ECOLOGY, BEHAVIOR AND BIONOMICS

An Annotated List of Insect Herbivores Foraging on the Seedlings of Five Forest Trees in Guyana

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Lista Comentada de Insetos Herbívoros Encontrados em Plântulas de Cinco Espécies Florestais na Guiana

RESUMO - Uma lista de insetos herbívoros de vida livre colecionados em plantas de cinco espécies de importância econômica, perto de Mabura Hill, Guiana é apresentada. As plantas hospedeiras incluem as seguintes espécies: *Chlorocardium rodiei* (Scomb) (Lauraceae), *Mora gonggrijpii* (Kleinh) Sandw. (Caesalpinaceae), *Eperua rubiginosa* Miq. (Caesalpinaceae), *Pentaclethra macroloba* (Willd.) Kuntze (Leguminosae) and *Catostemma fragrans* Benth. Bombacaceae). Cerca de 10.000 plântulas foram observadas com intervalos de um mês durante dois anos. Durante este período, 27.735 insetos pertencentes a 604 espécies foram colecionados. Os insetos mastigadores de folhas foram testados no laboratório, com a finalidade de identificar as espécies não herbívoras e as ocasionais. Os insetos sugadores mais comuns e abundantes são: Psyllidae, Cicadellidae, Derbidae, Membracidae, Achilidae; Galerucinae, Eumolpinae, Alticinae, Cryptocephalinae, Gelechiidae e Entiminae (insetos mastigadores de folhas). As espécies mais comuns (n ≥ 22 indivíduos) são generalistas. Ao início do segundo ano de coleta, metade das árvores mães ("estações", n=125) foram selecionadas para ser cortadas, imitando o processo madeireiro. Apresenta-se um teste preliminar comparativo da abundância das espécies mais freqüentes durante os dois anos de coleta, assim como entre as estações cortadas e as não cortadas. Os resultados sugerem que perturbações leves podem aumentam a abundância de apenas algumas espécies. Estes padrões não parecem ser similares para espécies congenéricas. Esta investigação visa fornecer informações para o parco estudo da entomofauna herbívora em plântulas numa floresta húmida tropical.

PALAVRAS-CHAVE: Insecta, *Catostemma, Chlorocardium*, *Eperua*, floresta húmida.

ABSTRACT - An annotated list of the free-living insect herbivores collected on the seedlings of five rainforest tree species of economic importance near Mabura Hill, Guyana, is presented. The host plants were *Chlorocardium rodiei* (Scomb.) (Lauraceae), *Mora gonggrijpii* (Kleinh.) Sandw. (Caesalpiniaceae), *Eperua rubiginosa* Miq. (Caesalpiniaceae), *Pentaclethra macroloba* (Willd.) Kuntze (Leguminosae,) and *Catostemma fragrans* Benth. (Bombacaceae). During the monitoring of approximately 10,000 seedlings at monthly intervals during two years, 27,735 insect individuals were collected representing 604 species. Leaf-chewing insects were further tested in captivity, to remove transient and non-feeding species. The most common higher taxa included Psyllidae, Cicadellinae, Derbidae, Membracidae and Achilidae for sap-sucking insects and Galerucinae, Eumolpinae, Alticinae, Cryptocephalinae, Gelechiidae and Entiminae for leaf-chewing insects. Most of the common species collected ($n \geq 22$ individuals) were generalists. At the onset of the second collecting year, half of the parent trees ("stations", $n = 125$) were felled to mimic selective logging. Preliminary tests comparing the abundance of the most common species during the successive collecting years and at the non-felled vs. felled stations are also presented. These tests suggest that moderate levels of disturbance increased the abundance of a few species only and these patterns were not necessarily similar for congeneric species. The present survey represents one of the few studies of insect herbivores on seedlings in tropical rain forests.

KEY WORDS: Insecta, *Catostemma, Chlorocardium*, *Eperua*, logging, rain forest.

Despite much theoretical attention related to tree regeneration and maintenance of local tree diversity in rain forests (Janzen 1970), insect communities that feed on seedlings are not well-known in the tropics. Most studies have concentrated on the damage and mortality sustained by the seedlings (Becker 1983, Clark & Clark 1985, de la Cruz & Dirzo 1987), more rarely on a few common insect species attacking the seedlings (Folgarait *et al*. 1995, Gombauld 1996). However, studies quantifying the whole community of herbivore insect foraging and feeding on seedlings with adequate sampling effort in the tropics are practically lacking, with the notable exception of New (1983) studying *Acacia* seedlings in Australia.

Typically, insects subsist at low densities on seedlings (Becker 1993, Basset 1999). Thus, one of the main problems facing entomologists may be that surveying adequate numbers of seedlings for prolonged periods of time represents a near-impossible task for a single researcher, particularly if seedling patches are rather scattered in the forest. A solution to this problem is to train and work with insect parataxonomists (Janzen 1992, Novotny *et al*. 1997, Basset *et al*. - in press). This study reports on insects collected on seedlings of five species of rainforest timber trees near Mabura Hill, central Guyana, with such a team of parataxonomists.

As in other large-scale surveys of tropical insects (see discussion in, Erwin 1995), the resulting species list that we were able to compile with the help of taxonomist colleagues is frustratingly simple and includes many unidentified and undescribed species. However, we are motivated by the paucity of data on communities of insect herbivores foraging on seedlings in tropical rain forests and by the reassuring thought that the material has been deposited in a safe repository and is available for further examination.

Insect sampling was part of a study reporting on the effects of selective logging on communities of insect herbivores at Mabura Hill. The present species list is augmented by preliminary tests of annual variability and of the impact of canopy opening for the most common insect species collected. More detailed analyses accounting for the effects of rainfall, leaf production and canopy opening at the specific level or at the level of the insect community will be presented elsewhere.

Material and Methods

Study Site and Study Plants. Insect sampling was performed in a plot of 0.92 km^2 of unlogged forest (Block 17), in the Camoudi compartment of the logging concession of Demerara Timbers Limited, 40 km South of Mabura Hill, central Guyana (5°13'N, 58°48' W, altitude = *ca*. 30 m). The main forest types in Block 17 include well- and poorly-drained mixed forests (ter Steege *et al.* 1996). Annual rainfall at Mabura Hill is high and variable, from 2500 to 3400 mm, while annual air temperature is about 25.9°C.

This study focused on the seedlings and foliage of felled trees of the following species, which are either important timber species in Guyana or relatively common in Block 17: *Chlorocardium rodiei* (Scomb.) (Lauraceae, known locally as 'Greenheart'); *Mora gonggrijpii* (Kleinh.) Sandw. (Caesalpiniaceae, 'Morabukea'); *Eperua rubiginosa* Miq. (Caesalpiniaceae, 'Water Wallaba'); *Pentaclethra macroloba* (Willd.) Kuntze (Leguminosae, 'Trysil'); *Catostemma fragrans* Benth. (Bombacaceae, 'Sand Baromalli'). A collecting station was defined as a fixed number of tagged seedlings (40 for *Chlorocardium* and *Catostemma*, 50 for *Mora* and *Eperua* and 15 for *Pentaclethra*) growing below the parent tree or in its vicinity. Fifty such collecting stations were chosen for each species in Block 17 (total of 250 stations and 9,750 seedlings). Seedlings which died during the course of the study were replaced by other non-tagged seedlings growing below the parent tree. Other characteristics of the study site, stations and plants are detailed elsewhere (Thomas 1999, Basset 1999).

Insect Collecting and Processing. The sampling protocols targeted free-living insect herbivores collected by hand or with small aspirators during day-time. This included leaf-chewing (e.g., Chrysomelidae, some Curculionidae, juvenile Lepidoptera, some Orthoptera) and sap-sucking insects (Homoptera and some Heteroptera). Meristem-feeders and stem-boring insects were not surveyed on a regular basis since their census would have destroyed the seedlings.

Most of the sampling protocol was performed by trained assistants. From October 1996 to September 1997, 11 monthly insect surveys were organized (Year 1). During October 1997, half of the parent trees at the stations were felled (n = 125). This felling mimicked a situation of selective logging, where only particular areas in the forest are cut and damaged. The size of the gaps created were between 175 m^2 and 600 m^2 [as measured with Runkle's (1981) method], and most were between 300-400 m^2, an area mostly equivalent to "medium-sized" gaps in Charles (1998). From January to November 1998, 11 other insect surveys were performed (Year 2). During both years of sampling, the following protocol was used. During each survey, all the tagged seedlings of the 250 collecting stations were inspected once, during day-time. As far as possible, insects flying away were recorded to the insect family. On average, one assistant spent at least 30 minutes at each collecting station, carefully inspecting each tagged seedling. Overall, sampling effort during the two study years amounted to 1,114 person-days of field work.

Juveniles of leaf-chewing insects (all caterpillars) were collected and reared with young foliage from seedlings grown for this purpose. Juveniles of sap-sucking insects were not collected but recorded to the nearest insect family. Leaf-chewing insects were kept in plastic vials with young leaves of the host-plant species there were collected from. The vials were kept for 3-4 days in Block 17 and records of leaf damage and frass were subsequently checked for. Insect species responsible for obvious damage were later assigned to the "feeding" category, others, including dead insects, to the "non-feeding" category. Only the former were assigned to morphospecies and are included in the present list. Insect specimens were mounted, assigned to morphospecies on the basis of morphological characters and examination of genitalia, issued with a unique specimen access number and recorded in a database. Whenever possible, taxonomist colleagues examined the material further (see acknowledgments), which was deposited in the collections of the Centre for Biodiversity, University of Guyana, Georgetown.

Whenever possible, feeding *in situ* of leaf-chewing insects was also recorded for the study hosts. For sap-sucking insects, host records could only be ascertained in the field for xylem-feeding species (e.g., exudation of droplets for some Cicadellinae). From this information, as well as from distributional records, both leaf-chewing and sap-sucking insects were classified as "specialist" and "generalist" categories in calculating Lloyd's index of patchiness (see Basset 1999, for further details). A species was considered to be a "specialist" if 80% or more of its individuals were collected on a single host species. In the present context, a specialist should be considered to be a species that showed a clear preference for one of the five host species studied, but without implication of monophagy.

Insect species were considered "common" if a total of 22 individuals per species were collected during the two study years (i.e., at least one individual collected per survey on average). For these common species, we tested whether their abundance was significantly different between Year 1 and Year 2 of sampling with a Mann-Whitney test. Data were pooled per survey to ensure that sample size was large enough for this test. Significance levels were corrected with the Bonferoni method to account for the number of simultaneous tests. For generalist species, records from all study hosts were considered; for specialists, only records from the major host were considered. Further, it was tested whether, during Year 2, the abundance of common species was significantly different between non-felled stations vs. felled stations with a Wilcoxon signed ranks test. As previously, the data were pooled per survey, Bonferoni corrections were applied and records from all hosts were considered unless the species tested was a specialist. The Mann-Whitney test explored whether the annual variability of species was high. A significant difference may result from differences in rainfall, leaf production, felling of stations or other factors between study years. The Wilcoxon test explored whether a significant difference could be more specifically related to a species' response to the felling of stations.

Results

A synoptic list of the insect herbivores collected on each study host is presented in Appendix I. Species identified at least to the generic level, along with common unidentified species are listed first by higher taxonomical order (order, family, subfamily), then by alphabetical order. In total, 27,735 insect individuals were collected during both study years, including juveniles, damaged and lost specimens. This included 3,148 leaf-chewing insects representing at least 179 species and 24,587 sap-sucking insects representing at least 425 species. The most common higher taxa included Psyllidae, Cicadellinae (particularly Cicadellinae, Coelidiinae and Idiocerinae), Derbidae, Membracidae (particularly Smiliinae) and Achilidae for sap-sucking insects and Chrysomelidae (particularly Galerucinae, Eumolpinae, Alticinae and Cryptocephalinae), Curculionidae (particularly Entiminae) and Gelechiidae for leaf-chewing insects. Aphididae were sometimes collected from *Mora gonggrijpii* in the Mabura Hill area, but not from the tagged seedlings in Block 17. Orthoptera were collected rarely on seedlings and included nymphs and non-feeding specimens of Acrididae and Pyrgomorphidae. On an isolated occasion, larvae of sawflies (Hymenoptera) were collected from non-tagged seedlings of *Catostemma fragrans* but could not be reared to adult stage. No Thysanoptera and Phasmoptera were collected from the tagged seedlings.

Most species were rare and many represented only by singletons. However, 61 species were considered to be common, including 51 species of sap-sucking and 10 species of leaf-chewing insects. About 85% of these common species were generalist (52 generalists and nine specialists). Most generalist species were represented by xylem-feeding Cicadellinae, by presumably phloem-feeding Cixiidae, Achilidae and Derbidae, and by leaf-chewing Eumolpinae and Entiminae. Specialist species included one species of Pseudococcidae, two of Psyllidae, three of Membracidae, one of Galerucinae, one of Cryptocephalinae and one of Gelechiidae. Lepidoptera larvae were relatively rare, representing only 6% of the total insect individuals collected. It is difficult to comment on the actual damage that seedlings sustained from sap-sucking insects. In addition to intake of sap, many sap-sucking species may be vector of various plant diseases (Nielson 1968), but this has been quantified rarely in studies assessing seedling mortality in rain forests (Clark & Clark 1985, Folgarait *et al*. 1995). Leaf damage due to leaf-chewing insects on seedlings was rather low, estimated to be less than 5%. Leaf damage other than by leaf-miners on *Chlorocardium rodiei* was rare, and it is probable that this is due to a better chemical protection from chewing- rather than sap-sucking insects (Basset 1999). Seedlings of *Mora gonggrijpii* were attacked by *Cryptocephalus esuriens* Suffrian, notably, but rarely sustained high damage. The same was true of the unidentified species of Gelechiidae (TORT001) and Galerucinae (CHRY007) attacking *Pentaclethra macroloba* and *Catostemma fragrans*, respectively. Seedlings of *Eperua rubiginosa* were attacked by various species, notably an unidentified Eumolpinae (CHRY008), but none of them were unusually common during the study years at the study site. However, seedlings of *E. rubiginosa* were attacked by a species of bud-galling Cecidomyiidae, which was common but not included in the present census.

The foliage of seedlings was also shelter to several herbivore species feeding on seeds of the study hosts. For example, Scolytidae attacking the seeds of *C. rodiei* (Hammond *et al*. 1994) were common on conspecific seedlings, but not included in the present census. Many of the weevil species of *Conotrachelus* and Zygopinae, whose adults occasionally perform maturation feeding on seedlings as reported here, may be boring conspecific seeds at the larval stage.

Whereas the number of leaf-chewing insects did not increase notably between both study years (1,611 and 1,537 individuals collected, respectively), that of sap-sucking insects increased from 7,412 to 17,175 individuals between Year 1 and 2, respectively. This difference was due mainly to an increase of the specialist psyllid *Isogonoceraia* sp. and its nymphs, feeding on *Eperua rubiginosa*. The abundance of this species was also significantly higher at felled vs. non-felled stations during the second year of collecting (Appendix I). The abundance of most of the common species did not change significantly between collecting years (62% of species with test not significant, see Appendix I) or between the non-felled vs. felled stations during Year 2 (70% of species with test not significant). The abundance of some specialist as well as generalist species was affected by the collecting years or the felling treatment. A trend was noted for specialist species to be more sensitive to collecting years than were generalists, but this was not significant (G-test, G = 3.65, P = 0.056).

When the number of cases for which at least one of the two tests performed was significant (n = 29 species), the most common situation occurred when the abundance of the species increased both during the second collecting year and at felled stations (n = 11 spe cies or 38% of cases). The second common situation included a significant decrease during the second collecting year but no significant change at the felled stations (n= 8 species or 28% of cases). Only one species, the cixiid *Pintalia* sp. (CIXI002) showed a significant decrease both during the second collecting year and at felled stations. Annual variability, when significant, induced mixed responses from insects: the abundance of 14 species increased, whereas the abundance of nine others decreased. However, when the effect of the felling treatment was significant, the abundance of the species often increased (16 species with higher abundance against two species with lower abundance; G-test, G = 4.34, $P < 0.05$).

Finally, the trends (or their absence) in the change of abundance of insect species either between collecting years or between non-felled and felled stations were not necessarily similar for congeneric species. This was obvious when comparing the results of the two tests for different species in the following genera: *Plectoderes, Pintalia, Amblyscarta, Ladoffa, Dasmeusa, Soosilius* and nr *Oragua*, for which this comparison was possible (Appendix I).

Discussion

As far as we are aware, the present list represents one of the very first attempts to characterise the entire community of insect herbivores foraging on seedlings in a tropical rain forest with a suitable sample size. As similar compilations become available from other sites in the Amazon basin or elsewhere in the Neotropical region, knowledge of the ecology of many herbivore species foraging in the forest understorey of tropical forests may greatly improve. Further, such compilations may also prompt taxonomic revisions and descriptions of particular insect groups, such as some tribes in the Derbidae, Cixiidae or Eumolpinae.

The most abundant leaf-chewing species that were collected on seedlings feed readily on the host from which they were collected and were sometimes observed feeding *in situ*. Although this could be only ascertained *in situ* for a few xylem-feeding species, it is probable that most of the very common species of sap-sucking insects also feed on the seedlings of the study hosts. Most of these insect species feeding on seedling appeared to be generalist species. The general impression of the study system is that many insect species may feed on the seedlings, but probably occasionally only, and few reach densities that may be detrimental to their hosts, with the possible exception of the spread of plant diseases, particularly by sap-sucking insects (Nielson 1968). The implications of high levels of generalist insects in the present system with reference to models of tree regeneration in tropical rain forests are discussed elsewhere (Basset 1999).

Relatively few larvae of Lepidoptera were collected from the seedlings. This may be related to the infrequency of their leaf flush and, as such, seedlings being a poor food resource for most insect herbivores (Basset 1999). Moving from one seedling to another in search of young foliage may be risky for lepidopteran larvae, but less so for alate adults such as chrysomelids and cixiids, for example. This interpretation is reinforced further by the significantly higher abundance of Lepidoptera larvae in parent trees, which offer more abundant food resources, in comparison with conspecific seedlings (Basset *et al*. 1999).

Since insect seasonality was low during collecting years (Basset - in press), it was possible to pool the insect data to ensure that sample size was high enough for the analyses. However, insect densities on seedlings were genuinely low, presumably because seedlings represent a marginal food resource for most of the species collected (Basset - in press). Thus, it is possible that lack of significant change in the abundance of many insect species either between years or between non-felled and felled stations may result purely from the low abundance of the insects. Nonetheless, the abundance of some insect species was significantly different between the two collecting years. The last surveys of Year 1

Appendix I. Synoptic and commented list of free-living insect herbivores foraging on seedlings in Block 17. Code = insect codes used in collections; Total = total number of individuals collected; S 1-11 = number of individuals collected during surveys 1 to 11; S 12-22 = number of individuals collected during surveys 12 to 22; number of individuals collected during surveys 1 to 22 on the study host, abbreviated by the first letter of their generic and specific names (Cr, Mg, Er, Pm, Cf); T Yr = test for increasing abundance during Year 1 vs. Year 2 (see methods); T Fe = test for increasing abundance at non-felled vs. felled stations (see methods); results of tests coded as follows: I = significant increase, D = significant decrease, n.s. = not significant. Notes detail whether the common species tested are generalist or specialist (see methods) and report of feeding *in situ* (F:), on host abbreviated as above.

Taxa	Code	Total	S 1-11	S 12-22	Cr	Mg	Er	Pm	Cf	T Yr	T Fe	Notes
HOMOPTERA												
Delphacidae												
Gen. sp. ?	DELP001	8	5	3	3	2	2	1	-	-	-	-
Gen. sp. ?	DELP003	1	0	1	-	-	-	-	1	-	-	-
Derbidae												
Herpis vittata F.	DERB008	55	22	33	23	3	13	5	11	n.s.	n.s.	Generalist
Herpis sp. nr *metcalfi*	DERB006	69	56	13	44	1	15	2	7	D	n.s.	Generalist
Mysidia sp.	DERB020	214	113	101	38	65	43	19	49	n.s.	n.s.	Generalist
Mysidia sp.	DERB007	89	46	43	14	14	22	11	28	n.s.	n.s.	Generalist
Gen. sp. ?	DERB022	597	13	584	211	30	91	8	257	I	I	Generalist
Gen. sp. ?	DERB003	148	109	39	11	37	41	23	36	D	n.s.	Generalist
Gen. sp. ?	DERB017	68	10	58	16	22	5	1	24	n.s.	n.s.	Generalist
Gen. sp. ?	DERB004	64	27	37	8	18	13	6	19	n.s.	n.s.	Generalist
Gen. sp. ?	DERB009	41	22	19	27	1	4	2	7	n.s.	n.s.	Generalist
Gen. sp. ?	DERB039	39	27	12	6	11	15	1	6	n.s.	n.s.	Generalist
Gen. sp. ?	DERB012	36	20	16	2	12	11	4	7	n.s.	n.s.	Generalist
Gen. sp. ?	DERB021	30	19	11	8	6	2	3	11	n.s.	n.s.	Generalist
Other Derbidae	66 spp.	275	138	137	49	82	73	24	47	-	-	-
Kinnaridae												
Southia sp. nr *opposita*	CIXI003	69	47	22	31	2	6	7	23	n.s.	n.s.	Generalist
Fulgoridae												
Nr *Locrona* sp.	FULG002	1	1	0	-	1	-	-	-	-	-	-

Nr *Scaralis* sp.	FULG001	1	1	0	-	-	1	-	-	-	-	-
Achilixiidae												
Gen. sp. ?	ACCX001	4	4	0	-	1	-	3	-	-	-	-
Achilidae												
Plectoderes collaris F.	ACHI002	132	54	78	27	16	14	27	48	n.s.	n.s.	Generalist
Plectoderes sp.	ACHI023	35	2	33	4	8	15	1	7	I	n.s.	Generalist
Plectoderes sp.	ACHI025	2	0	2	-	-	2	-	-	-	-	-
Plectoderes sp.	ACHI026	1	0	1	-	1	-	-	-	-	-	-
Sevia bicarinata F.	ACHI001	117	61	56	6	13	22	48	28	n.s.	D	Generalist
Sevia consimile Fennah	ACHI006	16	6	10	2	4	2	1	7	-	-	Known from Trinidad (L. O'Brien, pers. comm.)
Nr *Catonia* sp.	ACHI016	1	1	0	1	-	-	-	-	-	-	-
Gen. sp. ?	ACHI009	11	4	7	-	-	3	1	7	-	-	-
Other Achilidae	19 spp.	54	31	23	7	11	13	5	18	-	-	-
Dictyopharidae												
Taosa muliebris Walker	DICT006	2	0	2	-	1	-	-	1	-	-	-
Toropa ferrifera (Walker)	DICT001	14	8	6	3	1	3	6	1	-	-	-
Toropa picta Walker	DICT002	3	1	2	-	1	-	-	2	-	-	-
Toropa sp.	DICT004	1	1	0	-	-	1	-	-	-	-	-
Other Dictyopharidae	3 spp.	11	2	9	-	-	3	3	5	-	-	-
Cixiidae												
Bennarella sp.	ACCX002	18	12	6	15	-	2	1	-	-	-	-
Pintalia sp.	CIXI006	669	554	115	128	73	85	130	253	D	n.s.	Generalist
Pintalia sp.	CIXI002	415	355	60	101	12	82	25	195	D	D	Generalist
Pintalia sp.	CIXI009	110	91	19	23	12	35	19	21	D	n.s.	Generalist
Nr *Bothriocera* sp.	ACHI018	2	1	1	2	-	-	-	-	-	-	-
Nr *Bothriocera* sp.	ACHI020	1	0	1	-	-	-	1	-	-	-	-
Gen. sp. ?	CIXI008	22	16	6	-	3	6	8	5	n.s.	n.s.	Generalist
Other Cixiidae	11 spp.	88	54	34	11	21	18	10	28	-	-	-
Tropiduchidae												
Gen. sp.?	TROP001	2	1	1	-	1	-	-	1	-	-	-
Gen. sp.?	TROP004	1	0	1	-	-	1	-	-	-	-	-
Flatidae												

Nr *Anormenis* sp.	FLAT012	6	0	6	1	-	2	1	2	-	-	-
Nr *Locrona* sp.	FLAT004	3	1	2	-	2	-	-	1	-	-	-
Nr *Poekilloptera* sp.	FLAT016	1	0	1	-	-	-	-	1	-	-	-
Other Flatidae	5 spp.	14	8	6	2	5	1	0	6	-	-	-
Issidae												
Gen. sp. ?	ISSI002	11	5	6	1	1	1	3	5	-	-	-
Other Issidae	9 spp.	20	9	11	2	2	4	4	8	-	-	-
Acanaloniidae	3 spp.	5	3	2	3	-	-	-	1	-	-	-
Nogodinidae												
Nogodina reticulata F.	NOGO001	14	6	8	3	2	3	2	4	-	-	-
Gen. sp.?	NOGO002	1	0	1	-	-	-	1	-	-	-	-
Cicadidae												
Gen. sp. ?	CICD002	1	0	1	-	-	-	-	1	-	-	-
Cercopidae												
Gen. sp. ?	CERC001	11	7	4	2	2	2	1	4	-	-	-
Other Cercopidae	5 spp.	23	11	12	4	3	5	6	5	-	-	-
Membracidae												
Endoiastinae												
Scytodepsa sp.	MEMB012	44	10	34	1	8	-	12	23	n.s.	n.s.	Generalist
Tropidaspis sp.	MEMB049	3	0	3	-	1	2	-	-	-	-	-
Tropidaspis sp.	MEMB106	1	0	1	-	-	1	-	-	-	-	-
Other Endoiastinae	2 spp.	8	0	8	1	1	7	1	-	-	-	-
Stegaspinae												
Stegaspis fronditia L.	MEMB043	3	1	2	-	2	-	-	1	-	-	-
Nr *Lycoderes* sp.	MEMB051	4	0	4	-	-	1	1	2	-	-	-
Darninae												
Cyphotes sp.	MEMB095	1	0	1	-	-	1	-	-	-	-	-
Darnis lateralis F.	MEMB007	81	29	52	8	15	3	19	36	n.s.	n.s.	Generalist
Nr *Stictopelta* sp.	MEMB022	1	1	0	-	1	-	-	-	-	-	-
Heteronotinae												
Heteronotus nr *tridens* Burmeister	MEMB024	1	0	1	-	-	-	-	1	-	-	-
Membracinae												

Bolbonota sp.	MEMB032	3	3	0	-	-	-	3	-	-	-	-
Bolbonota sp.	MEMB089	1	0	1	-	-	1	-	-	-	-	-
Campylenchia sp.	MEMB093	1	0	1	-	-	-	1	-	-	-	-
Enchophyllum sp.	MEMB088	9	0	9	2	-	1	3	3	-	-	-
Leioscyta sp.	MEMB030	6	1	5	-	2	-	1	3	-	-	-
Leioscyta sp.	MEMB071	21	0	21	20	-	-	-	1	-	-	-
Membracis nr *foliata* L.	MEMB048	7	1	6	3	-	-	2	2	-	-	-
Membracis sp.	MEMB026	47	5	42	1	-	2	37	7	I	I	Specialist on Pm
Membracis sp.	MEMB041	1	1	0	-	-	-	-	1	-	-	-
Nassuna sp.	MEMB050	2	0	2	1	-	-	1	-	-	-	-
Notocera sp.	MEMB009	33	4	29	6	5	6	9	7	I	n.s.	Generalist
Potnia gladiator Walker	MEMB015	9	3	6	3	-	3	-	3	-	-	-
Sphongophorus nr *quelini* Fron.	MEMB054	1	0	1	-	-	-	1	-	-	-	-
Sundarion sp.	MEMB091	1	0	1	-	-	-	1	-	-	-	-
Nr *Aconophora* sp.	MEMB035	6	5	1	-	5	1	-	-	-	-	-
Nr *Cymbomorpha* sp.	MEMB047	1	1	0	-	-	-	-	1	-	-	-
Other Membracinae	6 spp.	21	1	20	2	2	2	14	1	-	-	-
Smiliinae												
Amastris sp.	MEMB029	1	1	0	-	-	-	1	-	-	-	-
Amastris sp.	MEMB062	1	0	1	-	-	-	1	-	-	-	-
Aphetea sp.	MEMB005	16	3	13	-	-	-	16	-	-	-	-
Aphetea sp.	MEMB039	3	2	1	-	1	-	2	-	-	-	-
Harmonides sp.	MEMB002	11	1	10	3	-	1	1	6	-	-	-
Harmonides sp.	MEMB010	1	0	1	-	1	-	-	-	-	-	-
Harmonides sp.	MEMB023	13	2	11	1	1	4	2	5	-	-	-
Harmonides sp.	MEMB031	1	1	0	1	-	-	-	-	-	-	-
Membracidae												
Smiliinae												
Harmonides sp.	MEMB081	2	0	2	1	-	-	-	1	-	-	-
Harmonides sp.	MEMB087	4	0	4	-	1	2	-	1	-	-	-
Smiliorhachis sp.	MEMB003	214	24	190	12	12	6	177	7	I	I	Specialist on Pm
Nr *Horiola* sp.	MEMB004	330	17	313	1	33	18	257	21	I	n.s.	Specialist on Pm
Other Smilinae	22 spp.	64	13	51	10	28	9	17	10	-	-	-

Other Membracidae	18 spp.	57	21	36	18	10	9	10	10	-	-	-
Aetalionidae												
Gen. sp. ?	AETA001	8	0	8	-	8	-	-	-	-	-	-
Cicadellidae												
Ledrinae												
Xedreota tuberculata (Osborn)	CICA023	18	5	13	2	3	3	1	9	-	-	-
Agallinae												
Agallia sp.	CICA061	18	11	7	-	4	4	-	10	-	-	-
Agallia sp.	CICA170	1	1	0	1	-	-	-	-	-	-	-
Idiocerinae												
Chiasmodolon sp.	CICA020	42	31	11	3	11	14	6	8	n.s.	n.s.	Generalist
Chiasmodolon sp.	CICA065	20	9	11	1	5	-	1	13	-	-	-
Gen. sp. ?	CICA036	39	12	27	12	15	4	2	6	n.s.	n.s.	Generalist
Other Idiocerinae	12 spp.	24	7	17	3	8	6	1	6	-	-	-
Cicadellidae												
Gyponinae												
Barbatana extera Freytag	CICA029	5	4	1	2	2	-	1	-	-	-	-
Curtara sp.	CICA027	1	0	1	-	-	-	1	-	-	-	-
Gypona bulbosa DeLong & Freytag	CICA008	16	2	14	1	9	2	2	2	-	-	-
Gypona flavolimbata Metcalf	CICA018	20	9	11	14	-	2	-	4	-	-	-
Gypona funda DeLong	CICA112	2	0	2	-	1	1	-	-	-	-	-
Gypona glauca F.	CICA030	3	2	1	-	1	1	-	1	-	-	-
Gypona offa DeLong & Freytag	CICA169	1	0	1	-	-	1	-	-	-	-	-
Polana sp.	CICA007	1	0	1	1	-	-	-	-	-	-	-
Other Gyponinae	5 spp.	7	2	5	1	4	0	1	1	-	-	-
Coelidiinae												
Baluba parallela Nielson	CICA016	37	9	28	1	4	6	7	19	n.s.	I	Generalist
Docalidia o'reilly Nielson	CICA060	3	1	2	-	-	-	1	2	-	-	-
Docalidia sp.	CICA024	42	12	30	7	3	4	3	25	n.s.	I	Generalist
Docalidia sp.	CICA129	7	3	4	-	1	1	1	4	-	-	-
Docalidia sp.	CICA130	5	5	0	1	-	-	1	3	-	-	-

Docalidia sp.	CICA131	2	2	0	-	-	1	1	-	-	-	-
Paracarinolidia sp.	CICA078	10	4	6	6	-	2	-	2	-	-	-
Cicadellidae												
Coelidiinae												
Stalololidia sp.	CICA052	1	1	0	-	-	1	-	-	-	-	-
Nr *Docalidia* sp.	CICA040	13	5	8	4	-	1	1	7	-	-	-
Other Coelidiinae	11 spp.	25	10	15	4	2	3	7	9	-	-	-
Xestocephalinae												
Xestocephalus desertorum (Berg)	CICA144	26	0	26	7	-	-	-	19	n.s.	n.s.	Generalist
Cicadellinae												
Acrocampsa pallipes F.	CICA005	32	7	25	11	4	1	9	7	n.s.	n.s.	Generalist
Amblyscarta invenusta Young	CICA006	147	25	122	29	27	28	25	38	I	I	Generalist
Amblyscarta sp.	CICA012	35	1	34	13	1	5	4	12	I	I	Generalist
Amblyscarta sp.	CICA011	3	1	2	-	-	-	3	-	-	-	-
Cardioscarta quadrifasciata L.	CICA025	25	11	14	5	11	1	-	8	n.s.	n.s.	Generalist
Dasmeusa pauperata Young	CICA001	168	38	130	25	20	31	20	72	I	I	Generalist
Dasmeusa sp.	CICA076	74	46	28	3	8	33	6	24	n.s.	n.s.	Generalist
Ladoffa aguilari Lozada	CICA058	13	11	2	1	1	7	3	1	-	-	-
Ladoffa comitis Young	CICA054	24	4	20	6	2	3	1	12	n.s.	n.s.	Generalist; F: Cf
Ladoffa ignota Walker	CICA003	48	12	36	9	3	17	6	13	n.s.	I	Generalist; F: Pm
Ladoffa sp.	CICA077	10	5	5	2	4	1	2	1	-	-	-
Macugonalia moesta (F.)	CICA062	62	62	0	39	10	9	2	2	D	n.s.	Generalist
Poeciloscarta cardinalis F.	CICA033	17	6	11	3	5	2	1	6	-	-	-
Soosiulus fabricii Metcalf	CICA004	1172	603	569	404	122	217	165	264	n.s.	n.s.	Generalist; F: Cr, Mg, Er, Cf
Soosiulus interpolis Young	CICA081	148	65	83	37	29	30	28	24	n.s.	n.s.	Generalist; F: Er
Nr *Oragua* sp.	CICA010	254	203	51	41	16	82	32	83	D	n.s.	Generalist
Nr *Oragua* sp.	CICA080	59	38	21	9	4	22	5	19	n.s.	n.s.	Generalist
Other Cicadellinae	10 spp.	16	8	8	1	4	4	4	3	-	-	-
Cicadellidae												
Typhlocybinae												
Joruma coccinea McAtee	CICA002	29	0	29	1	2	4	-	22	n.s.	n.s.	Generalist
Joruma nr *apicata* Caldwell	CICA022	12	2	10	1	-	2	-	9	-	-	-

Gen. sp. ?	CICA009	15	6	9	2	1	2	-	10	-	-	-
Other Typhlocybinae	15 spp.	49	3	46	4	6	3	6	30	-	-	-
Deltocephalinae												
Mattogrossus colonoides												
(Linnavuori)	CICA165	1	0	1	1	-	-	-	-	-	-	-
Osbornellus sp.	CICA015	7	3	4	2	3	-	2	-	-	-	-
Planocephalus flavicosta												
(Stal.)	CICA143	7	0	7	3	-	-	-	4	-	-	-
Taperinha sp.	CICA043	8	4	4	1	1	1	2	3	-	-	-
Other Deltocephalinae	8 spp.	10	4	6	2	0	2	3	3	-	-	-
Other Cicadellidae	11 spp.	29	8	21	6	-	3	4	16	-	-	-
Psyllidae												
Euphalerus sp.	PSYL001	118	3	115	-	118	-	-	-	I	I	Specialist on Mg; F: Mg (nymphs)
Isogonoceraia sp.	PSYL003	2932	698	2234	62	115	2682	12	61	I	I	Specialist on Er; F: Er (nymphs)
Notophyllura sp.	PSYL005	1	1	0	1	-	-	-	-	-	-	-
Gen. sp.?	PSYL007	2	0	2	-	-	-	-	2	-	-	-
Aleyrodidae	at least 8 spp.	41	21	20	6	2	10	1	22	-	-	-
Pseudococcidae												
Gen. sp. ?	COCC002	149	147	2	149	-	-	-	-	D	n.s.	Specialist on Cr
Other Pseudococcidae	3 spp.	10	0	10	8	-	1	1	-	-	-	-
HETEROPTERA												
Coreidae												
Pachylis nr *laticornis* F.	CORE002	15	9	6	1	1		13		-	-	-
Nr *Acanthocephala* sp.	CORE003	14	4	10	2	-	8	1	3	-	-	-
Nr *Merocoris* sp.	CORE009	2	0	2	-	2	-	-	-	-	-	-
Nr *Peranthus* sp.	CORE001	30	3	27	12	1	1	7	9	I	I	Generalist
Other Coreidae	6 spp.	18	4	14	11	2	1	2	2	-	-	-
Lygaeidae												
Gen. sp.?	LYGA001	1	1	0	1	-	-	-	-	-	-	-
Gen. sp.?	LYGA002	1	0	1	1	-	-	-	-	-	-	-

Cydnidae												
Gen. sp.?	CYDN001	6	6	0	-	1	1	2	2	-	-	-
Pentatomidae												
Arocera equinoxia												
(Westwood)	PENT003	6	2	4	-	1	1	3	1	-	-	-
Edessa sp.	PENT001	43	11	32	5	4	12	5	17	I	I	Generalist
Edessa sp.	PENT006	11	2	9	1	1	-	1	8	-	-	-
Edessa sp.	PENT007	4	1	3	1	-	-	2	1	-	-	-
Mormidea ypsilon (L.)	PENT008	2	2	0	-	-	-	-	2	-	-	-
Nr *Edessa* sp.	PENT009	1	1	0	-	1	-	-	-	-	-	-
Other Pentatomidae	9 spp.	14	2	12	7	2	2	3	-	-	-	-
Plataspididae												
Canopus sp.	PLAT001	253	122	131	6	156	30	6	55	n.s.	n.s.	Generalist
Scutellaridae												
Pachycoris sp.	SCUT002	4	2	2	4	-	-	-	-	-	-	-
Gen. sp.?	SCUT001	1	1	0	-	-	-	-	1	-	-	-
COLEOPTERA												
Scarabaeidae												
Melolonthinae												
Gen. sp.?	SCAB002	1	1	0	-	-	-	-	1	-	-	-
Gen. sp.?	SCAB003	2	1	1	1	-	-	-	1	-	-	-
Cerambycidae												
Cerambycinae												
Gen. sp.?	CERA006	1	0	1	-	-	-	1	-	-	-	-
Lamiinae												
Steirastoma ?breve Sulzer	CERA001	1	0	1	-	-	-	-	1	-	-	-
Nr *Jamesia* sp.	CERA005	2	0	2	-	-	-	-	2	-	-	-
Chrysomelidae												
Megalopodinae												
Gen. sp.?	CHRY088	1	0	1	-	-	-	-	1	-	-	-
Cryptocephalinae												
Cryptocephalus esuriens												
Suffrian	CHRY003	123	52	71	-	106	5	7	5	n.s.	n.s.	Specialist on Mg; F: Mg

Eumolpinae												
Otilea nr *crenata* F.	CHRY019	11	6	5	-	6	1	1	3	-	-	-
Gen. sp.?	CHRY008	113	55	58	2	10	53	3	45	n.s.	n.s.	Generalist; F: Mg, Er
Gen. sp.?	CHRY001	47	12	35	-	26	2	12	7	n.s.	I	Generalist; F: Mg, Pm
Gen. sp.?	CHRY010	32	30	2	-	21	4	2	5	D	n.s.	Generalist
Gen. sp.?	CHRY025	24	5	19	-	10	2	9	3	n.s.	n.s.	Generalist; F: Mg
Other Eumolpinae	31 spp.	117	46	71	5	36	30	11	35	-	-	-
Lamprosomatinae												
Nr *Lamprosoma* sp.	CHRY053	1	1	0	1	-	-	-	-	-	-	-
Galerucinae												
Gen. sp.?	CHRY007	372	212	160	2	-	2	2	366	n.s.	I	Specialist on Cf; F: Cf
Other Galerucinae	14 spp.	78	41	37	1	11	10	19	37	-	-	-
Alticinae												
Heikertingerella sp.	CHRY044	4	3	1	2	1	-	1	-	-	-	-
Utingaltica sp.	CHRY040	5	3	2	1	-	-	-	4	-	-	-
Wanderbiltiana sp.	CHRY009	16	10	6	7	1	4	2	2	-	-	-
Nr *Calipeges* sp.	CHRY013	5	0	5	2	2	-	-	1	-	-	-
Nr *Calipeges* sp.	CHRY027	3	1	2	-	-	2	-	1	-	-	-
Gen. sp.?	CHRY014	43	37	6	1	15	2	2	23	n.s.	n.s.	Generalist; F: Er
Other Alticinae	25 spp.	72	37	35	9	6	18	10	29	-	-	-
Apionidae												
Gen. sp.?	APIO001	1	1	0	-	-	-	1	-	-	-	-
Curculionidae												
Rhyncophorinae												
Mesocordylus sp.	CURC004	3	3	0	-	-	1	-	2	-	-	-
Entiminae												
Compsus sp.	CURC012	14	9	5	-	3	2	3	6	-	-	-
Gen. sp.?	CURC003	49	4	45	-	6	1	23	19	I	I	Generalist
Other Entiminae	7 spp.	53	9	44	15	20	3	13	2	-	-	-
Hylobinae												
Heilipus sp.	CURC041	1	0	1	-	1	-	-	-	-	-	-
Other Hylobinae	3 spp.	4	1	3	-	3	1	-	-	-	-	-

Prionomerinae												
Prionomerus sp.	CURC017	3	0	3	3	-	-	-	-	-	-	-
Curculionidae												
Cryptorhynchinae												
Conotrachelus sp.	CURC016	3	2	1	-	1	1	-	1	-	-	-
Conotrachelus sp.	CURC058	2	0	2	-	1	-	1	-	-	-	-
Conotrachelus sp.	CURC002	1	1	0	-	1	-	-	-	-	-	-
Conotrachelus sp.	CURC036	1	0	1	-	-	1	-	-	-	-	-
Conotrachelus sp.	CURC040	1	0	1	1	-	-	-	-	-	-	-
Conotrachelus sp.	CURC057	1	0	1	-	1	-	-	-	-	-	-
Cryptorhynchus sp.	CURC018	1	1	0	1	-	-	-	-	-	-	-
Penestes sp.	CURC015	1	1	0	-	-	-	-	1	-	-	-
Rhyssomatus sp.	CURC019	2	1	1	-	1	-	1	-	-	-	-
Other Cryptorhynchinae	5 spp.	5	1	4	-	2	1	1	1	-	-	-
Zygopinae												
Pseudopinarus	CURC005	27	9	18	2	4	5	6	10	n.s.	n.s.	Generalist
Other Zygopinae	15 spp.	31	7	24	1	21	5	1	3	-	-	-
Baridinae												
Gen. sp.?	CURC013	2	1	1	-	-	-	1	1	-	-	-
Gen. sp.?	CURC010	1	0	1	-	1	-	-	-	-	-	-
Gen. sp.?	CURC024	1	1	0	-	-	-	-	1	-	-	-
Other Curculionidae	2 spp.	2	0	2	-	2	-	-	-	-	-	-
DIPTERA												
Cecidomyiidae												
Gen. sp.?	-	-	-	-	-	-	-	-	-	-	-	Not censued, common specialist on Er; induces bud galls
Agromyzidae												
Gen. sp.?	-	-	-	-	-	-	-	-	-	-	-	Not censued, common specialist on Cf; leaf-miner
LEPIDOPTERA												
Gracillariidae												
Gen. sp.?	-	-	-	-	-	-	-	-	-	-	-	Not censued, common specialist on Cr; leaf-miner

Gen. sp.?	-	-	-	-	-	-	-	-	-	-	-	Not censued, specialist on Mg; leaf-miner
Oecophoridae	3 spp.	3	2	1	-	-	-	3	-	-	-	-
Gelechiidae												
Gen. sp.?	TORT001	40	24	16	-	-	-	40	-	n.s.	n.s.	Specialist on Pm
Tortricidae	2 spp.	3	1	2	-	-	-	3	-	-	-	-
Limacodidae												
Gen. sp.?	LIMA001	1	1	0	1	-	-	-	-	-	-	-
Gen. sp.?	LIMA002	1	1	0	-	-	-	1	-	-	-	-
Pyralidae												
Stenominae												
Gen. sp.?	-	-	-	-	-	-	-	-	-	-	-	Not censued, specialist on Cf; stem-borer
Other Pyralidae	5 spp.	6	4	2	-	3	2	1	-	-	-	-
Saturniidae												
Gen. sp.?	SATU001	4	4	0	4	-	-	-	-	-	-	-
Geometridae												
Gen. sp.?	GEOM001	6	2	4	-	-	-	6	-	-	-	-
Other Geometridae	at least 5 spp.	5	1	4	-	1	-	4	-	-	-	-
Hesperiidae												
Gen. sp.?	HESP001	5	1	4	-	4	-	1	-	-	-	-
Gen. sp.?	HESP002	2	1	1	-	-	-	2	-	-	-	-
Lycaenidae												
Thestius phloeus (Cramer)	LYCA001	4	2	2	-	-	-	-	4	-	-	Feed on *Vouacapoua americana* (Joly 1996)
Chalybs janais (Cramer)	LYCA003	1	1	0	-	-	-	1	-	-	-	On *Lonchocarpus* and *Calliandra* (G. Beccaloni, p.c.)
Notodontidae												
Gen. sp.?	NOTO002	4	0	4	-	4	-	-	-	-	-	-
Arctiidae												
Ctenuchinae												
Gen. sp.?	SESI001	1	1	0	-	-	-	1	-	-	-	-
Noctuidae	at least 4 spp.	5	3	2	-	2	-	2	1	-	-	-

and a few of Year 2 were performed during an El Niño event. Many changes in insect abundance may result from the rainfall factor, and particularly from its interaction with the leaf production of the host -plants.

However, a few species apparently benefited from an increase in canopy openness after the felling of the stations and were significantly more abundant at the felled stations, as shown by the preliminary tests reported here. Even if the gaps created were relatively modest in size (< 400 m^2 for most), this may have been important for some heliophilous species, such as some Cicadellidae, Membracidae, Pentatomidae or Entiminae, in the otherwise dark and shady understorey of Block 17. Alternatively, higher canopy openness may have increased the leaf production of seedlings and the abundance of insects that may depend more directly on the presence of young foliage, such as some Psyllidae and Chrysomelidae. This, in addition to the influence of rainfall, will be examined elsewhere.

Interestingly, the present compilation and preliminary tests suggest that congeneric insect species may not necessarily respond in a similar way to changes induced by rainfall and canopy openness. This further suggests that the ecology and requirements of these species may be different and that these factors need to be examined at the specific level. Even generalist species in this study system display preferences for particular host-plants or micro-habitats (Basset - in press). It may be expected that insect species will be finely distributed on different resources/micro-habitats in the forest understorey, although their distribution may be even finer in the canopy. In these conditions, insect species are likely to display a variety of responses to natural and man-induced forest disturbance (Charles 1998), which may parallel their phenotypic and genetic diversity.

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