Documenting plant diversity in Central French Guiana: The first step toward understanding biocomplexity

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Publication of the *Guide to the Vascular Plants of Central French Guiana* completes the first phase of a botanical inventory of central French Guiana. This floristic effort has stimulated studies of pollination biology, insect predation, forest ecology, and seed dispersal; and has promoted conservation and ecotourism. We provide examples of 1) bee pollination of species of *Corythophora* (Brazil nut family, Lecythidaceae); 2) attack of the wood of Lecythidaceae by species of cerambycid beetles; 3) life form, habitat, and nutritional mode composition of the species of the flora; 4) the importance of bats as dispersers of seeds; 5) use of plant diversity data in promoting conservation; and 6) ecotourism and how it can increase local income without damaging forest diversity and structure. We conclude that floristic inventories act as a catalyst for studies in many other disciplines and, as such, are the first step in understanding biocomplexity.

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Introduction

The plants of the Guianas have been collected and studied since the latter part of the 18th century beginning with Aublet (1775) and Linnaeus (1775). Moreover, there have been and continue to be long-term floristic projects such as the *Flora of Suriname*, *The Flora of the Guianas* (Lindeman & Mori 1989), and the *Checklist of* *the Plants of the Guianas* (Boggan *et al.* 1997). As a result, the plants of this part of South America are among the best known of all of the American tropics. Nevertheless, there is still a great deal that needs to be done to complete the inventory and as well as to understand the biocomplexity of Guianan ecosystems.

As part of the effort to document the flora of the Guianas, The New York Botanical Garden (NY) and the Institut de Recherche pour le Développement – Cayenne (IRD-CAY) have been engaged in a project called the *Guide to the Vascular Plants of Central French Guiana* since 1976. Our goals are to:

- document with herbarium collections the species of plants found in an area surrounding the village of Saül in central French Guiana (Mori *et al.* 2002b),
- furnish keys and descriptions, including photos and botanical line drawings, to facilitate the identification of plants (Mori *et al.* 1997, 2002a),
- promote studies of ecology, systematics, evolution, and conservation by providing others with the ability to identify plants included in their studies,
- encourage ecotourism as a way to generate income without destroying the forest, and
- supply data for conservation.

With the publication of the *Guide to the Vascular Plants of Central French Guiana* (Mori *et al.* 1997, 2002a), we have accomplished goals one through three. As a result of these efforts, considerable progress had been made in the other goals as well. In addition, the recent publication on the mosses of central French Guiana has expanded the inventory to the non-vascular plants (Buck 2003).

The steps we followed to gather the collections, write, and publish the *Guide* are described elsewhere (Mori & Gracie in review). Therefore, the purpose of this paper is to describe the kinds of studies that have been possible because of our floristic inventory. The *Flora of Barro Colorado Island* (Croat 1978) and the subsequent studies (Leigh *et al.* 1996) that have been stimulated by it serve as a model for what we are attempting to accomplish in central French Guiana.

As examples of the kinds of studies promoted by knowledge of the flora, we will discuss (1) the pollination of Lecythidaceae, (2) the attack of the wood of species of Lecythidaceae by cerambycid beetles, (3) the life forms, habitats, and nutritional modes of the flowering plants of central French Guiana, (4) the importance of bats as dispersers of the fruits of *Cecropia*, (5) ecotourism and how it can stimulate local economies without destroying biological diversity, and (6) knowledge of plants and how it can be used to make arguments for conservation. Additional information about our program of research in central French Guiana can be found at *Fungal and Plant Diversity of Central French Guiana* and *Bat/Plant Interactions in the Neotropics* at:

www.nybg.org/bsci/french_guiana
and
www.botanypages.org

Study area

The area of our study includes 1402.5 square km (140250 hectares) covered mostly by undisturbed, non-flooded forest between 200 m and 400 m elevation (Mori & Boom 1987; Oldeman 1974). It encompasses a rectangle in the geographic center of French Guiana between 3°30' and 3°45' N latitudes and 53° and 53°28'W longitudes (Fig. 1). The most obvious deviations from the predominant vegetation pattern are found in poorly drained areas often dominated by *Euterpe oleracea* Mart. (Arecaceae); on outcroppings of large, granitic rocks, i.e. *inselbergs* (de Granville & Sastre 1991), which occur as steep slopes surrounded by forests of varying height as at Pic Matécho;

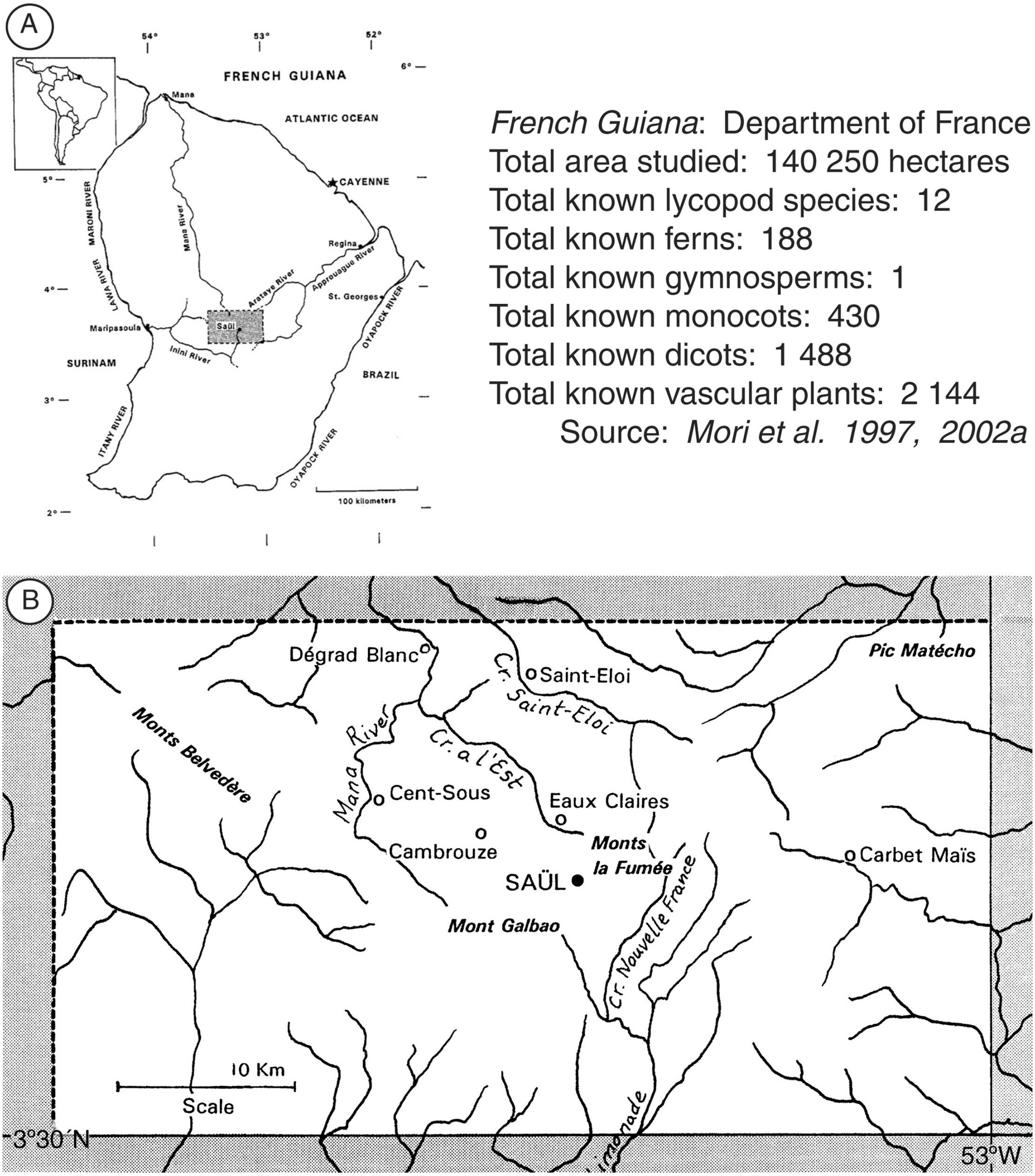

Fig. 1. Location of the study area. A. In relation to South America and French Guiana. B. The area covered by the *Guide to the Vascular Plants of Central French Guiana* (Mori *et al.* 1997).

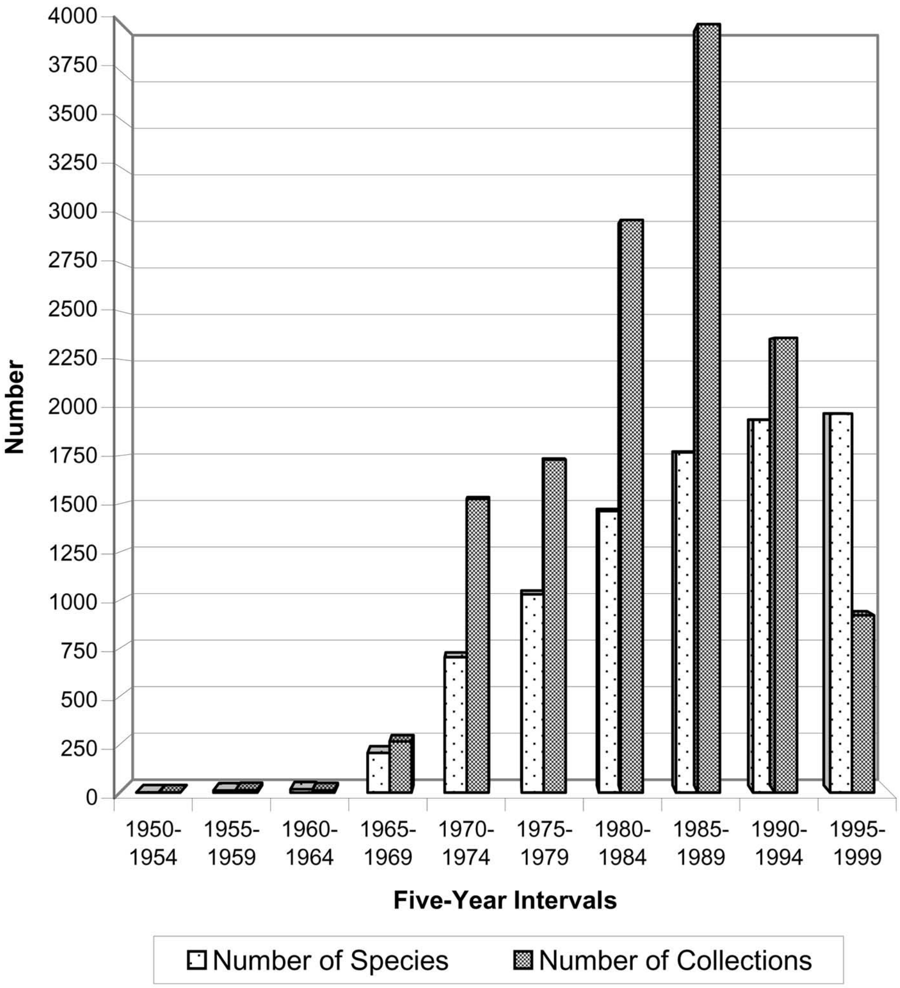

Fig. 2. Documenting plant diversity in central French Guiana. Left columns: Accumulation of vascular plant species recorded in central French Guiana over time. Right columns: Decrease in the number of specimens gathered; the number of specimen decreases as the flora of central French Guiana becomes better known.

and in limited areas of secondary vegetation found near the village of Saül and at scattered homestead sites. In addition, the zone extending from 500 m to the highest peak on Mont Galbao (762 m) consists of cloud forest. The study site does not contain any large lakes or rivers, but many small streams are present throughout the area. A small lake caused by impeded stream drainage near Pic Matécho is home to species so far found nowhere else in the area, *e.g.*, *Mayaca sellowiana* Kunth (Mayacaceae), *Nymphaea glandulifera* Rothschied (Nymphaeaceae), and *Tabebuia insignis* (Miq.) Sandwith (Bignoniaceae). There are no large areas of white sand and seasonally flooded ground and hence the associated vegetation types are lacking in central French Guiana.

Annual rainfall for central French Guiana, as recorded in the village of Saül, averages 2413 mm. There is a well defined dry season from July to November and a less pronounced and less reliable dry period for several weeks in February to March. Under the influence of NE or SE trade winds of moderate velocity (average 1,6 m/sec), temperatures vary only slightly through the year, averaging 27.1° C (Mori &

Prance 1987). The difference between the longest and shortest days of the year is approximately 35 min (List 1950).

The Vascular Plant Inventory

It is difficult to determine when enough collections have been accumulated to justify the production of a Flora. The collection process adds taxa new to science, taxa new to the flora, and new information about known taxa. If the goal of a project is simply to document the species found in a flora by providing a checklist, then only one collection per species is needed, and the total number of collections equals the total number of species in the flora. When our species accumulation curve (Fig. 2) began to level off, we decided that future discovery of species new to the flora would be minimal, and this was one consideration in determining when writing of the *Guide* could begin.

However, the format of the *Guide* required more information about species than just their presence, and this information was obtained by studying more than one collection per species. For example, information on phenology can be determined only after a species has been collected or observed for flowers and fruits throughout the year. In order to determine if we had enough collections to justify the publication of the *Guide*, we developed an indicator called the Index of Efficiency of Biodiversity Exploration (IEBE) (Mori & Gracie in review). An IEBE of one is only acceptable when the goal of the project is limited to a listing of the species found in the flora; hence, an IEBE number considerably greater than one was needed to insure that enough information was available to write our *Guide*.

Very high IEBE ratios might indicate that too many collections have been gathered for each species – thereby resulting in the accumulation of specimens that are expensive to handle and to archive, but which add little to botanical knowledge. On the other hand, a low IEBE indicates that not enough specimens are available to provide the information needed to describe all stages of a species' life cycle as well as its ecological and morphological variation. The IEBE value for central French Guiana is 7.0 (total number of collections [13488]/total number of species [1918]) suggesting that the number of collections per species for this area falls into the lower range of the number needed for initiating the preparation of the *Guide*. As the size of the area covered by floristic inventories increases, however, higher IEBE values are needed to understand the wider geographic distribution, larger ecological amplitude, and greater morphological variation characteristic of species over wider areas.

As botanical exploration progresses, the total number of collections per expedition or per period of time should diminish because the easy-to-collect common species are avoided as they are already represented by sufficient specimens (Fig. 2). The value of each collection increases because of the higher percentages of rare species and of new information in the collection. Therefore, the success of an expedition should not be judged solely on the total number of specimens gathered, but also on the quality of the specimens and the amount of new information they provide.

After we concluded that enough specimens were available to justify writing the *Guide*, we enlisted the help of nearly 80 taxonomic specialists studying the plants of the Neotropics. The combination of monographers and floristicians working together results in better monographs and floras. The monographer receives herbarium collections, pickled flowers and fruits, photographs, DNA collections, and notes about the ecology of the plants they study and, in return, the flora benefits by having the most up-to-date treatments.

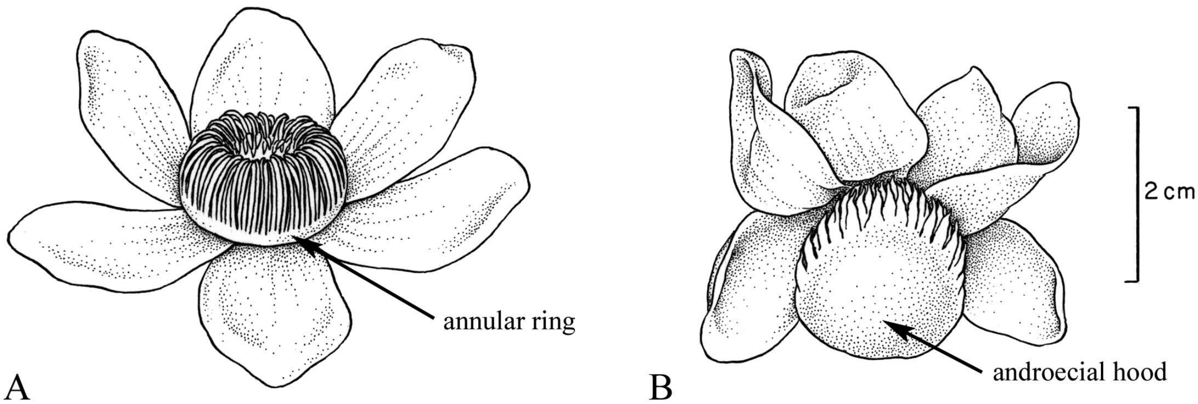

Fig. 3. Floral symmetry of Lecythidaceae in central French Guiana. A. *Gustavia hexapetala*, an actinomorphic-flowered species. B. *Eschweilera pedicellata*, a zygomorphic-flowered species.

Pollination of Lecythidaceae

The pollination biology of the Brazil nut family (Lecythidaceae) has been relatively well-studied in central French Guiana (Mori & Boeke 1987). Adaptation of Lecythidaceae for pollination has taken place, for the most part, in the androecium. There are two types of flowers, actinomorphic (Fig. 3A) and zygomorphic (Fig. 3B) and three different rewards offered to pollinators – fertile pollen, sterile pollen, and nectar. Radially symmetrical flowers, such as those of *Gustavia hexapetala* Aubl. (Fig. 3A), offer only fertile pollen as a reward; consequently the pollinator reward and the pollen that effects fertilization is morphologically and physiologically identical. Female bees move into the flower without restriction, collect pollen that is subsequently fed to their larvae, and receive pollen haphazardly deposited on their bodies. When the bees move to a flower of another tree, the pollen is deposited onto the stigma of another flower and that pollen eventually effects fertilization. Although numerous bees visit the flowers of *G. augusta* in central French Guiana, the principal pollinator is the night-flying bee, *Megalopta genalis*, which removes pollen from the poricidal anthers by vibrating its flight muscles in a process called buzz pollination.

The zygomorphic-flowered species offer either sterile pollen or nectar as a reward. We describe the pollination biology of the two species of *Corythophora* found in French Guiana as an example of species with sterile pollen as a reward and that of *Eschweilera pedicellata* (Rich.) S. A. Mori as a species with nectar as a reward (Fig. 3B).

Corythophora is a genus of three species, one of which, *C. rimosa* W. A. Rodrigues, includes subsp. *rimosa* and subsp. *rubra* S. A. Mori. The flowers are zygomorphic and sterile pollen is the pollinator reward. Depending on the species, the sterile pollen is either placed in the androecial hood or in the staminal ring. The fertile pollen is always found in some part of the staminal ring.

In central French Guiana, both *Corythophora amapaensis* and *C. rimosa* subsp. *rubra* are visited by bees for their sterile pollen reward (Mori & Boeke 1987) (Figs. 4A-C). The larger flowers of *C. amapaensis* Pires ex S. A. Mori & Prance are entered mostly by the large bees *Euglossa mixta* (Fig. 4D), *Epicharis* sp., *Eufriesea purpurata*, and *Xylocopa viridis*. All of the bees enter the flowers head first and pry open the androecial hood with their heads; hence, their ventral surfaces are oriented toward the androecial hood while their heads and backs contact the fertile anthers of the staminal ring. The bees stay in the flowers for three to five seconds, and, upon emerging, they have yellow (sterile) pollen on their heads and white (fertile) pollen on their backs. After the bees back out of the flowers, they hover for several seconds and transfer the yellow pollen to their pollen baskets.

The only insect observed to enter the flowers of *C. rimosa* was *Trigona capitata*. This bee makes frequent visits to the flowers. It enters the flowers with its ventral surface toward the androecial hood from which it collects yellow (fodder) pollen. Upon leaving the flowers, yellow pollen (sterile) is clearly visible in its pollen baskets while white pollen (fertile) from the staminal ring is deposited on its head and back.

The two species of C*orythophora* found in central French Guiana, although they are both canopy trees and grow in nearly the same habitat, are clearly different in floral structure. Even though they both offer pollen as a reward, the size of the flowers and the position of the anthers bearing the sterile pollen is different. In *C. amapaensis* the sterile pollen is found on the inside of the ring bearing the fertile stamens and in *C. rimosa* subsp. *rubra* the sterile pollen comes from sterile anthers on the staminal hood (Fig. 4C). Moreover, these two species are pollinated by different species of bees (Mori & Boeke 1987).

Eschweilera is a genus of 85 species. The flowers are zygomorphic and nectar is the pollinator reward. *Eschweilera pedicellata* produces relatively few flowers, 3-5 cm in diameter (Fig. 4B), scattered within the crown. The principal flower visitor is the large bee *Eulaema bomiformis* which has been observed entering the flowers with its ventral surface against the androecial hood. This bee presumably removes nectar from the apex of the coiled hood and gets pollen deposited onto its head and back.

Our knowledge of the pollination of Lecythidaceae in central French Guiana stems from an interest in explaining the differences in floral structure observed during our botanical inventory. Actinomorphic versus zygomorophic flowers, the different floral rewards, the position of the floral rewards, and the type of anther dehiscence all play roles in the pollination of these species.

Cerambycid attack on Lecythidaceae

Investigations of complex interactions between tropical plants and animals are among the most rewarding field studies, but there are daunting obstacles to overcome. One fundamental obstacle is plant identification, especially of trees or lianas. Even experienced field botanists are unable to identify most tree species with any degree of confidence based solely on vegetative characteristics. Because different trees species are fertile at different times of the year, and a particular species can bloom at different times from one year to the next, considerable effort must be expended to identify the local plants before any serious study of tropical plant/animal interactions can take place. In studies involving plants and insects, the identification of the insect partners can be an even greater obstacle – in part because any particular plant species is typically visited by many unrelated insect species. Although estimates vary widely, there is no doubt that many tropical insects are not yet described. Even when tropical insects have a name and a rudimentary description, specialists capable of teasing out the identity are few and far between.

A collaboration between Scott Mori, specialist in the Brazil nut family, and Gérard Tavakilian, specialist in wood-boring beetles (Cerambycidae), led to the discovery that a well defined guild of cerambycid beetles (Fig. 5) was reproducing exclusively in trees belonging to the Brazil nut family. Cerambycids lay their

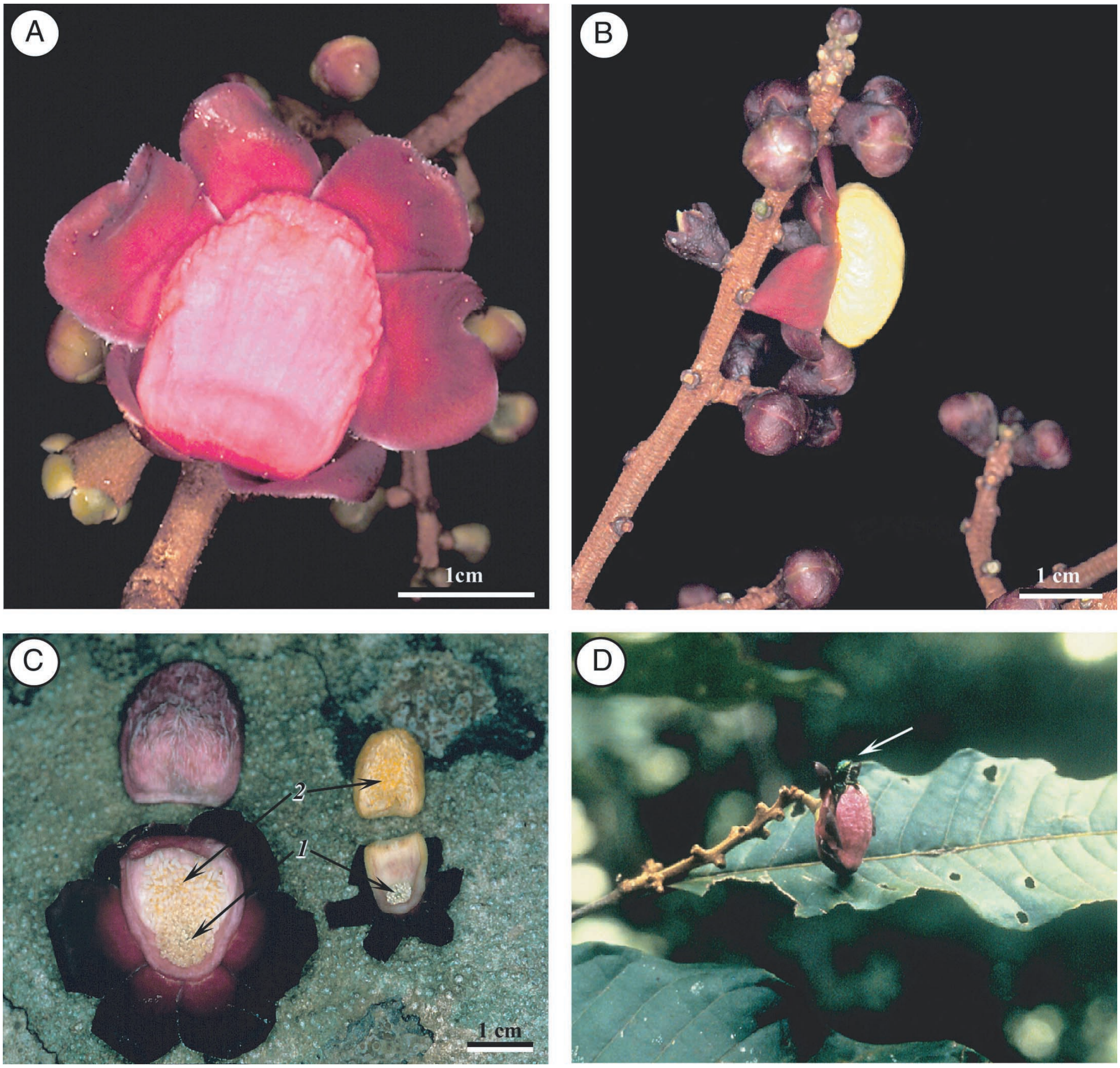

Fig. 4. Pollination rewards of species of *Corythophora* in central French Guiana. A. *C. amapaensis.* B. *C. rimosa* subsp. *rubra.* C. Fertile (1) and sterile (2) pollen locations in *C. amapaensis* (left) and *C. rimosa* subsp. *rubra* (right). D. A euglossine bee (arrow) visiting the flower of *C. amapaensis* (Photo by Jef Boeke).

eggs in dead wood and the galleries they produce allow entry of bacteria and fungi thereby facilitating the breakdown of wood to humus and the subsequent recycling of nutrients (Berkov & Tavakilian 1999).

The presence of plant and beetle taxonomists working in the same area, stimulated a year-long beetle rearing study in which graduate student, Amy Berkov, reared cerambycids (and other wood-boring beetles) from five

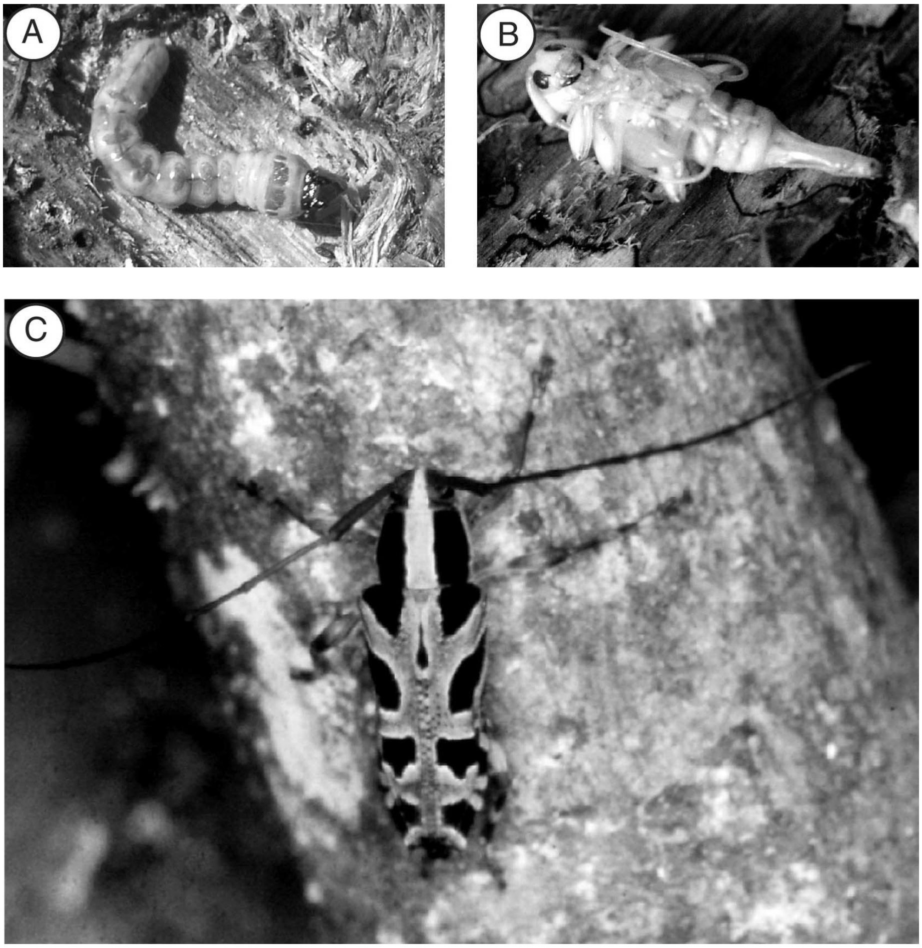

Fig. 5. Cerambycid beetles and their Lecythidaceae hosts. A. Late instar larva of *Xylergatina pulchra* from a branch of *Lecythis poiteaui* O. Berg. B. Pupa of *Xylergatina pulchra* from *Eschweilera coriacea.* C. An adult of *Colobothea* sp. on a branch of *Gustavia hexapetala* Aubl.

species of Lecythidaceae (Berkov 1999, 2002; Berkov & Tavakilian 1999; Berkov *et al.* 2000). Her study, designed to quantify the host, seasonal, and stratum specificity of the beetles, revealed 52 new host plant records for 38 cerambycid species (including 12 that may represent undescribed species). Approximately 70% of the cerambycid species were associated preferentially with a single host genus. Overall, many more cerambycids (individuals and species) emerged from branches cut during the dry season, although *Eschweilera coriacea* (DC.) S. A. Mori was well-colonized during the rainy season. The ratio of stratum specialists: stratum generalists was roughly 1:1, but only four cerambycid species appeared to be canopy stratum specialists. Although few cerambycid species were reared exclusively from canopy branches, during the rainy season almost all cermbycid reproductive activity took place in the canopy. This change in stratum selection suggests that in tropical forests with extended wet seasons, fewer insects reproduce in wood of branches found on the ground in the wet season than in the dry season.

Berkov's ongoing ecological study would not have been possible without the taxonomic expertise of Mori and Tavakilian, and is coming full circle to make a small contribution back to beetle taxonomy. Several cerambycid species that originally appeared to make seasonal changes in host association actually included multiple mtDNA haplotype groups (8-11% sequence divergence), and now appear to be complexes of cryptic species (Berkov unpublished data). Berkov is currently extending her study to other regions of Amazonia to see if she can explain better this taxonomically complex group of little brown beetles, and to evaluate the stability of host-plant associations throughout Amazonia.

Life form, habitat, and nutritional mode

Our botanical inventory has made possible ecological studies. For example, we were able to determine the different life forms, habitats occupied, and the nutritional modes of the flowering plants of central French Guiana (Mori *et al.* 2002c) by constructing a database derived from our checklist (Mori *et al.* 2002b) and the information provided in the *Guide to the Vascular Plants of Central French Guiana* (Mori *et al.* 1997, 2002a).

The flowering plants of central French Guiana comprise 1918 native species (Mori *et al.* 2002c), including 549 species of herbs, 44 species of vines, 45 species of subshrubs, 269 species of shrubs, 245 species of lianas, and 766 species of trees. The habitat of the flowering plants is primarily terrestrial. A total of 1653 species or 86% of the flora occurs in this habitat. However, the reproductive cycles of a majority of the flowering plants take place in the crowns of trees. When the number of species of trees is added to the numbers of epiphytes, hemi-epiphytes, and aerial endophytes, the crowns of trees are the site of about 68% of the flowering plant reproductive activity in this forest. Heterotrophic vascular plants, with 36 species, make up 1.9% of the flora.

Because the forests of central French Guiana have not been disturbed on a large scale by humans in the recent past (Mori & de Granville 1997), the life form, habitat, and nutritional mode compositions reported by Mori *et al.* (2002c) should provide baseline data needed to distinguish pristine from disturbed habitats. Hence, these data can be used for conservationists to identify relatively undisturbed forests for protection in biological reserves.

Bats as dispersers of *Cecropia*

Bats play an important role in the pollination and dispersal of tropical plants. However, details of this interaction in lowland Neotropical forests have not been adequately studied partly because there are few areas in the Neotropics that have published inventories of the plants and the bats. An exception is found in central French Guiana where a published flora (Mori *et al.* 1997, 2002a) and bat fauna are available (Charles-Dominique *et al.* 2001). As part of our effort to describe bat/plant interactions, we have recently completed a study of the role of bats in dispersing the diaspores of *Cecropia* (Cecropiaceae) in French Guiana (Lobova *et al.* 2003).

Cecropia is a Neotropical genus of pioneer plants. A review of the literature on bat/plant dispersal revealed that 15 species of *Cecropia* are consumed by 32 species of bats. In French Guiana, bats we captured in primary and secondary forests yielded 936 fecal samples with diaspores, among which 162 contained diaspores of *C. obtusa* Trécul., *C. palmata* Willd., and *C. sciadophylla* Mart. We discovered that the dispersal unit of *Cecropia* is the fruit (Figs. 6A, B), not just the seed (Fig. 6F), and that bats consume the infructescence, digest pulp derived from the enlarged, fleshy perianth (Fig. 6A), and defecate the fruits (Fig. 6C). We suggest that the mucilaginous pericarp of

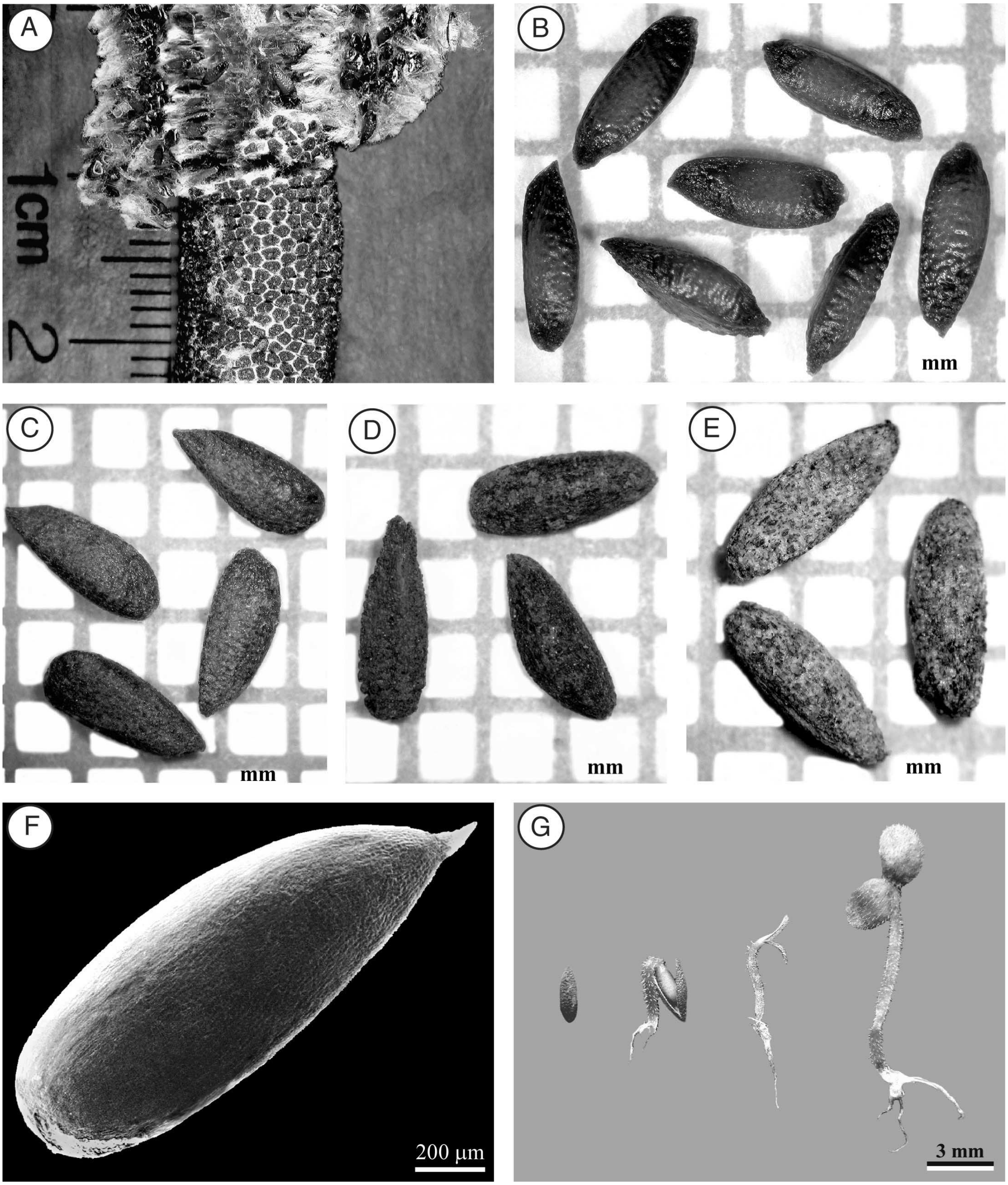

Fig. 6. Fruits, seed, and seedlings of *Cecropia obtusa.* A. Part of dry infructescence showing fruits enclosed in perianth. B. Fruits. C. Fruits from bat feces. D. Fruits from soil seed bank (clay soil). E. Fruits from soil seed bank (sandy soil). F. Seed. G. Germination, fruit (left), dehisced fruit and young seedling (middle left), more advanced seedling (middle right), and still more advanced seedling (right).

Cecropia facilitates endozoochory. The exocarp and part of the mesocarp may be lost after passage through the digestive tract of bats (Fig. 6C), but fruits buried for a year in the soil seed bank remain structurally unchanged (Figs. 6D, E) and seeds retained within soil keep their ability to germinate for up to nine years. Bat dispersal is not necessary for seed germination (Fig. 6G), but it increases seed survival and subsequent germination by removing the perianth and some of the mucilaginous tissue from the fruit. Our study confirms that species of *Cecropia* are important colonizers of disturbed vegetation and that this genus possesses a set of adaptations that facilitates dispersal by bats and adapts the diaspores for longevity in the soil until light conditions are favorable for seed germination.

Ecotourism

We have made the argument that ecotourism is a way to protect the environment and, at the same time, preserve the tropical ecosystems of the Guianas (Mori *et al.* 1998). Because of its pristine nature and the existence of books that enable visitors to identify plants in general (Mori *et al.* 1997, 2002a), orchids (Veyret 1991), trees (Office National des Forêts 2001), vegetation types (de Granville 1986), birds (GEPOG 2003; Tostain *et al.* 1992), mammals (Hansen & Richard-Hansen 2000), snakes (Chippaux *et al.* 1988; Rogé & Sauvanet 1987; Starace 1998), amphibians (Lescure & Marty 2000), some insects (Hequet 1996), and even poisonous animals (Marty 2002), central French Guiana is an ideal travel destination for those wishing to learn about the plants and animals inhabiting tropical lowland forests. It is already visited by many Europeans interested in tropical nature, but even those not interested in knowing the names of the plants and animals they observe, are drawn to the forests of French Guiana by the natural beauty they find there (Richard-Hansen & Le Guen 2001). The publication of user-friendly guides to the plants and animals and beautiful books about nature enhances the visitor experience and thereby helps promote an appreciation for wilderness areas. As the result of increased ecotourism, local people will have sources of income that depend on the preservation rather than the destruction of the forests surrounding them.

Conservation

In 1974, a plan for conserving the diversity of French Guianan ecosystems was developed (de Granville 1974) and central French Guiana was among the areas proposed as reserves. The presence of relatively undisturbed forests in a region of high plant diversity as demonstrated by our botanical inventory has been an impetus to continuing efforts to set aside this area as a biological reserve (Deviers & Raynaud 1994; Mission pour la Création du Parc de la Guyane 1999). These efforts have resulted in the establishment of a biological reserve (*Arrêté de Protection de Biotope* called the *Forêt de Saül*) in central French Guiana.

Botanical inventories can have a more direct application in conservation planning. Once the species of an area are known, then studies of their biogeography can provide guidelines for conservation planning. For example, a study of the Lecythidaceae of central French Guiana (Mori 1991) reveals that a considerable number of species are distributed within the northeastern confines of the Amazon, Negro, and Orinoco Rivers thereby supporting the recognition of a Guayana Lowland Floristic Province. Moreover, within this area, there is evidence supporting recognition of an eastern and western element within the overall Guayana region. As much as 55% of all of the Guianan species of Lecythidaceae would be protected if a large biological reserve were established in central French Guiana. Species composition of Lecythidaceae changes markedly at the Essequibo River in Guyana. The protection afforded by the large Iwokrama Reserve, added to that of the proposed central French Guiana reserve, would raise the number of protected species of Lecythidaceae to 83%. In order to complete the protection of Guianan species of Lecythidaceae, smaller reserves protecting habitats not found within the two proposed larger reserves would have to be established. For example, the establishment of a reserve in the savannas of southwestern Guyana would protect *Lecythis brancoensis* (R. Knuth) S. A. Mori and *L. schomburgkii* O. Berg, the preservation of periodically inundated forest along the Comté River would preserve *L. pneumatophora* S. A. Mori, and the continued safeguarding of Brownsberg National Park in Surinam would insure the continuation of *Corythophora labriculata* (Eyma) S. A. Mori & Prance, the only known endemic of this family in Surinam.

Conclusions

The first step in understanding the biocomplexity of tropical forests is knowledge of the plants and animals that inhabit them. We have demonstrated that detailed floristic study in central French Guiana has stimulated research in different fields, ecotourism, and conservation. We recommend that similar inventories be made throughout the Neotropics as was first recommended by the Committee on Research Priorities in Tropical Biology in 1980.

Acknowledgements

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