		
Prepona antimache	U	C
Apaturinae		
Adelpha gelania	U	C
Nymphalinae		
Marpesia petreus	U	C
Hypanartia paullus	U	C
Anartia jatrophe	U	C
Siproeta stelenes	U	C
Lycaenidae		
Chlorostrymon maesites	U	C
Electrostrymon angelica	U	C
Megalopygidae		
Megalopyge krugii *	U	
Pyralidae		
Pyraustinae		
Sparagmia gigantalis *	U	
Pantographa limata	U	
Terastia meticulosalis	U	
Azochis rufidiscalis	U	
Margaronia flegia	U	
Margaronia costata	U	C
Margaronia elegans *	U	
Margaronia nitidalis	U	
Margaronia marginepuncta	U	
Margaronia sibillalis	U	

Taxon	Foraging location
Margaronia sp.	U
Sylepta onophasalis	U
Sylepta elevata	U
Sylepta ceresalis	U
Sylepta silicalis	U
Sylepta sp. a	U
Sylepta sp. b	U
Pycnarnon receptalis	U
Mesocondyla concordalis	U
Mesocondyla sp.	U
Crocidolomyia palindalis	U
Neoleucinodes elegantalis	U
Pyrausta cerata	U
Pyrausta cardinalis	U
Pyrausta sp.	U
Phostria humeralis	U
Phostria simialis	U
Phostria prolongalis	U
Desmia tages *	U
Desmia ufeus	U
Maruca testulalis	U
Pilocrocis ramentalis	U
Pilocrocis infuscalis	U
Pilocrocis lauralis	U
Epipagis mopsalis	U
Syngamia florella	U
Syngamia cassidalis	U
Syngamia sp.	U
Herpetogranma phaeropteralis	U
Herpetogranma perusialis	U
Lygropia lelex	U
Bradina hemingalis	U
Hileithia ductalis	U
Diasemia ramburialis	U
Samea carrelalis	U
Lamprosema zoilusalis	U
Lamprosema indicata	U
Lamprosema stenialis	U
Lineodes metagrammalis	U
Argyractis serapionalis	U
Argyractis sp. a	U
Argyractis sp. b	U
Cataclysta sumptiosalis	U
Cataclysta miralis	U
Scoparia sp.	U
Gonopionea sp.	U
Condolorrhiza sp. a	U
Condolorrhiza sp. b	U
Undulambia sp.	U
Pyralinae	
Pyralis manihotalis	U
Epipaschiinae	
Jocara ferrifusalis	U
Jocara sp.	U
Tetralopha scabridella	U

Taxon	Foraging location
Tetralopha sp.	U
Pococera atramentalis	U
Crambinae	
Argyria lacteela	U
Diatraea saccharalis	U
Crambus sp.	U
Chrysauginae	
Pachymorphus subductellus	U
Caphys bilinea	U
Parachma sp.	U
Schoenobiinae	
Rupela sp. a	U
Rupela sp. b	U
Rupela sp. c	U
Thyrididae	
Rhodoneura leuconotula	U
Rhodoneura thiastoralis	U
Rhodoneura myrsusalis	U
Pterophoridae	
Oidaematophorus basalis	U
Sphenarches caffer	U
Adaina sp. a	U
Adaina sp. b	U
Platyptilia sp.	U
Geometridae	
Microgonia vesulia	U
Sphaecelodes vulneraria	U
Semaeopus perletaria	U
Drepanodes hamata	U
Cambogia mexicaria	U
Racheospila sanctae-crucis	U
Racheospila gerularia	U
Racheospila herbaria	U
Racheospila sp.	U
Pleuroprucha rudimentaria	U
Hammaptera chloronotata	U
Tricentrogyna vinacea	U
Tricentrogyna floridora	U
Cloropteryx paularia	U
Sterrha sp.	U
Scopula sp. a	U
Scopula sp. b	U
Scopula sp. c	U
Psaliodes sp.	U
Bronchelia sp.	U
Phrygionis sp.	U
Semiothisa sp.	U
Sphingidae	
Manduca sexta	U
Erinnyis alope	U
Erinnyis ello	U
Pholus fasciatus	U
Xylophanes tersa	U
Pachylia ficus	U
Aellopos fadus	U

Taxon	Foraging location
Aellopos sp.	U
1 other sp.	U
Notodontidae	
Rifargia distinguenda	U
Proelymniotis aequipars	U
Disphragis baracoana	U
Disphragis sp.	U
Arctiidae	
Pericopinae	
Ctenuchida virginalis	U
Hyalurga vinosa	U
Arctiinae	
Eupseudosoma involutum	U
Ecpantheria icasia	U
Ecpantheria sp.	U
Utethesia ornatrix	U
Phegoptera bimaculata	U
Tricypha proxima	U
Lomuna negripuncta	U
Talaria sp.	U
Ctenuchinae	
Cosmosoma auge	U
Cosmosoma achemon	U
Lymire flavicollis	U
Correbida terminalis	U
Nyridela chalciope	U
Eunomia colombina	U
Euceron sp.	U
Noctuidae	
Blosyris mycerina	U
Ophisma tropicalis	U
Gonodonta sicheus	U
Gonodonta incurva	U
Mocis diffluens	U
Mocis megas	U
Prodenia pulchella	U
Prodenia rubrifusa	U
Prodenia eridania	U
Heliothis virescens	U
Eulepidotis addens	U
Heterochroma berylliodes	U
Heterochroma sp.	U
Ephrodes cacata	U
Sylectra erycata	U
Condica cupentia	U
Messala obvertens	U
Speocropia scriptura	U
Mastigophorus demissalis	U
Phlyctaina irregularis	U
Mamestra soligena	U
Gonodes liquida	U
Metalectra analis	U
Lascoria phormisalis	U
Anepischetos porrectalis	U
Anepischetos mactatalis	U
Phalaenophana eudorealis	U

Taxon	Foraging location	
Carteris oculatalis	U	
Callipistra floridensis	U	
Callipistra jamaicensis	U	
Plusia admonens	U	
Araeoptera vilhelmina	U	
Afrida tortriciformis	U	
Nymbis garnoti	U	
Leucania rosea	U	
Leucania sp.	U	
Plusiodonta sp. a	U	
Plusiodonta sp. b	U	
Calpe sp.	U	
Diptherigia sp.	U	
Bleptina sp. a	U	
Bleptina sp. b	U	
Antiblemma sp.	U	
Diomyx sp.	U	
Tortricoides orneodalis	U	
Tortricoides sp. a	U	
Tortricoides sp. b	U	
Thursania sp.	U	
Physula sp.	U	
Pseudaletia sp.	U	
Lascoria sp.	U	
Zale sp.	U	
Nola bistriga	U	
Order DIPTERA		
Suborder Nematocera		
Tipulidae*		
Tipulinae		
Dolichopeza puertoricensis	U	C?
Brachypremna unicolor	U	C?
Limoniinae		
Helius albitarsus	U	C?
Limonia diva	U	C?
Limonia gowdeyi	U	C?
Limonia cinereinota	U	C?
Limonia tibialis	U	C?
Limonia myersiana	U	C?
Limonia subrecisa	U	C?
Limonia rostrata antillarum	U	C?
Limonia tetraleuca	U	C?
Limonia domestica	U	C?
Limonia sp. k	U	C?
Limonia sp. hh	U	C?
Limonia willistoniana	U	C?
Limonia schwarzi	U	C?
Limonia sp. aa	U	C?
Limonia hoffmani	U	C?
Limonia divisa	U	C?
Limonia trinitatis	U	C?
Limonia sp. t	U	C?
Limonia sp. bb	U	C?
Atarba sp.	U	C?
Elephantomyia westwoodi	U	C?
Polymera geniculata pallipes	U	C?

Taxon	Foraging location	
Hexatoma sp. a	U	C?
Hexatoma sp. b	U	C?
Psiloconopa portoricensis	U	C?
Psiloconopa caliptera	U	C?
Teucholabis sp. gg	U	C?
Gonomyia pleuralis	U	C?
Gonomyia puer	U	C?
Gonomyia subterminalis	U	C?
Trentepohlia nivetarsis	U	C?
Trentepohlia sp. kk	U	C?
Shannonomyia leonardi	U	C?
Shannonomyia sp. p	U	C?
Shannonomyia sp. m	U	C?
Blephariceridae		
Paltostoma argyrocincta	U	
Mycetophilidae*		
Leia sp.	U	C?
Manota sp.	U	C?
Platyura sp. d	U	C?
Platyura sp. n	U	C?
Platyura sp. o	U	C?
Platyura sp. x	U	C?
Platyura sp. y	U	C?
Megopthalmida sp.	U	C?
Boletina incompleta	U	C?
Boletina sp.	U	C?
Neompheria sp.	U	C?
Zygomyia sp. h	U	C?
Zygomyia sp. aa	U	C?
Zygomyia sp. bb	U	C?
Zygomyia sp. cc	U	C?
Exechia sp. a	U	C?
Exechia sp. c	U	C?
Exechia sp. q	U	C?
Exechia sp. u	U	C?
Exechia sp. dd	U	C?
Rhymosia sp.	U	C?
Mycetophilia sp. f	U	C?
Mycetophilia sp. m	U	C?
Mycetophilia sp. p	U	C?
Mycetophilia sp. r	U	C?
Mycetophilia sp. s	U	C?
Mycetophilia sp. w	U	C?
Sciaridae (33 spp.)*	U	C
Cecidomyiidae (30 spp.)	U	C
Psychodidae (37 spp.)*	U	C
Scatopsidae		
Rhegmoclema sp.	U	C
Aldrovandiella sp.	U	C
Dixidae		
Dixa sp.	U	C?
Chaoboridae		
Chaoborus brasiliensis	U	C
Chaoborus sp. e	U	C
Chaoborus sp. c	U	C

Taxon	Foraging location		
Culicidae			
Toxorhynchites portoricensis		U	C
Aedes mediovittatus		U	C
Aedes taeniorhynchus		U	C
Aedes serratus		U	C
Culex nigripalpus		U	C
Culex pipiens quinquefasciatus		U	C
Culex sp.		U	C
Wyeomia sp.		U	C
Uranotaenia sp.		U	C
Mansonia flaveolus		U	C
Simuliidae (2 spp.)		U	C
Ceratopogonidae			
Monohelea johannseni		U	C
Culicoides hoffmani		U	C
Polpomyia sp. n		U	C
Atrichopogon sp. r		U	C
Atrichopogon sp. s		U	C
Atrichopogon sp. t		U	C
Stilobezzia bimaculata		U	C
Stilobezzia sp. h		U	C
Stilobezzia sp. q		U	C
Dasyhelea sp. b		U	C
Dasyhelea sp. e		U	C
Dazyhelea sp. ee		U	C
Dasyhelea sp. ff		U	C
Dasyhelea sp. jj		U	C
Forcipomyia glauca		U	C
Forcipomyia fuliginosa		U	C
Forcipomyia genualis		U	C
Forcipomyia corsoni		U	C
Forcipomyia pluvialis		U	C
Forcipomyia sp. a		U	C
Forcipomyia sp. c		U	C
Forcipomyia sp. d		U	C
Forcipomyia sp. f		U	C
Forcipomyia sp. g		U	C
Forcipomyia sp. j		U	C
Forcipomyia sp. k		U	C
Forcipomyia sp. l		U	C
Forcipomyia sp. v		U	C
Forcipomyia sp. x		U	C
Forcipomyia sp. y		U	C
Forcipomyia sp. aa		U	C
Forcipomyia sp. bb		U	C
Forcipomyia sp. cc		U	C
Forcipomyia sp. hh		U	C
Chironomidae			
Orthocladiinae			
Corynoneura sp. (near water)		U	
Cricotopus sp. (near water)		U	
Diplosmittia sp. (near water)		U	
Limnophyes sp. (near water)		U	
Parametriocnemus sp. (near water)		U	
Thienemanniella sp. (near water)		U	
Pseudosmittia sp. (near water)		U	

Taxon	Foraging location		
Unknown Orthoclad genus 1 (near water)		U	
Unknown Orthoclad genus 2 (near water)		U	
Chironomini			
Nilothauma? n. sp. (near water)		U	
Paralauterborniella? sp. (near water)		U	
Polypedilum sp. 1 (near water)		U	
Polypedilum sp. 2 (near water)		U	
Polypedilum sp. 3 (near water)		U	
Polypedilum sp. 4 (near water)		U	
Stenochironomus cf. *innocuus* (near water)		U	
Stenochironomus sp. 1 (near water)		U	
Xestochironomus furcatus (near water)		U	
Xestochironomus cf. *nebulosus* (near water)		U	
Tanytarsini			
Tanytarsus sp. 1 (near water)		U	
Tanytarsus sp. 2 (near water)		U	
Rheotanytarsus sp. (near water)		U	
Tanypodinae			
Ablabesmya sp. (near water)		U	
Dialmabatista sp. (near water)		U	
Labrundinia sp. (near water)		U	
Larsia sp. (near water)		U	
Pentaneura sp. (near water)		U	
About 50 unidentified spp.*	L	U	C
Suborder Brachycera			
Tabanidae			
Stenotabanus brunettii		U	
Rhagionidae (1 sp.)		U	
Xylophagidae (1 sp.)		U	
Stratiomyidae			
Hermetia illucens		U	
Hermetia sexmaculata		U	
Nothomyia nigra		U	
3 other spp.		U	
Asilidae			
Andrenosoma chalybeum		U	C
Empididae (6 spp.)		U	C
Dolichopodidae*			
Condylostylus graenicheri		U	C
Condylostylus flavicornis		U	C
Condylostylus sp. r		U	C
Condylostylus sp. d		U	C
Pelastoneurus sp.		U	C
Neurigona sp.		U	C
Thrypticus sp.		U	C
Chrysotus flavohirtus		U	C
Chrysotus sp. a		U	C
Chrysotus sp. c		U	C
Chrysotus sp. h		U	C
Chrysotus sp. j		U	C
Chrysotus sp. g		U	C
Chrysotus sp. l		U	C
2 other spp.		U	C
Phoridae			
Chaetopleurophora formosa		U	C?
Diploneura picea		U	C?

Taxon	Foraging location		
Macrocerides brevicornis		U	C?
Megaselia basichaeta		U	C?
Megaselia defecta		U	C?
Megaselia fausta		U	C?
Megaselia perspicua		U	C?
Megaselia subfava		U	C?
Megaselia subinflava		U	C?
Megaselia violata		U	C?
Metopina reflexa		U	C?
Pseudacteon simplex		U	C?
Puliciphora borinqensis		U	C?
Puliciphora parvula		U	C?
51 other spp.		U	C?
Syrphidae			
Meromacrus cinctus		U	
Ornidia obesa		U	
Eristalis cubensis		U	
Baccha capitata		U	
Baccha latiuscula		U	
Baccha deceptor		U	
Baccha parvicornis		U	
Baccha gracilis		U	
Baccha cylindrica		U	
Eristilis albifrons		U	
?*Mesograpta arcifera*		U	
Mesograpta sp. *verticalis* or *floralis*		U	
Mesograpta violacea		U	
Mesograpta sp.		U	
?*Parapenium banksi*		U	
Volucella tricincta		U	
Pipunculidae (1 sp.)		U	
Micropezidae			
Taeniaptera lasciva		U	
Taeniaptera sp.		U	
Systellapha scurra		U	
Systellapha sp.		U	
Neriidae (3 spp.)		U	
Lonchaeidae			
Lonchaea sp.		U	C
Silba sp.		U	C
Otitidae			
Euxesta thomae		U	
Euxesta sp.		U	
Tephritidae			
Anastrepha sp.		U	C
1 other sp.		U	
Clusiidae (3 spp.)	L	U	
Odiniidae			
Odinia biguttata	L	U	C
Agromyzidae			
Melanagromyza sp.		U	C
Milichiidae (2 spp.)		U	
Sepsidae			
Paleosepsis scabra		U	
Lauxaniidae			
Pseudogriphoneura albovittata		U	C

Taxon	Foraging location		
Pseudogriphoneura octopunctata		U	C
Pseudogriphoneura sp.		U	C
Neogriphoneura sordida		U	C
Poecilominettia picticornis		U	C
Sapromyza sp.		U	C
Minetta octopuncta		U	C
?Chamaemyiidae (1 sp.)		U	C
Heleomyzidae (1 sp.)		U	C
Sphaeroceridae (4 spp.)	L	U	
Curtonotidae (1 sp.)		U	C
Drosophilidae			
Drosophila sp. d		U	C
Drosophila sp. e		U	C
Drosophila sp. f		U	C
Aulacigaster sp.		U	C
4 other spp.		U	C
Ephydridae (1 sp.)		U	C
Chloropidae			
Oscinella lutzi		U	C
Pentanotaulax sp.		U	C
Muscidae			
Neomuscina sp.		U	C
Neodexiopsis ditiportus		U	C
Neodexiopsis rex		U	C
Neodexiopsis cavalata		U	C
Neodexiopsis discolorisexus		U	C
Neodexiopsis crassicrurus		U	C
Neodexiopsis maldonadoi		U	C
Bithoracochaeta sp.		U	C
4 other spp.		U	C
Calliphoridae			
Phaenica rica	L	U	C
Sarcophagidae			
Paraphrissopoda capitata		U	
Sarcophaga sp. a		U	
Sarcophaga sp. d		U	
11 other spp.		U	
Tachinidae			
Euphasiopteryx dominicana		U	
Eucletoria armigera		U	
Tachinophyta sp.		U	
At least 17 other spp.		U	C
Hippoboscidae (1 sp.)	On bats		
Streblidae			
Aspidoptera sp.	On bat host: *Artibeus jamaicensis*		
Megistropoda aranea	On bat host: *Artibeus jamaicensis*		
Icterophilia sp.	On bat host: *Monophyllus redmani*		
Trichobius sp. nr. *sparsus*	On bat host: *Monophyllus redmani*		
Trichobius sp.	On bat hosts: *Artibeus jamaicensis, Monophyllus redmani*		

Taxon	Foraging location		
Order HYMENOPTERA			
Suborder Apocrita			
Braconidae			
Apanteles carpatus		U	C
Heterospilus sp.		U	C
Xenarcha sp.		U	C
Ecphylus sp.		U	C
Orthostigma sp.		U	C
Spathius sp.		U	C
Macrocentrus sp.		U	C
Clinocentrus sp.		U	C
Ichneumonidae (4 spp.)		U	C
Mymaridae (13 spp.)*		U	C
Trichogrammatidae (3 spp.)		U	C
Eulophidae (14 spp.)*		U	C
Encyrtidae (7 spp.)		U	C
Eupelmidae (1 sp.)		U	C
Agaonidae			
Blastophaga sp.		U	C
Torymidae (1 sp.)		U	C
Pteromalidae (at least 1 sp.)		U	C
Cynipidae			
Hypolethria sp.		U	C
Kleidotoma sp.		U	C
2 other spp.		U	C
Ceraphronidae			
Ceraphron sp. a		U	C
Ceraphron sp. b		U	C
Ceraphron sp. c		U	C
Ceraphron sp. d		U	C
Ceraphron sp. h		U	C
Aphanogmus sp.		U	C
Aphanogmus sp.		U	C
Aphanogmus sp.		U	C
Aphanogmus sp.		U	C
Diapriidae (12 spp.)		U	C
Scelionidae (17 spp.)*	L	U	C
Platygasteridae (9 spp.)		U	C
Bethylidae (4 spp.)		U	C
Dryinidae (1 sp.)	L	U	C
Formicidae			
Ponerinae			
Amblyopone falcata	L		
Anochetus mayri	L		
Hypoponera puntatissima	L		
Hypoponera opacior	L		
Odontomachus brunneus	L		
Odontomachus bauri	L		
Pachycondyla stigma	L		
Platythyrea punctata	L		
Myrmicinae			
Cyphomyrmex minutus	L		
Macromischa leptothorax	L		
Monomorium ebeninum	L		
Monomorium floricola	L	U	C
Mycocepurus smithi	L		

Taxon	Foraging location		
*Myrmelachista ramulorum**		U	C
Wasmannia auropunctata	L		
Pheidole moerens	L		
Pheidole subarmata	L		
Pheidole sp.	L		
Solenopsis azteca	L		
Solenopsis corticalis	L		
Solenopsis geminata	L		
Solenopsis sp. a	L		
Solenopsis sp. b	L		
Strumigenys eggersi	L		
Strumigenys gundlachi	L		
Strumigenys rogeri	L		
Tetramorium bicarinatum	L		
Dolichoderinae			
Linepithema mellea (formerly *Iridomyrmex melleus*)	L	U	C
Tapinoma littorale	L		
Tapinoma melanocephalum	L		
Formicinae			
Brachymyrmex heeri	L	U	C
Paratrechina cisipa		U	
Paratrechina longicornis	L	U	
Paratrechina myops	L	U	
Paratrechina steinheili	L	U	
Paratrechina sp. a	L	U	
Paratrechina sp. b	L		
Paratrechina sp. o	L		
Paratrechina sp. r	L		
Camponotus sp. 1	L?		
Camponotus sp. 2	L?		
Scoliidae			
Campsomeris atrata	L	U	
Pompilidae			
Pepsis ruficornis		U	
Vespidae			
*Mischocyttarus phthisicus**		U	
*Polistes crinitus**		U	
Sphecidae			
Sphex ichneumoneus		U	
2 other spp.		U	
Halictidae (2 spp.)		U	
Apidae			
*Apis mellifera**		U	C
Centris haemorrhoidalis		U	
*Xylocopa mordax**		U	

Sources: Assignment of taxa to the foraging locations is based on personal observations by J. Alvarez, R. W. Garrison, W. J. Pfeiffer, and M. R. Willig, and on knowledge of general habitat associations pertaining to certain arthropod groups. The list augments that of Drewry (1970b).

Note: This list includes arthropods in soil (S), litter (L), understory (U), and canopy (C) strata.

* Major component of the food web based on abundance and/or size.