



Host utilization of the Brazil nut family (Lecythidaceae) by sympatric wood-boring species of *Palame* (Coleoptera, Cerambycidae, Lamiinae, Acanthocinini)

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Estimates of the total number of arthropod species in existence are based, in part, upon assumptions about both the host specificity of tropical insects and their restriction to the forest canopy. It has been difficult to evaluate these estimates because of the paucity of available data. A newly discovered association between wood-boring beetles (Cerambycidae) and their host plants in the Brazil nut family (Lecythidaceae) inspired a year-long rearing project in the Neotropical rain forest of French Guiana. Branches severed from five species of Lecythidaceae yielded 1813 cerambycids belonging to 37 species. Three cerambycid species—*Palame anceps* (Bates), *P. crassimana* Bates, and *P. mimetica* Monné—accounted for almost half of the individuals reared. Each demonstrated a different pattern of host fidelity. *Palame crassimana* emerged from four of the five potential hosts, *P. anceps* emerged exclusively from a single host, and *P. mimetica* made a seasonal change in host affiliation. Although *Palame* spp. emerged from both ground level and canopy branches, they made a seasonal shift in stratum: they reproduced at both levels during the dry season, but exclusively at canopy level during the rainy season. Even specialized tropical insects may show greater flexibility in host utilization than some current hypotheses suggest.

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ADDITIONAL KEYWORDS:—host specificity – canopy arthropods – forest stratum – insect seasonality – insect–plant interactions – *Couratari stellata* – *Eschweilera coriacea* – *Gustavia hexapetala* – *Lecythis poiteaui*.

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INTRODUCTION

Estimates of the number of arthropod species

The global arthropod fauna comprises close to one million described species (see references in Hammond, 1992). Various authors have proposed that if undescribed species could also be enumerated, there would prove to be between 2.5 and 10 million extant insects (Gaston, 1991a). A great controversy was instigated 16 years ago with the publication of a brief paper speculating, based on the results of an experiment in which the canopies of 19 individuals of the tropical tree *Luehea seemanii* were fogged with insecticide, that there might actually be more than 30 million species of arthropods (Erwin, 1982).

Erwin sorted the beetles into morphospecies, and placed them in guilds (herbivore, predator, fungivore and scavenger). Faced with a lack of sufficient data on the degree of host specificity within the various guilds, he estimated percentages, and calculated the number of beetles hypothetically dependent upon *Luehea seemanii*. He multiplied this figure by 50 000 tropical tree species, estimated that beetles constitute 40% of the total canopy fauna, and surmised that the ground fauna would contribute half as many species as the canopy. Subsequent studies convinced Erwin that he had substantially underestimated the potential number of insect species (Erwin, 1988). Other authors (Basset, 1992; Gaston, 1991a, b; Hodkinson & Casson, 1991) maintain that his figures are seriously inflated because the premises on which they depend (the bulk of tropical insects being undescribed, often restricted to the canopy, and having a high degree of host specificity) are flawed.

The debate has continued to reverberate (Erwin, 1991; Gaston, 1991a; May, 1988; Stork, 1988). There are profound implications for conservation, because the figures extrapolated from limited data sets are used to generate hypotheses about current and projected rates of extinction as tropical forests are destroyed (Stork, 1997, and references therein). Subsequent analyses of the faunal overlaps of con-specific versus unrelated trees have suggested that Erwin may have overestimated the host fidelity of tropical insects (Kitchling *et al.*, 1997; Mawdsley & Stork, 1997). These studies also analysed the chaotic profusion of insects harvested after the

release of insecticides into the forest canopy. Fogging experiments do not adequately sample concealed feeders including wood-borers, and cannot reveal life history attributes of the insects that are efficiently sampled.

Objectives

Cerambycids, due to the prolonged larval period spent in intimate contact with the tissues of the host plant, may be prone to the development of host-specific associations. When trees belonging to more than 45 plant families were investigated for their cerambycid associates in French Guiana, Lecythidaceae was one of two families that not only gave rise to a clearly defined guild of specialist beetles, but was conspicuously avoided by generalists (Tavakilian, 1993; Tavakilian *et al.*, 1997). The objective of this study was to further investigate this association by quantifying whether different cerambycid species emerged from (1) five different species of Lecythidaceae, (2) branches at canopy stratum or ground stratum, and (3) branches cut during the dry season or the rainy season. The first two variables were selected to address Erwin's assumptions about the specialization of tropical insects.

Cerambycidae

Cerambycids constitute one of the largest groups of insects in the world, with approximately 35 000 described species (Lawrence, 1982). The family has clearly undergone a massive diversification in concert with the angiosperms (Farrell, 1998). They have a cosmopolitan distribution, but are particularly diverse in the tropics. Over 1400 species have been documented in French Guiana (Hequet & Tavakilian, 1996), while there are fewer than 1000 cerambycid species in the United States and Canada (Arnett, 1988). Cerambycids play a very important ecological role in the reduction of wood to humus. They can also make an unfavourable economic impact, because they are prone to attack cut logs before they are processed and thereby degrade the quality of the resulting lumber (Linsley, 1958).

Adult beetles feed on a wide range of plant parts including flowers, nectar, fruits, leaves, roots, and bark. The adults essentially live to mate, usually on the host tree. The olfactory response, mediated by sensilla on the antennae, is presumed to be critical in the location of an appropriate site for mating and oviposition. Most larvae feed underneath bark, and pupate in wood or bark (Linsley, 1959, 1961). The more primitive taxa, whose larvae often develop in long-dead or decomposing wood, are generally polyphagous, while those taxa whose larvae develop in living wood are the most narrowly host specific. Most cerambycids, however, attack damaged or dying trees where persistent bark protects the immature stages from desiccation (Linsley, 1959, 1961).

Three cerambycid species belonging to the genus *Palame* Bates—*Palame anceps*

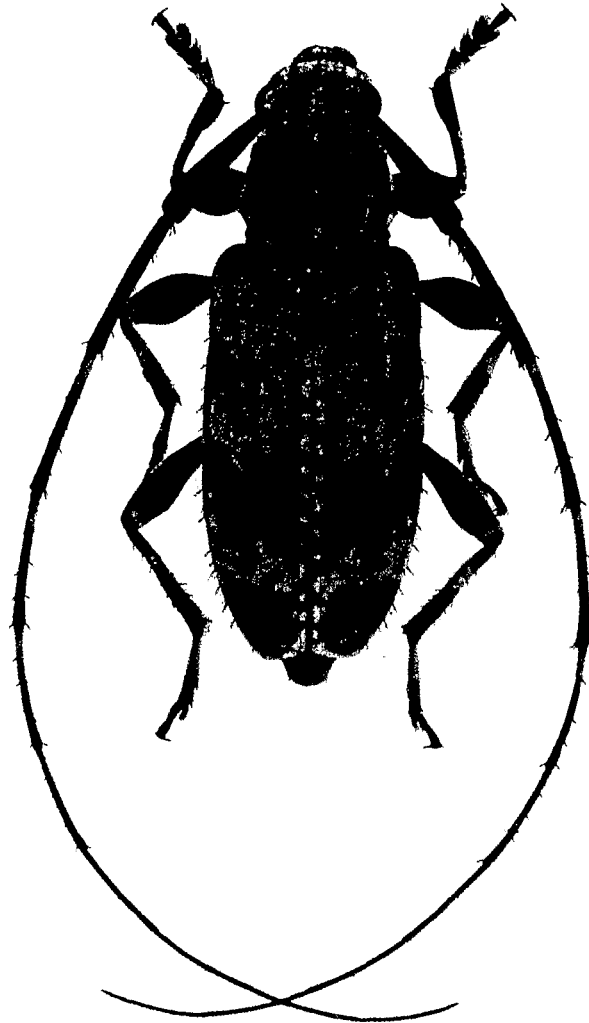


Figure 1. *Palame crassimana* Bates (bicolor form), female, 8 mm, Lecythidaceae specialist.

(Bates), *P. crassimana* Bates (Fig. 1), and *P. mimetica* Monné—accounted for almost half of the individual cerambycids reared during this study. In French Guiana, these three species are apparently associated exclusively with trees belonging to the Brazil nut family (Tavakilian, 1993; Tavakilian *et al.*, 1997). Like many of the beetles associated with Lecythidaceae, they are cryptic, crepuscular insects belonging to the huge tribe Acanthocinini (subfamily Lamiinae). *Palame anceps*, *P. crassimana*, and *P. mimetica* are well documented in both Brazil and French Guiana (Monné & Giesbert, 1994; Tavakilian *et al.*, 1997). *Palame crassimana*, which includes at least three morphological forms (Tavakilian, pers. obs.), also occurs in Guyana and Peru, and *P. mimetica* also occurs in Venezuela (Martins & Monné, 1972; Monné, 1985). *Palame* includes two additional species, *Palame aeruginosa* and *P. vitticole*, currently known only from Brazil (Monné, 1985).

Lecythidaceae

Lecythidaceae is a comparatively small plant family (comprising about 300 woody species belonging to 20 genera) with a Pan-tropical distribution (Mori & Prance, 1993). The greatest diversity is found in the Neotropical subfamily Lecythidoideae, and 52 species belonging to seven genera are found in the Guianas (Mori & Prance, 1993; Prance & Mori, 1979). Although there are some small understory trees, the majority are canopy trees or emergents (Mori & Prance, 1993). In several lowland tropical forests, this family is extremely important, both in terms of the number of individuals and species present (Mori & Boom, 1987). They are most easily identified in the field by the fallen androecia of their distinctive flowers, or by their conspicuous woody fruits.

The five species investigated in this study were *Corythophora amapaensis* Pires ex S. A. Mori & Prance, *Couratari stellata* A. C. Smith, *Eschweilera coriacea* (A. P. de Candolle) S. A. Mori, *Gustavia hexapetala* (Aublet) J. E. Smith, and *Lecythis poiteaui* Berg. These trees, representing the five genera of Lecythidaceae commonly encountered in French Guiana, were selected because they were relatively abundant at the study site. All species are canopy trees or emergents, with the exception of *G. hexapetala*, a slender understory species. They flower profusely and leave the ground carpeted with fallen corollas, also with the exception of *G. hexapetala*, which produces relatively few flowers over a long period of time. *Lecythis poiteaui* flowers during the early rainy season, *G. hexapetala* peaks during the late rainy season, and the remaining taxa flower during the dry season. *Corythophora amapaensis* (F. G. and Amapá, Brazil) and *L. poiteaui* (F. G., Surinam, and eastern Amazonia) have somewhat restricted distributions, while *C. stellata* (Guianas, western and central Amazonia), *E. coriacea* (Guianas, the Amazon Basin, and west of the Andes in Panama and Columbia), and *G. hexapetala* (Guianas, Amazonia, and north-central Venezuela) are widespread (Mori & Prance, 1990, 1993).

MATERIAL AND METHODS

Study site in central French Guiana

This study was conducted in the lowland moist forest surrounding Les Eaux Claires, a homestead approximately 7 km N of the village of Saül, French Guiana (3°37–39'N, 53°12–13'W). The forest surrounding Saül persists in a relatively undisturbed state (Mori & Boom, 1987), and the flora of central French Guiana is fairly well-known (Mori *et al.*, 1997, in prep.). The region is quite hilly, although most localities are between 200 and 400 meters above sea level (Mori & Brown, 1994). The headwaters for French Guiana's major river systems arise here and the area is dissected by many streams (Mori *et al.*, 1997), but the soils are generally well-drained. Rainfall measurements made at Les Eaux Claires from mid-September, 1995, through mid-August, 1996, using a Tru-Chek rain gauge, documented a cumulative rainfall of 2374 mm. There are usually two dry periods: a well-defined dry season between July and November, and a second, abbreviated dry spell during March or early April.

Experimental design

Prior to the dry season cut, five trees in each of the selected species of Lecythidaceae (*Corythophora amapaensis*, *Couratari stellata*, *Eschweilera coriacea*, *Gustavia hexapetala*, and *Lecythis poiteauii*) were located at the study site by S. A. Mori. All trees were located within 1 km of the homestead, either along the Route de Bélizon, a dirt road that originates in Saül and passes Les Eaux Claires, or along the Sentier Botanique, a trail that ascends a ridge E of Les Eaux Claires. Each tree was assigned an identifying letter, and its location, diameter breast height (DBH), estimated height, and fertility status were recorded. Herbarium vouchers were collected and are on deposit at CAY and NY. Small wood samples were also collected from the study trees and preserved in methanol for part of an ongoing investigation into the chemical attributes of cerambycid host plants.

The cerambycids investigated in this study typically lay their eggs in freshly killed wood, and therefore branches were severed from the study trees using various rope climbing technologies (Perry, 1978). The first cut took place in mid dry season (September 15–24, 1995). Two individual branches were sawn from each sample tree approximately 60 cm from the fork. The branch stubs that remained attached to the tree were girdled to kill them. Equivalent lengths were sawn from the branches on the ground. These canopy and ground level samples hereafter referred to as 'Snacks', and the leftover branches, hereafter referred to as 'Debris', were all labelled.

The rainy season cut took place about 6 weeks after the onset of the rainy season (January 4–10, 1996). At this time, all dry season snacks were placed into individual cages constructed from plastic screen. The debris was also collected, but due to a shortage of cage materials, varying numbers of branch segments from a particular tree species were consolidated in a single cage, hereafter referred to as a 'Big Cage'. The big cages contributed additional data about associations between cerambycid species and host tree species, as well as stratum preference and seasonality, but it was not possible to document the individual host tree for emerging cerambycids.

We initially followed the dry season protocol during the rainy season cut, but several modifications were made due to the time constraints of the principal tree climber and inclement weather. One replicate was dropped from each of the five tree species, leaving a total of 20 trees in the study. We reluctantly curtailed the canopy portion of the experiment, and only prepared canopy snacks for *E. coriacea* and *L. poiteauii* (nocturnal observations of cerambycid visits had suggested that these species would be the most productive). A single branch was severed from each of the remaining trees, and two snacks were sawn from the same branch. A couple of days into the rainy season cut, we realized that many of the canopy snacks girdled during the dry season cut had not actually died, but had simply resprouted! Thenceforth, the canopy snacks were prepared by completely severing the 60 cm samples and rigging them upon pulleys, so that they dangled in the canopy. All of the *E. coriacea* and half of the *L. poiteauii* canopy snacks were placed on pulleys, but *L. poiteauii* canopy snacks were left girdled on two of the four replicates. The branches prepared during the rainy season were collected late March through April. Snacks were placed in individual cages, and debris was again consolidated in big cages.

All cages were monitored continuously for the emergences of adult beetles through mid-August, 1996. The branches that still seemed productive at this time were the rainy season canopy snacks, and their cages continued to be monitored by a local assistant through November, 1996. Each beetle was given a preliminary identification

to species, measured from the anterior portion of the scape to the tip of the elytra, and preserved in alcohol. Species were subsequently determined and individuals were sexed by the second author. Some of the rarer cerambycids were retained in Cayenne, and the others were transported to the American Museum of Natural History for dry-mounting. A list of all emergences is available on request.

Statistical tests (contingency tables analysed by G -test, using the program JMP SAS) probed for non-random associations between beetle and branch. They were run for the number of individuals reared in the following complexes: (1) *Palame* species \times Tree species, (2) *Palame* species \times Season, (3) Season \times Stratum (all *Palame* spp.), (4) *P. crassimana* Form \times Tree species, (5) *P. crassimana* Form \times Season, and (6) *P. mimetica* Tree species \times Season. Data from the snacks and the big cages were pooled in these tests because, in the case of *Palame* spp., the vast majority of individuals associated with ground level branches emerged from debris in the big cages. The host associations of the few individuals that did emerge from the snacks were fully consistent with those from the big cages (Berkov, 1999). Due to modifications in protocol, there were different numbers of available branch sections in each comparison. We do not feel that this biased our results because most were quite sparsely colonized (even eliminating totally non-productive branches from the analysis, the range of emergences from snacks was 1–99, the mean \pm SE was 12.01 ± 2.01 , and the median was 6).

RESULTS

The branch segments ($n=406$) prepared during these experiments gave rise to a total of 1813 individual cerambycid beetles belonging to 37 species (Table 1). Three species belonging to *Palame* Bates were overwhelmingly well-represented, accounting for 48% of the individuals reared. *Palame* spp. demonstrated very different patterns of host plant utilization, ranging from restricted to widespread within Lecythidaceae (Table 2). Each species was present throughout the year, although there were different peaks in abundance (Fig. 2). (In subsequent discussions of seasonality, 'dry season' and 'rainy season' refer to the time that the branches were cut, although most emergences from dry season branches occurred during the rainy season, and some emergences from rainy season branches occurred during the subsequent dry season). *Palame* spp. were present at canopy and ground level, although there was a seasonal shift in stratum (Fig. 2).

Palame anceps (Bates), ($n=160$, Table 2) was associated exclusively with *Eschweilera coriacea*. These beetles were present throughout the year, although there was a rainy season spike (Fig. 2). *Palame anceps* was associated with both forest strata, but 83% of the emergences from branches cut during the dry season were from those left at ground level (Table 3). On the contrary, *P. anceps* emerged solely from canopy level snacks prepared during the rainy season. The rainy season ground level snacks were completely devoid of beetles, and even the debris gave rise to a diminished and impoverished complement of cerambycids that did not include *Palame* spp.

Palame crassimana Bates, ($n=402$, Table 2) proved to be the only cerambycid in this study that arose in substantial numbers from four of the five Lecythidaceae species investigated. *Palame crassimana* was also present throughout the year, although in this case 83% of the individuals arose from dry season branches (Table 3).

TABLE 1. Cerambycid species reared from Lecythidaceae at Les Eaux Claires, French Guiana. Cerambycid species are listed in alphabetical order, and those not previously reared from Lecythidaceae are marked with an asterisk. TOTAL: total number of individuals reared. Host Plant: individuals reared from each of the five host trees (CA = *Corythophora amapaensis*, CS = *Coulatari stellata*, EC = *Eschweilera coriacea*, GH = *Gustavia hexapetala*, and LP = *Lecythis poiteaui*). H/S: Beetle species represented by at least two host records are classified according to their host specificity as generalists (G), or specialists associated with a single plant species (S/SP), genus (S/GEN) or family (S/FAM). There are insufficient data (ISD) to classify beetles represented by a single host record. A beetle is considered a specialist at the designated level when 90% of the host records are in accord. Host spp: the total number of hosts documented to date (it is assumed that continued sampling would generate additional host records). Data from Tavakilian *et al.* (1997) were included in the classification of specificity and the number of documented hosts. Stratum: individuals reared from branches left at ground (G) or canopy (C) stratum. S/P: classification of stratum preference (G = ground, C = canopy, G/C = both strata, ISD = insufficient data). We hypothesize a stratum preference for beetles represented by at least 10 individuals from at least two hosts, when at least 95% of the individuals emerged from branches at a particular level. In the classifications of host specificity and stratum preference each snack was considered a separate host. All branch segments in a big cage were considered a single host because it was impossible to precisely trace the source of an emerged beetle

Cerambycid species	# Reared	Host Plant					H/S	Host spp.	Stratum		S/P
		CA	CS	EC	GH	LP			G	C	
<i>Carterica</i> sp.*	9	-	-	-	9	-	S/SP	1	9	-	ISD
<i>Carterica</i> sp.*	2	-	-	-	2	-	S/SP	1	2	-	ISD
<i>Ceragenia lebrueuri</i> Buquet in Guérin-Méneville*	1	-	-	-	-	1	G	3	1	-	ISD
<i>Colobothea bisignata</i> Bates*	4	-	2	-	2	-	S/FAM	2	1	3	ISD
<i>Eburodacrys sexmaculata</i> (Olivier)*	1	-	-	-	-	1	G	4	-	1	ISD
<i>Eburodacrys</i> sp. 1282*	3	-	-	3	-	-	G	2	3	-	ISD
<i>Eupromerella clavator</i> (Fabricius)*	20	-	-	-	20	-	G	2	20	-	G
<i>Hesychotypa jaspidea</i> (Bates)*	6	-	5	-	-	1	G	3	6	-	ISD
<i>Hesychotypa liturata</i> (Bates)*	2	-	-	-	2	-	G	3	2	-	ISD
<i>Mecomelopus triangularis</i> (Laporte & Gory)*	15	2	-	-	-	13	G	35	15	-	G
<i>Nealcidion badium</i> Monné & Delfino*	1	-	-	-	1	-	ISD	1	1	-	ISD
<i>Neobaryssinus marianae</i> (Martins & Monné)	18	-	18	-	-	-	S/GEN	3	5	13	G/C
<i>Neoeutrypanus mutilatus</i> (Germar)	93	9	2	2	-	80	S/FAM	7	67	26	G/C
<i>Neoeutrypanus nobilis</i> (Bates)*	5	-	-	5	-	-	ISD	1	-	5	ISD
<i>Neoeutrypanus</i> sp. 915*	69	-	-	-	-	69	S/SP	1	2	67	C
<i>Neopalame</i> sp. 851	10	10	-	-	-	-	S/FAM	2	4	6	G/C
<i>Nesozineus</i> sp.*	3	-	-	-	3	-	S/SP	1	1	2	ISD
<i>Oedopeza apicale</i> (Gilmour)*	9	-	1	-	8	-	G	8	9	-	ISD
<i>Oedopeza leucostigma</i> Bates	232	-	2	229	-	1	S/FAM	6	224	8	G
<i>Oreodera melzeri</i> Monné & Fragoso*	1	-	-	-	-	1	G	2	1	-	ISD
<i>Oreodera simplex</i> Bates*	158	-	-	158	-	-	S/SP	1	157	1	G
<i>Ozineus</i> sp.*	66	-	-	66	-	-	S/SP	1	43	23	G/C
<i>Palame anceps</i> (Bates)	160	-	-	160	-	-	S/GEN	5	50	110	G/C
<i>Palame crassimana</i> Bates	402	114	-	93	39	156	S/FAM	13	208	194	G/C
<i>Palame mimetica</i> Monné	316	3	-	29	2	282	S/FAM	15	217	99	G/C
<i>Peribocum pubescens</i> (Olivier)	102	2	-	-	7	93	S/FAM	17	91	11	G/C
<i>Pistonax albolinitus</i> (Bates)*	1	1	-	-	-	-	ISD	1	1	-	ISD
<i>Stratone rufotestacea</i> Thompson	1	1	-	-	-	-	S/FAM	2	1	-	ISD
<i>Sympersasmus thoracicus</i> (White)*	1	-	-	-	-	1	G	4	1	-	ISD
<i>Taurolema bellatrix</i> Thomson*	11	-	-	-	11	-	S/SP	1	-	11	C
<i>Xenofrea lineatipennis</i> Zajciw*	3	-	-	-	-	3	S/SP	1	-	3	ISD
<i>Xenofrea</i> sp. 662*	16	-	-	16	-	-	S/SP	1	4	12	G/C
<i>Xenofrea</i> sp. 714*	2	-	-	2	-	-	ISD	1	-	2	ISD

continued

TABLE 1. *continued*

Cerambycid species	# Rearcd	Host Plant					H/S	Host spp.	Stratum		S/P
		CA	CS	EC	GH	LP			G	C	
<i>Xylogates elaineae</i> Gilmour	35	-	-	33	-	2	S/FAM	7	12	23	G/C
<i>Xylogatina pulchra</i> (Lane)	24	-	-	-	-	24	S/FAM	12	24	-	G
Genus sp. 229*	10	-	1	-	7	2	S/FAM	3	-	10	C
Genus sp.*	1	-	-	1	-	-	ISD	1	-	1	ISD
TOTAL	1813	142	31	797	113	730			1182	631	

TABLE 2. *Palame* spp. reared from five Lecythidaceae tree species. CA = *Corythophora amapaensis*, CS = *Couratari stellata* (* = eliminated from the statistical analysis because no *Palame* emerged), EC = *Eschweilera coriacea*, GH = *Gustavia hexapetala*, LP = *Lecythis poiteaui*. Emergences from both snacks and big cages are included. ($G=684.8$, $df=6$, $P=0.0000$)

Beetle species	Tree species					Total
	CA	CS*	EC	GH	LP	
<i>P. anceps</i>	0	0	160	0	0	160
<i>P. crassimana</i>	114	0	93	39	156	402
<i>P. mimetica</i>	3	0	29	2	282	316
All <i>Palame</i> spp.	117	0	282	41	438	878

Emergences from canopy and ground stratum branches were almost equally divided (Table 3), but, like *P. anceps*, during the rainy season *P. crassimana* reproduced exclusively at canopy level.

It should be noted here that two of the morphological forms currently treated as *Palame crassimana* Bates were reared during the described experiments. Although we presently lack sufficient data to describe these forms as separate species (Berkov, 1999), in this locality they are clearly behaving as such. The abundant 'bicolor form' reproduced almost exclusively during the dry season, and the less common 'unicolor form' almost exclusively during the rainy season (Table 4). Should additional data support the delimitation of these forms as separate species, this would affect our interpretation of *P. crassimana* phenology. It would not, however, significantly alter our perception of *P. crassimana* (bicolor form) as the 'least picky' Lecythidaceae specialist. The bicolor form did emerge from four of the five potential hosts, while the unicolor form emerged exclusively from *Eschweilera coriacea* (Table 4).

Palame mimetica Monné ($n=316$, Table 2) made a partial seasonal switch in host plant utilization. The vast majority of individuals that emerged from dry season branches (98%) were associated with *Lecythis poiteaui* (Table 5). In contrast, 54% of the individuals that emerged from rainy season branches were associated with *Eschweilera coriacea* (which did not yield a single individual during the dry season). *Palame mimetica* was present throughout the year, although, like *P. crassimana*, 83% of the emergences were from dry season branches (Table 3). Like other *Palame* spp., *P. mimetica* made a seasonal shift in stratum: 83% of dry season emergences were from ground level branches, while rainy season emergences were solely from canopy snacks (Table 3).

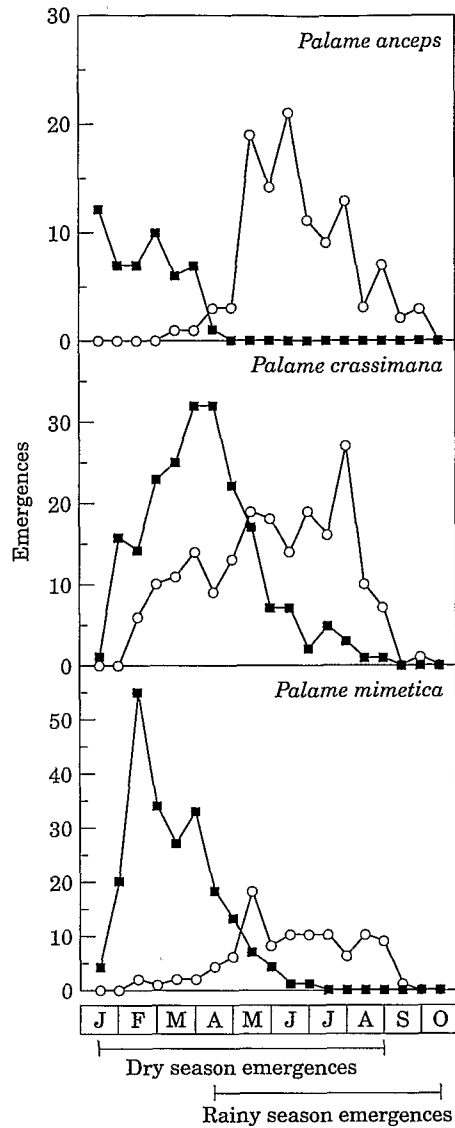


Figure 2. Emergences from (■) ground and (○) canopy stratum branches for three *Palame* species. The dry season branches were cut in September and collected in January, and the rainy season branches were cut in January and collected in April. During the dry season, *Palame* spp. reproduced at both forest strata, but during the rainy season they reproduced exclusively at canopy stratum.

DISCUSSION

Host affinities of Palame spp.

In this study, *Palame anceps* was associated exclusively with *Eschweilera coriacea*, *P. crassimana* was associated with four of the five Lecythidaceae taxa investigated, and *P. mimetica* was primarily associated with *Lecythis poiteaui* during the dry season, but

TABLE 3. Seasonal change in stratum association. The number of individuals reared from Ground and Canopy level branches prepared during the Dry and Rainy seasons is listed. Emergences from both snacks and big cages are included. (*Palame* spp. \times Season: $G=125.8$, $df=2$, $P=0.0000$; Season \times Stratum, for All *Palame* spp.: $G=441$, $df=1$, $P=0.0000$).

Beetle species	Stratum	Season		Stratum Total
		Dry	Rainy	
<i>P. anceps</i>	Ground	50	0	50
	Canopy	10	100	110
Seasonal total		60	100	
<i>P. crassimana</i>	Ground	208	0	208
	Canopy	125	69	194
Seasonal total		333	69	
<i>P. mimetica</i>	Ground	217	0	217
	Canopy	45	54	99
Seasonal total		262	54	
All <i>Palame</i> spp.	Ground	475	0	475
	Canopy	180	223	403
Seasonal total		655	223	

TABLE 4. Two morphological forms of *Palame crassimana* reared from Lecythidaceae. The number of individuals belonging to the 'Bicolor' and 'Unicolor' forms reared from the four host Tree species (CA = *Corythophora amapaensis*, EC = *Eschweilera coriacea*, GH = *Gustavia hexapetala*, and LP = *Lecythis poiteau*) during the Dry and Rainy seasons is listed. Emergences from both snacks and big cages are included. (Form \times Tree species: $G=260.8$, $df=3$, $P=0.0000$; Form \times Season: $G=326.2$, $df=1$, $P=0.0000$)

Form	Season	Tree species				Total
		CA	EC	GH	LP	
Bicolor form	Dry	109	22	37	153	321
	Rainy	0	0	0	1	1
Total Bicolor		109	22	37	154	322
Unicolor form	Dry	0	2	0	0	2
	Rainy	0	66	0	0	66
Total Unicolor		0	68	0	0	68

TABLE 5. *Palame mimetica*: Seasonal change in host association. The number of individuals reared from branches severed from the four host Tree species (CA = *Corythophora amapaensis*, EC = *Eschweilera coriacea*, GH = *Gustavia hexapetala*, and LP = *Lecythis poiteau*) during the Dry and Rainy seasons is listed. Emergences from both snacks and big cages are included. ($G=120.1$, $df=3$, $P=0.0000$)

Season	CA	EC	Tree species		Total
			GH	LP	
Dry	3	0	2	257	262
Rainy	0	29	0	25	54
Total	3	29	2	282	316

made a seasonal change in host utilization (Table 2). We believe that interspecific variability in host chemistry is most likely to account for the noted distribution patterns, and would like to propose some hypotheses.

Palame anceps was not the only cerambycid in this study that emerged solely from *Eschweilera coriacea*. Of the five tree species investigated in this study, *E. coriacea* gave rise to the complement of cerambycids showing the greatest host fidelity (Table

1; Berkov, 1999). Wood extracts and partitions analysed by TLC (thin layer chromatography) suggest that *E. coriacea* is exceptionally rich in saponins, a class of bitter-tasting, toxic compounds prevalent in Lecythidaceae. We hypothesize that there may be a correlation between host toxicity and the degree of specialization demonstrated by xylophagous associates. Extracts derived from the wood samples collected from each tree in this study have been screened in a series of anti-microbial bioassays (Rovira *et al.*, in press), and preliminary data do indicate that *E. coriacea* is unusually toxic.

Four of the five Lecythidaceae species investigated gave rise to *Palame crassimana* (*Couratari stellata* was the lone exception). *Couratari stellata* produces a foetid odour so strong that individual trees are often smelled before they are seen. This species gave rise to an extremely impoverished complement of cerambycids (Table 1), and although *Palame* spp. accounted for almost half of the beetles reared during this project, not a single individual emerged from *C. stellata* (Table 2). *Gustavia hexapetala*, which gave rise to relatively few individuals of *P. crassimana*, produces an odour that is slightly less offensive. Numerous cerambycid species were reared from *G. hexapetala*, but they were represented by few individuals, and several were atypical for Lecythidaceae (Table 1). The distinctive 'bouquet' apparently arises from a combination of nitrogen and sulfur compounds (Berkov, 1999), and our working hypothesis is that the putrid-smelling compounds act as deterrents to Lecythidaceae specialists seeking oviposition sites.

Palame mimetica, associated almost exclusively with *Lecythis poiteaui* during the dry season, made a partial host switch to *Eschweilera coriacea* during the rainy season (Table 5). Not only did 54% of the individuals reared from rainy season branches emerge from *E. coriacea*, but individuals were associated with three of the four available sample trees (Berkov, 1999). *Lecythis poiteaui* was the only tree species in this study that was in bloom at the time of the rainy season cut. The flowers are fairly typical of their genus in morphology: large and showy, with the androecium expanded on one side to form an open hood bearing many staminodia. They are, however, atypical in their adaptations for pollination. While many Lecythidaceae bear diurnal flowers pollinated by bees (Mori & Boeke, 1987), *L. poiteaui* anthesis is nocturnal, and the bat-pollinated flowers have the very pungent, characteristically musky odour frequently associated with this syndrome. *Palame mimetica* may be making a seasonal rejection of a favoured host plant that no longer smells right.

Stratum affinities of Palame spp.

Palame spp. emerged from both ground and canopy level branches cut during the dry season, and were particularly well represented at ground level. All three species emerged exclusively from canopy level snacks cut during the rainy season (Table 3). We originally believed that canopy level branches would be inherently less hospitable due to the increased exposure to light, a greater chance of desiccation, and the reduced stability of dead branches dangling in the canopy (which, given the windier microclimate, might be prone to plummet to the ground carrying a fragile load of easily bruised larvae). Contrary to our expectations, canopy branches were well-colonized throughout the year (with the exception of those girdled branches that resprouted and yielded to vastly diminished numbers of cerambycids). Canopy

level was incontestably the stratum of choice during the rainy season (Fig. 2), and *Palame* spp. (as well as other cerambycid species) proved quite capable of exploiting this somewhat ephemeral, but certainly renewable, resource.

The distributions of many insects are influenced by available moisture. During the extended dry season in a seasonal tropical forest, insects have proved to be more abundant and diverse in moister habitats (Janzen & Schoener, 1967). On the other hand, insects in seasonally inundated forests may need to escape the influx of water. Options for terrestrial arthropods are proposed to include (1) survival of the immersion (by egg or dormant adult) in the soil or under loose bark, (2) migration to adjacent *terra firme*, (3) wholesale death followed by recolonization, or (4) migration up the trunks or into the canopy (Adis, 1984; Irmiler, 1979). The majority of beetle species investigated by Irmiler (1979) did migrate to a higher forest stratum. This study suggests that some insects living in more uniformly moist, non-inundated forests also make a seasonal migration to the treetops. Several possible explanations may contribute to this phenomenon.

Branches sections left at ground level during the rainy season were in an extremely wet environment, and quite a few sprouted new foliage. As noted, dry season canopy snacks that resprouted gave rise to very few cerambycids (Berkov, 1999). It is possible that the still living branches failed to provide cues to satisfy female cerambycids seeking oviposition sites, or a persistent vascular flow might have been detrimental to larvae. The ground level branches that did die were particularly prone to fungal attack, not likely to be advantageous for developing larvae. Finally, during the rainy season the atmosphere at ground level might simply be so saturated with water that the volatile molecules that initially attract a cerambycid to a potential host plant fail to circulate efficiently. Whatever the explanation, the capacity to breed even in very small dead branches at canopy level seems to assure reproductive success throughout the year.

Approximations of tropical insect specificity

We believe that one of the most important legacies of Erwin's 1982 paper was the attention it drew to the dearth of empirical research illuminating the dynamics of plant-insect interactions in tropical forests. It is not our intention to enter the fray by generating any sort of estimate of the potential number of arthropods, but we would like to comment upon some of the assumptions made in the initial paper (that many tropical insects are restricted to the canopy and/or highly host specific) that led to the conclusion that the vast majority of tropical arthropods are as yet undescribed.

We hypothesized a stratum preference for beetles represented by at least 10 individuals from at least two hosts, when at least 95% of the individuals emerged from branches at either ground or canopy level (Table 1). Eighteen of the 37 cerambycid species reared in this study were sufficiently abundant to classify. Of the 18 species, only three (17%) were restricted to the canopy level branches, and five (28%) were associated almost exclusively with ground level branches. Ten species (55%), including *Palame* spp., were present at both ground and canopy level. This is not consistent with the Erwin's assertion that two out of three tropical insects are restricted to the canopy, although, as with *Palame* spp., there may be a seasonal association.

Our results also deviated from stratum preferences reported for cerambycids in a lowland tropical forest in Sulawesi (Hammond, Stork & Brendell, 1997). Hammond *et al.* hypothesized that although 25% of the species sampled were not sufficiently abundant to classify, 57% were tree-crown specialists, 7% were ground specialists, and only 11% were stratum generalists. Our results, as percentages of all species reared, were 51% insufficient data, 8% canopy specialists, 13% ground specialists, and 27% stratum generalists. The sampling regime in Sulawesi was comprehensive, but only adult cerambycids were sampled, which may have biased the results.

Erwin formulated his estimates about host-specificity by sorting beetles into guilds delimited by feeding strategy: herbivore, predator, fungivore and scavenger. He thought that herbivores would be more likely to become dependent upon specific host plants than, for instance, predators (typically opportunistic in their search for food). If one accepts a seminal role for host plant chemistry in the development of host specificity, different types of herbivory should also predispose different insects to different degrees of host fidelity (some of the following are reviewed in Basset, 1992). Leaf miners, which spend their larval period entirely surrounded by and consuming living plant tissue, should be prone to great selectivity. Insects feeding upon plant parts harbouring high levels of defensive compounds, such as seeds, should be predisposed to selective feeding strategies. Herbivores that macerate living plant tissue should show greater host fidelity than those that suck sugar-rich sap from the vascular tissue. Xylophagous species that spend the larval period surrounded by freshly killed tissue (with cellular contents still somewhat intact) should show greater specificity than those attacking wood in an advanced state of decay.

Are these predictions well-supported? About 90% of the caterpillars in a Costa Rican deciduous forest seem to feed locally on either a single host plant species or on a restricted group of taxonomically or chemically related hosts (Janzen, 1988), but no distinction was made between the specificity of concealed versus exposed feeders. The majority (75%) of the coleopteran seed predators at the same site appear to be locally monophagous, but polyphagous over their geographic range (Janzen, 1980, 1981). A variety of adult bugs that feed on floral resources and seeds are primarily associated with a single plant species or plant part at any one time, but may attack numerous unrelated hosts throughout the year (Janzen, 1981). Grasshopper species at La Selva, Costa Rica, range from being monophagous to polyphagous, but those that oviposit into or on the host plant, rather than in the soil, have the most restricted host ranges (Marquis & Braker, 1994). Leaf beetle species belonging to the chrysomelid subfamily Alticinae usually show high specificity, but may nevertheless be found feeding on different host plants at the end of the season (Jolivet, 1988). Most species of phloem-tapping treehoppers at La Selva are indeed polyphagous (Marquis & Braker, 1994). Scolytids that feed on phloem do appear to have much narrower host ranges than those that feed on xylem (Mattson *et al.*, 1988). Generalizations about feeding strategy seem logical, but in the case of *Palame*, three species with similar life history attributes and some overlap in host utilization showed different patterns of host fidelity.

Characteristics of host plant taxa must also be examined. Erwin (1982) investigated the arthropod fauna of a single tree species, but was this tree typical of its family (Tiliaceae) or of other trees composing tropical forests? In French Guiana, extensive sampling (200 tree species representing 38 families) demonstrated that different plant families give rise to vastly differently ratios of specialist to generalist cerambycids

(Tavakilian *et al.*, 1997). An analysis of free-living herbivores collected from ten taxonomically unrelated trees in Papua New Guinea also suggests that different trees host highly variable proportions of specialists (Basset, 1996a, b). The family Tiliaceae (order Malvales) has not been well investigated, but seems unlikely to host a highly specialized fauna. In French Guiana, Malvales hosted a cerambycid fauna in which generalist species outnumbered specialist species two to one (Tavakilian *et al.*, 1997). *Argyrodendron actinophyllum* (family Sterculiaceae, order Malvales) appears to support a free-living herbivore fauna including few specialists (Basset, 1992). Lecythidaceae, on the other hand, hosts a relatively specialized cerambycid fauna. Species of Lecythidaceae hosting the most specialized complements of cerambycids are highly toxic (Rovira *et al.*, in press), extremely abundant, have widespread geographic distributions, and numerous congeners (Berkov, 1998).

Sampling protocol can also make a profound impact upon experimental results. Cerambycids have been reared from Lecythidaceae at two localities in French Guiana (Tavakilian *et al.*, 1997, and this study). The mission of the first project was to reveal the identities of cerambycids associated with as many tree species as possible. Ensuing cuts were taxonomically diverse, simulating a natural disaster such as a hurricane. Ovipositing cerambycids were able to select their favoured hosts from a broad menu of felled trees. Entire trees were cut, but only a small portion of each tree was caged. Lecythidaceae, as sampled in this scenario, gave rise predominately to specialist species (65%) and very few generalist species (6%). Most specialists were classified as family level specialists.

At Les Eaux Claires, the objective was to elucidate the associations between a select group of cerambycids and their host plants in the Brazil nut family. Branches were cut from replicates of five tree species, creating an unnatural abundance of freshly killed Lecythidaceae. Although branches were cut in lieu of trees, much of the wood was ultimately caged. Lecythidaceae, as sampled in this scenario, gave rise to numerous generalist species (27%), although they were typically represented by very few individuals (Table 1). More generalists may have oviposited in Lecythidaceae because it was abundantly available, or they were simply more likely to be documented because more of the available wood was caged. With adequate replication, specialists had ample opportunity to select their favoured host, and *Palame crassimana* was the only Lecythidaceae specialist that emerged in abundance from several host species.

Erwin (1982) included wood-borers in the herbivore guild (Basset, 1992), thereby implying that 20% might be dependent upon a single host species. Basset (1992, 1996b) suggested that cerambycids should be considered scavengers, and that many wood-borers are actually generalists. In French Guiana, when a cerambycid feeding strategy can be proposed, specialists outnumber generalists by more than three to one (Tavakilian *et al.*, 1997). Many species are classified as family level specialists, and those that currently appear to be monophagous are expected to accumulate additional host records over time.

Although Lecythidaceae is one of two plant families associated with a very well-defined guild of specialist cerambycids, compared to other specialized tropical herbivorous insects (see references in Gaston, 1993 and Marquis, 1991) they appear to have relatively broad host ranges (Table 1). We caution against making overly simplistic comparisons among studies, in part because the results are so sensitive to modifications in protocol. In this study, the mean number of host species for all cerambycid species reared \pm SE was 4.7 ± 1.09 , but the mean was 7.06 ± 2.00 for the cerambycid species reared from Lecythidaceae in Tavakilian *et al.* (1997).

Finally, Erwin (1982) projected that for each currently described arthropod species, at least 29 unnamed species (almost 97% of the presumed total) were still waiting in the wings. A comprehensive sampling of Hemiptera in Sulawesi revealed a mean of 62.5% undescribed species per family, leading to a surprisingly low estimate (1.84–2.57 million) of the global arthropod fauna (Hodkinson & Casson, 1990). In this study, 30% of the cerambycid species reared have not yet been described. Almost 42% of the cerambycid species documented in French Guiana over 15 years are currently being described (Hequet & Tavakilian, 1996; Tavakilian, in prep.). It is clear that many tropical insects do await description, but the 30% revealed in this study do not begin to approach Erwin's estimate. Cerambycids are, of course, among the megafauna of the insect world and relatively well-investigated.

In short, in French Guiana the majority of cerambycid species that attack freshly cut wood are likely to be host specific but not monophagous. Stratum generalists appear to be slightly more common than stratum specialists. Relatively few species are restricted to the canopy, although it appears that a seasonal association can make a dramatic impact on insect life history. These results are not consistent with Erwin's assumptions about the specificity of tropical insects.

Studies of tropical insects are difficult to compare due to differences in protocol, geographic location, forest type and other confounding variables. Nevertheless, the results of this study are in accord with a growing body of literature suggesting that many tropical insects may be somewhat flexible in their requirements. Seasonal or regional changes in patterns of host utilization appear to be rather common. We suspect that monophagy as most narrowly defined (one insect species dependent upon a single plant species) is actually a relatively uncommon phenomenon in high diversity tropical forests. Strict monophagy is likely to be an artifact of sampling protocol: many insects may have the capacity to exploit related, if less than optimal hosts, when the need arises.

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REFERENCES

- Adis J. 1984. Seasonal igapó-forests of central Amazonian blackwater rivers and their terrestrial arthropod fauna. In: Sioli H, ed. *The Amazon: Limnology and landscape ecology of a mighty tropical river and its basin*. Dordrecht: Junk Publishers, 245–268.
- Arnett RH. 1988. Present and future of systematics of the Coleoptera in North America. In: Kosztarab M, Schaefer CW, eds. *Systematics of North American insects and arachnids: Status and needs*. Blacksburg, Virginia: Virginia Polytechnic Institute and State University, 165–173.
- Basset Y. 1992. Host specificity of arboreal and free-living insect herbivores in rainforests. *Biological Journal of the Linnean Society* 47: 115–133.
- Basset Y. 1996a. Local communities of arboreal herbivores in Papua New Guinea: Predictors of insect variables. *Ecology* 77: 1906–1919.
- Basset Y. 1996b. How many species of host-specific insects feed on a species of tropical tree? *Biological Journal of the Linnean Society* 59: 201–216.
- Berkov A. 1999. Neotropical cerambycid beetles and their Lecythidaceae host plants: Variations on a theme. D. Phil. Thesis, The City University of New York.
- Erwin TR. 1982. Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin* 36: 74–75.
- Erwin TR. 1988. The tropical forest canopy: The heart of biotic diversity. In: Wilson EO, ed. *Biodiversity*. Washington, DC: National Academy Press, 123–129.
- Erwin TR. 1991. How many species are there?: Revisited. *Conservation Biology* 5: 330–333.
- Farrell BD. 1998. “Inordinate fondness” explained: Why are there so many beetles? *Science* 281: 555–558.
- Gaston KJ. 1991a. The magnitude of global insect species richness. *Conservation Biology* 5: 283–292.
- Gaston KJ. 1991b. Estimates of the near-imponderable: A reply to Erwin. *Conservation Biology* 5: 564–566.
- Gaston KJ. 1993. Herbivory at the limits. *Trends in Ecology & Evolution* 8: 193–194.
- Hammond PM. 1992. Species inventory. In: Groombridge B, ed. *Global Biodiversity, status of the Earth's living resources: A report compiled by the World Conservation Monitoring Center*. London: Chapman & Hall, 17–39.
- Hammond PM, Stork NE, Brendell MJD. 1997. Tree-crown beetles in context: a comparison of canopy and other ecotone assemblages in a lowland tropical forest in Sulawesi. In: Stork NE, Adis J, Didham RK, eds. *Canopy arthropods*. London: Chapman & Hall, 184–223.
- Hequet V, Tavakilian G. 1996. *Longicornes de Guyane*. Cayenne, French Guiana: Silvolab.
- Hodkinson ID, Casson D. 1991. A lesser predilection for bugs: Hemiptera (Insecta) diversity in tropical rain forests. *Biological Journal of the Linnean Society* 43: 101–109.
- Irmiler U. 1979. Abundance fluctuations and habitat changes of soil beetles in central Amazonian inundation forests (Coleoptera: Carabidae, Staphylinidae). *Studies on Neotropical Fauna and Environment* 14: 1–16.
- Janzen DH. 1980. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. *Journal of Ecology* 68: 929–952.
- Janzen DH. 1981. Patterns of herbivory in a tropical deciduous forest. *Biotropica* 13: 271–282.
- Janzen DH. 1988. Ecological characterization of a Costa Rican dry forest caterpillar fauna. *Biotropica* 20: 120–135.
- Janzen DH, Schoener TW. 1967. Differences in insect abundance and diversity between wetter and dryer sites during a tropical dry season. *Ecology* 49: 96–110.
- Jolivet P. 1988. Food habits and food selection of Chrysomelidae. Bionomic and evolutionary perspectives. In: Jolivet P, Petitpierre E, Hsiao TS, eds. *Biology of Chrysomelidae*. Dordrecht: Kluwer Academic Publishers, 1–24.
- Kitchling RL, Mitchell H, Morse G, Thebaud C. 1997. Determinants of species richness in assemblages of canopy arthropods in rainforests. In: Stork NE, Adis J, Didham RK, eds. *Canopy arthropods*. London: Chapman & Hall, 131–150.
- Lawrence JF. 1982. Coleoptera. In: Parker S, ed. *Synopsis and classification of living organisms*. New York: McGraw Hill, 482–553.
- Linsley EG. 1958. The role of Cerambycidae in forest, urban and agricultural environments. *The Pan-Pacific Entomologist* 34: 105–124.
- Linsley EG. 1959. The ecology of the Cerambycidae. *Annual Review of Entomology* 4: 99–138.

- Linsley EG. 1961. *The Cerambycidae of North America: Part I. Introduction*. Berkeley: University of California Press.
- Marquis RJ. 1991. Herbivore fauna of Piper (Piperaceae) in a Costa Rican wet forest: Diversity, specificity, and impact. In: Price PW, Lewinsohn TM, Fernandes GW, Benson, WW, eds. *Evolutionary ecology in tropical and temperate regions*. New York: John Wiley & Sons, Inc., 179–208.
- Marquis RJ, Braker HE. 1994. Plant-herbivore interactions: Diversity, specificity & impact. In: McDade LA, Bawa KS, Hespenhede HA, Hartshorn GS, eds. *La Selva: Ecology and natural history of a Neotropical rain forest*. Chicago: The University of Chicago Press, 261–281.
- Martins UR, Monné MA. 1972. Caracterização de dois generos de Acanthocinini (Col., Cerambycidae). *Revista Brasileira de Entomologia* 16: 61–66.
- Mattson WJ, Lawrence RK, Haack RA, Herms DA, Charles PJ. 1988. Defensive strategies of woody plants against different insect-feeding guilds in relation to plant ecological strategies and intimacy of association with insects. In: Mattson WJ, Levieux J, Bernard-Dagan C, eds. *Mechanisms of woody plant defenses against insects: Search for pattern*. New York: Springer Verlag, 3–38.
- Mawdsley NA, Stork NE. 1997. Host-specificity and the effective specialization of tropical canopy beetles. In: Stork NE, Adis J, Didham RK, eds. *Canopy arthropods*. London: Chapman & Hall, 104–130.
- May RM. 1988. How many species are there on Earth? *Science* 241: 1441–1449.
- Monné MA. 1985. Sinopse do gênero *Palame* Bates, 1864 (Coleoptera, Cerambycidae, Lamiinae, Acanthocinini). *Revista Brasileira de Entomologia* 29: 299–304.
- Monné MA, Giesbert EF. 1994. *Checklist of the Cerambycidae and Disteniidae (Coleoptera) of the Western Hemisphere*. Burbank, California: Wolfsgarden Books.
- Mori SA, Boeke JD. 1987. Pollination. In: Mori SA, et al., The Lecythydaceae of a lowland Neotropical forest: La Fumée Mountain, French Guiana. *Memoirs of the New York Botanical Garden* 44: 137–155.
- Mori SA, Boom BM. 1987. The forest. In: Mori SA, et al., The Lecythydaceae of a lowland Neotropical forest: La Fumée Mountain, French Guiana. *Memoirs of the New York Botanical Garden* 44: 9–29.
- Mori SA, Brown JL. 1994. Report on wind dispersal in a lowland moist forest in central French Guiana. *Brittonia* 46: 105–125.
- Mori SA, Cremers G, Gracie C, Granville JJ de, Hoff M, Mitchell JD. 1997. Guide to the vascular plants of central French Guiana, Part 1. Pteridophytes, gymnosperms, and monocotyledons. *Memoirs of the New York Botanical Garden* 76: 1–422.
- Mori SA, Prance GT. 1990. *Lecythydaceae—Part II. The zygomorphic-flowered New World genera (Couroupita, Corythophora, Bertholletia, Couratari, Eschweilera, & Lecythis)*. *Flora Neotropica Monograph* 21. Bronx, New York: The New York Botanical Garden.
- Mori SA, Prance GT. 1993. *Flora of the Guianas 53. Lecythydaceae*. Gorts-van Rijn, ARA, ed. Koenigstein, Germany: Koeltz Scientific Books.
- Perry DR. 1978. A method of access into the crowns of emergent and canopy trees. *Biotropica* 10: 155–157.
- Prance GT, Mori SA. 1979. *Lecythydaceae—Part I. The actinomorphic-flowered New World Lecythydaceae (Asteranthos, Gustavia, Grias, Allantoma, & Cariniana)*. *Flora Neotropica Monograph* 21. Bronx, New York: The New York Botanical Garden.
- Rovira I, Berkov A, Parkinson A, Tavakilian G, Mori S, Meurer-Grimes B. (In press). Antimicrobial activity of Neotropical wood and bark extracts. *Pharmaceutical Biology*.
- Stork NE. 1988. Insect diversity: Facts, fiction and speculation. *Biological Journal of the Linnean Society* 35: 321–337.
- Stork NE. 1997. Measuring global biodiversity and its decline. In: Reaka-Kudla ML, Wilson DE, Wilson EO, eds. *Biodiversity II: Understanding and protecting our biological resources*. Washington, D.C.: Joseph Henry Press, 41–68.
- Tavakilian G. 1993. Etude exhaustive des insectes xylophages de la famille des Cerambycides (Coleoptera) sur un site amené à disparaître lors de la mise en eau du barrage de Petite-Saut. Progress Report for Electricité de France.
- Tavakilian G, Berkov A, Meurer-Grimes B, Mori S. 1997. Neotropical tree species and their faunas of xylophagous longicorns (Coleoptera: Cerambycidae) in French Guiana. *The Botanical Review* 63: 303–355.