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Pollination Ecology and the Rain Forest

Sarawak Studies

With 76 Illustrations, 12 in Full Color

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Cover illustration: Concepts of coevolution, ecological fitting, and loose niches, applied to ecological interactions among plants and pollinators. Adapted from the island biogeographic model of MacArthur and Wilson, 1963.

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Preface

Rain Forest Biology and the Canopy System, Sarawak, 1992–2002

The rain forest takes an immense breath and then exhales, once every four or five years, as a major global weather pattern plays out, usually heralded by El Niño–Southern Oscillation. While this powerful natural cycle has occurred for many millennia, it is during the past decade that both the climate of Earth and the people living on it have had an increasing influence on the weather pattern itself, with many biological consequences. In Southeast Asia, as also in most of the Neotropics, El Niño accompanies one of the most exuberant outpourings of nature's diversity. After several years of little activity, the incredibly diverse rain forests suddenly burst into flower—a phenomenon referred to as General Flowering in Asia. Plant populations are rejuvenated and animals are fed, but the process involves a delicate and complex balance.

When the canopy access system was under construction at Lambir Hills National Park in the early 1990s, it made use of an underlying technology that was already in place: bridges. For centuries, bridges have spanned the natural chasms over rivers. This existing network of bridges and the people who built and use them produced the technology we needed to gain access to the canopy. Bridge builders were our natural allies in the quest for biological knowledge of the high canopy. We saw the two massive tree towers take shape, then the walkways between them, all in a setting that would make any naturalist or explorer dizzy with excitement, if not vertigo. Studies at the top of the living envelope of forest

were finally to gain a firm footing and would soon be incorporated with the more traditional, earthbound observations. Professor Tamiji Inoue recognized that the special environment of the rain-forest canopy held the future for tropical scientific exploration.

Now, over a decade later, technology has placed at our disposal a new canopy access system—an immense construction crane towering 80 meters high, with a jib reaching 75 meters across the surrounding forest, and a remote-controlled gondola that can travel from the ground to well above the canopy. This represents a revolution in the study of tropical rain forests. It may also represent a final frontier in natural history studies, in one of the most important, but little known, biomes on Earth.

Students of the rain forest strive to see the entire forest and its denizens, across both space and time. Of the 367 species of mammals, birds, reptiles, and frogs at Lambir Hills National Park, the disturbed or open habitat species are increasing, while forest animals such as hornbills and primates are in decline or have disappeared (Shanahan and Debski 2002). An unusually severe drought and an El Niño in 1997 and 1998 increased tree mortality by seven times (Nakagawa et al. 2000) and led uniformly to local extinctions of mutualistic insects (Harrison 2000). Also following that event was an outbreak of certain insect herbivores (Itioka et al. 2003). Many changes and dynamics continue apace.

Similar themes are emerging elsewhere. At the other side of the world, in Costa Rica, a gathering to commemorate the fortieth anniversary of the Organization for Tropical Studies recognizes a worldview with particular resonance for the tropics. One of the speakers is Dr. Edward O. Wilson, a spokesman for, and well-known pioneer of, themes about the rain forest that have captured attention with their urgency; for example:

- In 1988, the term *biodiversity* was introduced, yet even today, 90% of the world's species remain undescribed and unappreciated. Half of them live only in the tropical forests.
- The second-greatest block of rain forest on the planet is in Borneo. It is representative of what remains on Earth in the standing tropical forests, now diminished from 12% to 6% of the planet's surface, since the precipitous advance of human populations.
- In the small but biodiverse region of Costa Rica, national parks and preserves now include 37% of all land, an increase from 20% a short time ago. Why? One reason is purely economical, because the water provided by forest is more valuable than one of its popular economic alternatives—beef cattle that would be produced on land cleared of its natural vegetation.
- Currently, the poor outnumber the rest of humanity by about 75:1, and almost 100 million people live in absolute poverty. However, future generations will pay the heaviest price. It will stem from the loss of biodiversity and the services, quality of life, culture, and potential for development that biodiversity provides.

- Our collective retirement funds lie, now and in the future, in the sustained partnership of people and their environment, not in the short-term profit taking that leads to erosion of all that is valued by society.

Even though the pessimists seem to outnumber the optimists, we still agree with Dr. Wilson and the participants of that tropical conference in the Americas. We need to act, we need to reason, and we need to understand. From a tract of rain forest in the north of Borneo, the information given here brings us a little closer to seeing the scientific reality of the rain forest. We are striving to keep in step with the race to realize our potential before the great forests are taken away, for, as Professor Inoue once remarked, these places are the windows in which we can behold the entire history of life on Earth. As presented in the closing chapter of this work, expressed by our friend the late Professor Inoue, who died tragically during the Sarawak studies, there is enduring relevance in rain-forest research. Maintaining the human birthright—the preservation of nature’s masterpieces while fulfilling the true goals of our lives and histories—is still the primary purpose of science.

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Acknowledgments

This book was compiled after more than 10 years of extensive ecological studies in lowland dipterocarp forest at Lambir Hills National Park, Malaysia. The work was conducted by cooperative projects that included the Forest Department Sarawak, Malaysia; the Japan Science and Technology Agency; Ehime University; Harvard University; Kyoto University; Osaka City University; Smithsonian Tropical Research Institute; and other universities and organizations from the United States and Japan.

Sarawak is endowed with true splendors of nature and recognized as one of the world's centers of species diversity. Like almost all tropical forests, those of Sarawak are threatened and may even disappear under strong economic pressures. The authorities of this Malaysian state have made serious and strenuous efforts to enlarge protected areas and to conserve biodiversity, as symbolized by the state emblem of the rhinoceros hornbill. As biologists, we greatly appreciate opportunities to wander, as Beccari did a century ago, the Great Forests of Borneo. We wander even farther now, to climb up to the canopy and conduct studies in the Lambir Hills forest, which is blessed with an amazingly high biodiversity and a safe system of canopy access, permitting biologists to go where none have gone before.

Rather than attempting to cover all the topics studied so far in this part of Borneo's rain forest, the present volume highlights interactions between plants and animals in the context of dynamic natural environments. Encouraged by recent attention given to the significance and real inspiration provided by bio-

diversity and biological interactions, we climbed to the canopy to observe firsthand the flowering, fruiting, sexual recombination, predation, fighting, and parasitism that occur there, and in the forest below. In addition, long-term monitoring of insects and plants has revealed that the forest's biological activities are very dynamic, with a cycle of more than one year under mild, uniform climate conditions with little seasonality. The tight links in regeneration of dipterocarp forests and rhythms of the global climate, related to El Niño, are exciting to recognize as major factors in rain-forest biology; at the same time, such links are cautionary signs, indicating the sensitive and fragile nature of the ecosystem. We hope our studies can contribute to the conservation of tropical forests by emphasizing that pollination and diversity are truly partners, and that they have been understudied or, unfortunately, altogether neglected not only in schemes for conservation, but also in research on forest ecology.

This book owes much to many people. First, we would like to apologize that it is impossible to list everyone who contributed to studies in Lambir Hills and to this book. Ms. Lucy Chong and many other staff members from the Forest Department, Sarawak supported fieldwork and management of the projects. The local people at Lambir have taken us to many interesting sites while providing fascinating knowledge about the forest. A large number of researchers and students conducted studies and contributed to Lambir projects, but they do not appear in this book as authors. In particular, Dr. Lee and professors Ogino and Yamakura played leading roles to establish our field site. We acknowledge the support and editorial assistance of Dr. Rhett Harrison. We also are grateful to Springer for unflinching support for this book. The studies were funded by various sources, including the Ministry of Education, Science, Sports, and Culture (nos. 04041067, 06041013, 09NP1501) and Japan Science, Technology Corporation (Core Research for Evolutionary Science and Technology Program) and the Research Institute for Humanity and Nature Project (P2-2) in Japan. This publication was supported by the Japan Society for the Promotion of Science (Grant 165296).

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1. Large Processes with Small Targets: Rarity and Pollination in Rain Forests

David W. Roubik

1.1 Ecological Interactions Among Plants, Animals, Microbes, and Fungi

Perhaps nowhere on Earth has there been such a remarkably long period of uninterrupted tropical forest evolution, some 36 million years (Morley 2000), as within the old forest in Borneo. An example of tropical forest ecology from this area is Lambir Hills National Park, Sarawak, shown in Plates 1–12.

For studies of terrestrial ecology in forests to be realistic they must consider the movement of organisms and turnover of populations. At the base of the food chain, plants are fixed in space; the fungi that grow with them are also immobile. Their reproductive propagules, however, exhibit impressive mobility. Animals locate and harvest their food as they explore the forest and feed on fungi, roots, wood, sap, dung, leaves, fruit, nectar, pollen, seeds, or flowers. In turn, the predators that follow such prey include the human hunters, and a large, forest-wide cycle is created. The cycle depends on very small ecological targets: flowers, fruits, seeds, pollen grains, the sites in which seeds, microbes, or fungi can grow, and the receptive stigmata of flowers.

On a grand scale, the forest displays periodic migrations within its bounds. Feeding groups of several hundred white-lipped peccaries *Tayassu*, which follow the fruit drop of palms along waterways in the Amazon basin, are matched by the movement of bearded pigs *Sus*, moving in number to find patches of fruit on the ground, during a heavy fruiting year in Southeast Asia. Preceding such

consumer migrations, there is always a burst of flowers opening and petals dropping to the ground, and the noisy commotion of pollinators high in the trees. Yet the forest canopy in Southeast Asia may remain relatively silent for years, because most of the fruiting and flowering occurs in a supra-annual fashion, generally once every four or five years (Inoue and Nakamura 1990; Inoue et al. 1993). One wonders if the intensity of those rare events is greater than the flowering peaks and annual glut of fruits taking place each year in the more predictably seasonal forests of Asia, Africa, or the Neotropics. Most observers who have witnessed both phenomena believe that the annual peaks in flowering and the resulting fruit are more intense in such seasonal forests than in their counterparts in the rain forest of Southeast Asia, although not lasting as long.

Why is the Lambir Hills National Park, Sarawak, which is located in the floristically rich north of Borneo, extremely valuable when left intact? The giant trees in the ocean of forest have often been measured in terms of their economic value or the ways in which plantations can be made by selecting certain species (Panayotou and Ashton 1992; Appanah and Weinland 1993; Guariguata and Kattan 2002; Okuda et al. 2003). Such forests lay outside the experience of most people, even biologists, yet few natural environments are so rich in detail and offer such great potential for insight. Lambir Hills yields insights that further the development of classical theory or concepts, as seen in the physical sciences, art, or music. We certainly have theories that address biology, culture, and many other disciplines, but tropical field biologists primarily begin their work by observing a concrete, physical world—one that is often full of surprises. When the studies are concluded, we are closer to understanding the forests and their component species; often we come away with concepts and perspectives that we had never before imagined.

What shapes the lives and evolution of living things in the rain forests? In terms of interactions (see Fig. 1.1), consider three guiding principles: *coevolution* (Janzen 1980), *ecological fitting* (Janzen 1985), and *loose niches* (Roubik 1992; Roubik et al. 2003). The first implies tight and sustained interactions over many generations, as part of the general process known as *adaptive radiation*. The interacting populations are affected genetically in significant ways.

For instance, pollinating *fig wasps* or beetles have the right size and physiological traits to fly to their host plants and to pollinate them, for which they must live their lives in synchrony with the highly specialized flowers. The flowers often have only one important pollinator, which they sustain by providing food and access to flowers. In contrast, in *ecological fitting* there is no coevolution, but interactions can be subtle and complex. The organisms may come from different places, having evolved their characteristics in other circumstances, but now combine to form an ecological relationship. The third process, the loose niches, derives from population cycles, with the strength of interaction tied to the changing abundance of participants. Modern participants may have a coevolutionary history or not, but the modern interactions often demand behavioral adjustments by the animals. The three types of relationships combine in highly diverse communities, where the highest proportions of coevolutionary relation-

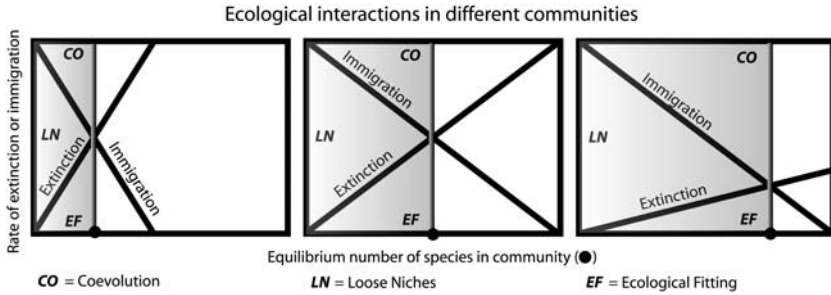


Figure 1.1. Concepts of coevolution, ecological fitting, and loose niches—applied to ecological interactions among plants and pollinators. Empirical data indicate loose pollination niches include 50% of plant species (Roubik et al. 2003); other interaction categories are complementary (shown by shaded triangles). Differing extinction and immigration rates determine local species richness; the richest community has the largest proportion of coevolved interactions (adapted from the island biogeographic model, MacArthur and Wilson 1963).

ships may exist (see Fig. 1.1). Undeniably, all such matters concern the weather, changing climate, geomorphology, continental drift, sea level, and oceans—not just life in and under the rain forest canopy. Such variables affect the origin, presence, and extinction of players in the game. The biological setting is traditionally known, thanks to G.E. Hutchinson, as the ‘ecological theater’ and the ‘evolutionary play.’

In the rain forest, there is a relentless dynamic centering on events that can be as explosive as a volcanic eruption. An individual tree, group of plants, or entire population bursts into flower, dispensing pollen and nectar. As they drop the last of their flowers, the plants begin to sprout offspring in the form of seeds and fruit, which are afterwards dropped or carried away. Consumers, certainly including humans and animals of all kinds, come in as though filling a vacuum. They have taken their cue for the localized event from its coincident weather patterns or, if from nothing else, the colors or fragrances of flowers or fruit.

The major consumers in tropical forest include folivores and plant pathogens, which are not strictly tied to reproductive botany. Their dynamics are similar to animals that use the fruit, flowers, and seeds, but they seem to operate on a much smaller spatial scale. They are not, after all, moving to and from objects that are *designed* to be attractive. Quite the contrary, herbivores using particular leaves or small seeds often find them by searching the appropriate habitats, seeking a chance encounter with their small targets. While dispersal of seeds to forest openings or gaps seems rarely to involve a distance greater than 100 meters (Dalling et al. 2002; Levey et al. 2002; see Higgins and Richardson 1999), the dispersal of pollen by pollinators to flowers can easily cover distances of several to dozens of kilometers. Fungal spores or microbes that can infest seeds or growing plants are transmitted by wind, water, or animals, while invertebrates in pursuit of host plants may walk, crawl, or fly a moderate distance.

Consumers that are not feeding on leaves—the pollinators, frugivores, and granivores—may require areas encompassing tens to hundreds of kilometers: the scale that is ultimately important to Lambir Hills. Particularly in a forest with so many species, the canopy and understory both share the all-important environmental and ecological factor of rarity. Ecological and evolutionary processes that cause or maintain rarity are clear, and constitute the flip side of species richness and biological diversity. The second unifying theme is the double standard of the rain forest. Large-scale events, like general flowering or a severe drought, are uncommon, while the normal, annual flowering of certain trees and understory plants in a warm and humid environment has taken place consistently for millions of years.

1.2 Pollen, Seeds, and the Red Queen

Because of their relatively slow evolutionary rates, long-lived plants' best chances for keeping up with the evolutionary advances of natural enemies include diversifying offspring and maximizing seed and pollen dispersal to favorable sites. Within the lifetime of an individual plant, generations of insects or pathogens may produce new genetic combinations that allow toxic or unpalatable foliage to be eaten and digested. Not to be forgotten is the fact that immigrant species may arrive from other communities, providing a chance for ecological fitting (Janzen 1985). Such community building is complementary to evolution, or, coevolutionary fitting between a particular host and mutualist (see Fig. 1.1). A functioning community is a product of biogeography, ecology, behavior, and genetics. Under the *Red Queen* hypothesis, genetic dynamics are not all that pertain to unequal life spans. For plants, the evolution of a breeding system and pollination ecology are among consequences that can be traced to the Red Queen. An invertebrate, fungus, or microbe may, as natural enemies, genetically overcome any conceivable defense of the trees (Summers et al. 2003; Arnold et al. 2003; Normark et al. 2003). The Red Queen hypothesis rests on this premise (Hamilton 2001; Summers et al. 2003). A further consideration is the population buildup in small, fast-breeding insects (Itioka et al. 2003), which can go through multiple generations even during a single flowering or fruiting event. Pollination ecology helps plants to persist.

Once they have located their target resource, insects or pathogens sometimes consume almost all its seeds or leaves. Even though they may not kill a reproductively mature host, they diminish its potential reproduction (Strauss 1997). But, if they repeatedly cause extensive damage, they threaten their own survival and propagation. One may reasonably expect them to follow options to the evolutionary arms race. One of the most attractive is mutualism (if you can't beat them, join them). That selective pressure, in particular, may be a basis for the evolution of rather unusual pollination systems—wherein pollination is by species that use flowers or seeds as breeding sites or consume foliage when no flowers are present—and the existence of plants that do not participate in the

general, community-wide flowering peak emphasized in this book (Itioka et al. 2003; Momose et al. 1998c). Exceptions involve ecological fitting or coevolution.

Fungi and bacteria not only feed the trees, but also kill their offspring. Mutualist fungi upon which the root systems of many tropical trees depend for nutrient acquisition (Turner 2001) or for defense of the foliage (Arnold et al. 2003) might have a starting point similar to that of herbivores that, over evolutionary time, have been converted into pollinators. Even some pathogenic fungi have been found playing a role in pollination in the Lambir Hills environment (Sakai et al. 2000). The transition from pathogen or herbivore to mutualist seems prevalent among the Dipterocarpaceae and their pollinators, root or seed associates. Because this plant family is so abundant at Lambir Hills, possessing by far the greatest stem area in the forest, and because a plant's natural enemies tend to evolve feeding specializations that are most effective on related host species (Janzen 2003), the evolutionary ecology of the Lambir Hills plant community is bound to the biology of abundant families maintaining a large biomass, like the euphorbs and dipterocarps.

Perhaps for a hardwood tree like Belian, *Eusideroxylon*, deaths from drought, fire, or specialist natural enemies are equally important. Woody plants with extremely hard wood and capable, especially among dipterocarps, of countering the breach of an insect mandible with copious resin (Langenheim 2003), are far from defenseless. It is no surprise that highly *eusocial* bees, most of the genus *Trigona*, are both abundant and ecologically diverse in Borneo, because they exploit the dipterocarp resin to build nests and defend their colonies (Plate 9F, G). Lodged within cavities in the dipterocarp trees, the bees obtain much pollen and nectar from their flowers, while also serving as pollinators.

Nonetheless, it is instructive to consider that millions upon millions of seeds are produced in order to maintain a tree population by contributing a single reproductive individual. Extremely large tropical trees make numerous tiny flowers, often dominated by social bees (Whitmore 1984; Momose et al. 1998c; Roubik et al. 2003), but these flower visitors are not prone to disperse pollen among trees (Roubik 1989). If no other individual is flowering within a short distance, in most cases not a single seed is produced (Ghazoul et al. 1998). This is largely because the mature seeds are derived only from non-self pollen in more than 85% of all tropical trees that have been investigated (Bawa 1990; Loveless 2002). Contrary to agricultural and domesticated plants, in which *outcrossing* and genetic diversity in seeds decrease fitness of the parents (Richards 1997), differences at the genetic level are strongly favored in tropical trees and become accentuated with rarity (Shapcott 1999; Loveless 2002). Loveless indicates, from studies of 176 tropical tree populations and nearly 100 species, average *heterozygosity* per locus is relatively high: 53%. Selection for inbreeding and uniformity among progeny would produce levels close to 0%.

If the entire lifetime of a tree could be witnessed, we would observe, in slow motion, behavior like that of a highly intelligent animal as it escapes from natural enemies and propagates its genes. Although it may stand rooted in the ground, a tree with a seed crop more than 40 m from the forest floor can disperse

its seeds far by wind. Trees in varied tropical forests show 8% to 30% of species disperse seeds in this manner (Regal 1977; Mori and Brown 1994). Most seed dispersers consume the fruit or seeds (thereby not killing them), but some passively carry the seeds (Levey et al. 2002). Some ovipositing seed predators are used as pollinators (Pellmyr 1997) and some pollinators are also used as seed dispersers (Dressler 1993; Wallace and Trueman 1995). Such cases imply that natural selection and evolution have forged a beneficial relationship from a one-sided detrimental one. On the other hand, an adult tree may buy time. Its options for success include making seeds have as wide a variety of pollen-donating parents as possible and dropping developing seeds that have not received sufficiently diverse pollen (Willson and Burley 1983; Kenta et al. 2002). Many cohorts of seeds and pollen may be made over many years; trees also are paying dispersers to carry seeds to favorable sites, where species-specific pathogens or insects are unlikely to find them. Last but not least, because wind is inadequate and self-pollinated seeds usually do not survive, animals must accomplish out-crossing pollination. Flowering trees and other plants reward pollinators, both for bringing in and for dispersing pollen, with some extremely rare or important floral resources. These include oviposition sites, antimicrobial floral resins, sweet nectar, high-quality protein in pollen, and emblems of foraging prowess that impress choosy females (Roubik and Hanson 2004).

At the base of this remarkable chain of life are tiny capsules containing genes. The currency in plant reproduction is pollen, one of the smallest natural forest materials. Pollen is protein for pollinators, but it carries genetic information that includes capacity for reproduction, the avoidance of natural enemies, and colonization ability. Exactly the same qualities apply to seeds, except that they result from maternal ovules combined with paternal pollen nuclei.

We believe that every seed has a micro-site where mutualists and the physical qualities of soil, nutrients, mutualist fungi, microbes, water, heat, and light are optimal. Such a site has much in common with a *conspecific* stigma needed for successful pollination in a forest of more than 1000 different plant species. Spatially, the odds are great that a pollen grain or seed will fail. Furthermore, the intricacies of compatibility between pollen and ovule show that the quality of pollinator ecology is key to the success of plant reproduction (Wiens et al. 1987). We also believe that the fate of either a pollen grain or a seed depends on the rareness or distribution of its enemies (Janzen 1983; Bawa 1994; Wright 2002; Terborgh et al. 2002; Olesen and Jordano 2002; Ricklefs 2003; Degen and Roubik 2004). Seeds are normally destroyed, either on the mother plant or on the way to another site, by insects or pathogens. Of course many are consumed by larger animals, which either defecate or drop them where they can grow, or digest them as food. Pollen grains, in parallel, most often nourish pollinator offspring (Thomson 2003), but sometimes they are taken by non-pollinating flower visitors and consumed in situ by thrips, microbes, or larger consumers, both invertebrate and vertebrate. Only rarely does a pollen grain experience mortality after reaching its germination site, although it often is out-competed by other pollen grains in fertilizing the target ovule; most ovules fail to produce a seed (Mulcahy 1979; Wiens et al. 1987; Thomson 1989).

Because plants are fixed in space, every natural enemy strikes twice with a single blow. Not only is an individual plant affected, so are its neighbors and progeny. Few plants escape herbivores, and these have remarkably precise defenses, chemical, intrinsic (e.g., Arnold et al. 2003) and mutualistic. Among the most impressive defoliators are caterpillars, which normally are adept at circumventing the defenses of a small number of plant species (Janzen 1984, 2003). When a pest outbreak occurs, the caterpillars spread between plants, or the next generation of adults lays its eggs on those plants nearest to the former host. Moreover, like their host plants, when the herbivores are hyperabundant, their natural enemies, including faster-reproducing viruses, locate and then decimate their populations.

To date, the root cause of diversity in an ecological community does not seem to fit the expectations of any single model (see Fig. 1.2 and below); there are too many exceptions, not enough data, and knotty problems with the application of both statistics and theoretical models (Leigh 1999; Hubbell 2001; Wright 2002; Terborgh et al. 2002; Uriarte et al. 2004).

The processes of extinction and colonization, which generate community richness in species, are tied to regional and local conditions (Fig. 1.1; Ricklefs 2004). While the Red Queen provides support for the well-known Janzen-Connell hypothesis, neither is established as the sine qua non of tree diversity in hyperdiverse forests (Condit et al. 1992; Gilbert et al. 1994; Wright 2002; Delissio et al. 2003; Normark et al. 2003; Uriarte et al. 2004). In addition, no convincing evidence exists that the number of tree species drives the species richness of herbivores (Odegaard 2003). The knowledge gap widens considerably when either the history of colonization or the relative tendencies for extinction or speciation are considered (Colinvaux 1996; Morley 2000; Dick et al. 2003; Ricklefs 2003). Nonetheless, the Red Queen demonstrates why it is important that seed and seedling mortality seem highest near the mother tree (Givnish 1999; Leigh 1999). After mortality occurs, surviving seed and seedling density still remain relatively high near a parent tree (Hubbell 1980; Condit et al. 2000). The density-dependence of tree mortality has been clearly demonstrated in data from Malaysia and Panama (Peters 2003). It is appealing to apply so-called negative density-dependent models to populations, because as any city-dweller is already aware, every outbreak has a focus. Diseases, like other natural enemies, are broadcast from their points of origin. Sedentary organisms depend much on the sites to which they are attached, making the distributions of individual species naturally aggregate in space, thus perpetuating the Red Queen and other phenomena dominated by spatiality. Another phenomenon of equal importance concerns the distribution of pollinators and flowers.

1.3 Flowering in the Face of Adversity

Flowers form the basis for plant populations to both purge *lethal mutations* and increase their fund of *genetic variation* available for short-term opportunities or necessities. Those necessities generally involve escape from natural enemies.

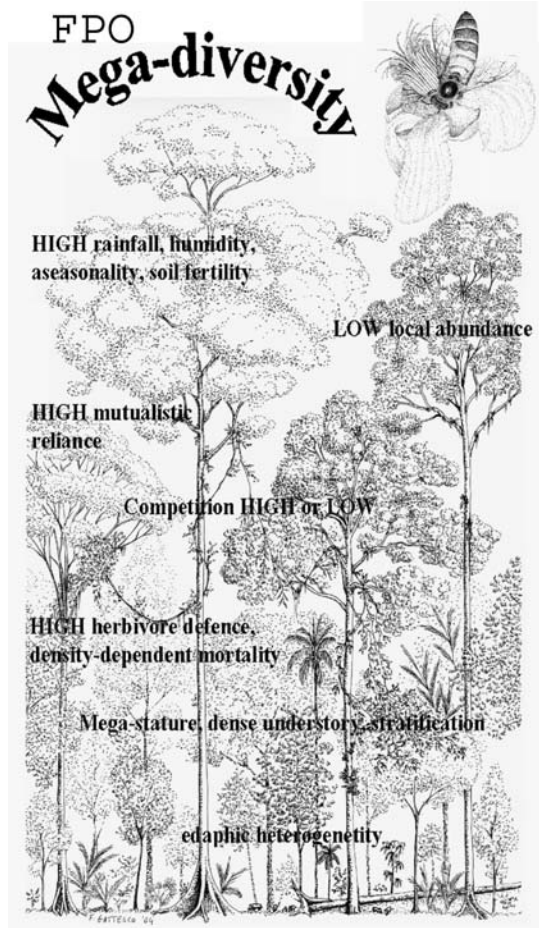


Figure 1.2. The mega-diversity phenomenon, viewing major factors that promote the astonishing richness of life in the ever-wet tropical forests of Borneo (adapted from Givnish 1999; original drawing by F. Gattesco).

Moreover, flowers and their parts represent a commitment in sexual reproduction. Without adverse conditions, and with no genetic mutations, it can be argued that plants would be better served by maintaining a single, female sex that would clonally produce its seeds or offshoots. The *cost of sex* hypothesis raises these points for all organisms (e.g., Kumpulainen et al. 2004). As already mentioned, outbreeding is advantageously avoided in flowering crops (Richards 1997). If asexual breeding or clonal reproduction were favored by natural selection, then flowers and pollen could be done away with altogether. That is certainly not the case for tropical trees, nor for wet tropical forests in particular. For example, our study area at Lambir and a similarly biodiverse area called Yasuní National Park in eastern Ecuador have roughly one-third of their tree species totally com-

mitted to sexual reproduction (Valencia et al. 2004b). The male flowers or the female flowers are on different individual trees. No selfing is allowed!

To be at least somewhat rare, or to be dioecious (Bawa 1980), seems an integral part of tropical plant life. Wind pollination will not work in this setting, unless the plant is a grass or gap specialist. Such plants may grow in high densities where there are intermittent winds—a condition also found in secondary growth trees like Neotropical *Cecropia* and Paleotropical *Macaranga*, which grow along river banks and, now, roadways. In these special cases, mutualist ants may be essential, to protect trees from herbivores which easily locate them (Chapters 13–15). A mutualism between ants and *Macaranga* has been traced to seven million years of coevolution (see Chapter 14).

Rarity, in contrast, brings special problems for maintaining beneficial relationships with mutualists, whether as defensive agents, nutritional suppliers, or dispersers of pollen and seeds. In light of the data presented in this book, it would seem that in the case of flowers and seeds rareness in space is characteristic of the understory, or of the non-emergent vegetation (except gap specialists). Rareness in time, often in addition to scarcity, is more common in flowering and fruit production among trees. Considering pollinators, resource rareness in time seems to promote generalization and diversity in interactions (ecological fitting and loose niches), while rareness in space favors specialization and sometimes tight coevolution (see Chapters 4, 9–12).

The *pest pressure hypothesis*, or *escape hypothesis*, (Gillet 1962; Losos and Leigh 2004) has been the basis for much discussion of why so many plant species coexist in a single tropical forest. Its key argument is provocatively simple: Rarity is a product of specialized natural enemies, which frees up space for competitors. The direct complement, although often neglected, is that intelligent or abundant pollinators *permit* plant rarity in general, both in space and in time (Janzen 1970; Regal 1977; Roubik 1993). There may be an added benefit for the plant in a synergism that naturally follows rarity, encouraging animal pollination and plant rareness to evolve together; and yet pollination occasionally involves *exaptations* that, incorporated as pollinator rewards, become less effective as herbivore deterrents (Armbruster 1997). The key concept is also a simple one, found in sexual selection models for animals (West-Eberhard 2003) and plants (Willson and Burley 1983). There must be considerable economic or ecological superiority in an individual that can send its pollen grain, or attract pollen to its stigma, over the many vicissitudes of weather, time, space, and interactions. A ‘spatial filter’ helps to select the mate, causes genetic remixing among parental gametophytes in seeds and the spreading of new alleles, and encourages rapid and diversified evolution of interactions. The patterns in evolution of flower shape, size, color, smell, and other varied features (Regal 1977; Endress 1994) benefit from the synergism that increased rarity creates. Pollinators are thus selected for spatial and temporal memory, color vision, and olfactory acuity (Dobson 1987; Chittka et al. 1994; Lunau 2000). The predicted results can be considered both from aspects of flowering phenology (see Chapters 3–5) and from qualities of the flowers that permit successful interaction with pollinators (see Chapters 6–12).

When seeds and flowers are both attacked intensely by herbivores, flowers like those of dipterocarps may evolve to be large and fleshy, thereby becoming attractive as oviposition sites or feeding sites for some insects. Most thrips that visit flowers of tropical trees are not their pollinators, and most beetles consume flowers or leaves rather than pollinate them, but both of these animals are important pollinators among dipterocarps and other plants at Lambir Hills. The seeds evolve nutritionally attractive arils or fleshy fruit, and repellents or deterrents, to ensure dispersal by the right animal. However, when the two consumer groups constantly overwhelm tree fecundity, the evolutionary result is thought to be masting, or making resources for the natural enemy populations particularly scarce for long periods of time (but see Herrera et al. 1998). If successful, the masting plant will have to contend with ever more generalized seed predators, which it may then attempt to satiate. We are just beginning to discern whether seed predators are relatively specialized to host trees while the prediction that pollinators often tend to be generalists compared to their flowers (Olesen and Jordano 2002; Roubik et al. 2003) seems upheld. Why should this be so?

1.4 Patterns in Mutualist Biodiversity

The mutualists that are given special domiciles as well as food in plants are products of a long and sustained evolutionary history, well documented in the ant genus *Crematogaster* and the pioneer plant *Macaranga*, in the fig genus *Ficus* and the agaonid wasps, and in other insects and flowers. The diversity and range of different mutualisms demonstrate how finely resources such as a mutualistic genus can be divided among plants, fungi, or organisms receiving the benefits. Often, the mutualism is largely specific to participating species. In the forest of Lambir Hills, our accumulated studies reveal more varied pollinators than are known for any other rain forest, yet variations among interacting species are largely unknown. The understory holds an unusually wide array of organisms in the plant-pollinator mutualism, from fungi to slugs to cockroaches, and from dung beetles to hordes of stinging bees, moths, butterflies, beetles, fruit bats, and squirrels. In contrast, the forest canopy does not display this diversity. Although reduced coevolution between flower visitors and hosts is likely when the host has flowers only once every four or five years, and loose pollination niches beget generalist associations, an ecological fitting seems more likely when the pollinators of the same dipterocarp trees are thrips in Peninsular Malaysia but beetles on Borneo (Sakai et al. 1999b). Many other canopy flowers are visited extensively and seem pollinated by the perennial, colonial stingless bees, or honey bees.

The most abundant tropical forest bees are the eusocial, perennial colonies. There are more than 60 local species of stingless bees in some Neotropical forest, about three times as many as in Lambir Hills (and five times as many genera). In addition, there are up to 50 species of long-tongued traplining bees (most are euglossines) in the same Neotropical forests (Roubik 1990, 1998; Roubik and Hanson 2004), compared to less than a dozen at Lambir Hills,

although four genera are found in each. Why is Lambir Hills poor in these key forest pollinators, both solitary and social? The perennial bees possessing large colonies, and the proportion of flowering angiosperm species visited by them, seem comparable in Southeast Asia and the Neotropics (Roubik 1990; Roubik et al. 2003; Wilms et al. 1996). The proportions of different animal pollinators do not differ appreciably in the two of the best-studied tropical wet forests: La Selva, Costa Rica (Kress and Beach 1994), and Lambir Hills, Sarawak.

Nonetheless, if one compares the tall, dense forest at Lambir Hills with outstanding examples of mature, Neotropical forests (see Chapter 16) there are obvious differences in mutualists that pollinate. Regardless of differences in forest stature, total annual rainfall, or its seasonality, there are far fewer pollinating bee species in the Asian tropical forests, and generally far fewer in the tropics than in many warm, temperate areas (Roubik 1989, 1990, 1996; Michener 2000). The understory of the forest at Lambir Hills is packed with immature, emergent trees, so that relatively few individuals are ever in flower there. Flower abundance is low. The sheer numerical and temporal dominance of the honey bees in Asia and the stingless bees is impressed upon all tropical field biologists. These bees are scavengers in forests, especially those with periodic flowering. In equatorial Africa, Asia, and America, bees are extremely fond of sodium and concentrate on removing it from vertebrate skin or the carcasses and feces left by predators. Bees that are stinging or biting pests are so practiced at locating sodium, which has no smell, that they use other vertebrate products to find its source. Their olfactory senses and exploratory behavior are strongly developed, and they rapidly locate floral and other potential resources, especially in the canopy of large forest trees. As alternative resources in times of scarcity, the colonies can use the colony food stores, or forage for non-floral food (Roubik 1989).

The explanations for social forager dominance in tropical forests hinge on floral scarcity. Social bees are generalized in flower choice, are good competitors, and can bring nest mates to resources at any level above the ground, thereby dominating many flowering plants and possibly curtailing evolution of more specialized or seasonal competitors (see Roubik 1996b, 2002; Roubik et al. 1999). An added feature is that the extremely tall emergent trees in Sarawak constitute a foraging environment absent in other tropical forests (Richards 1952; Allen 1956; Momose et al. 1998a). Momose and collaborators advanced a mathematical model stressing the importance of rapid reproduction for plants of small stature in the understory and in gaps, often having specialized mutualists then predicted that the generalist pollinators, honey bees, and stingless bees would be favored for emergent trees. The argument that a protracted periods without flowers further reduces development of a rich bee community in the tropics of Southeast Asia (Roubik 1990) is compatible with this view. However, the negligible response to increased flowering during a general flowering by forest bees specializing on understory flowers has further implications (see Chapter 11). More data on flower use and further attempts at realistic models are needed. There are at least three alternative hypotheses to account for unexpected low species richness: a *lack* of evolution of specialization and de-specialization

(Thompson 1994), a *lack* of dynamic-refugia (Colinvaux 1996), and *isolation* from adequate source populations (see Fig. 1.1; Ricklefs and Schluter 1993).

A key factor in the pollination ecology of the forests of Southeast Asia is thought to be the large interval between general flowering periods and the predominance of *Apis*, usually two abundant species. The prominent migratory honeybees, giant *Apis dorsata* may escape predation from the sun bear *Helarctos* by nesting in *Koompassia*, a legume that is the tallest emergent tree. Honeybees generalize on many flower species. Their migratory pattern of populating the rain forest is testimony to the many loose niches that exist there, promoted perhaps most strongly by the periods of non-General Flowering that may last for 20 years (Wood 1956). These migratory flower visitors may compensate for, and take advantage of, the local poverty of pollinators created by an intermittent, general flowering phenomenon, and a low abundance of flowers in the understory.

Comparative studies can be used to assess the impact of social bee dominance on rain forest pollination ecology. Studies in the Neotropics pointed to the role of stingless bees (where formerly there were no *Apis*) in molding plant breeding systems. Dioecy would evolve to avoid inefficiency of pollen capture and wastage of pollen and ovules (Bawa 1980). The wet forest of Sri Lanka, at Sinharaja, has many tree species with mixed breeding systems (Stacy and Hamrick 2004). That is, self-compatibility and hermaphroditic flowers are not rare, even though honey bees are common. However, stingless bees, having only one species, are rare (Karunaratne 2004). Does the low incidence of dioecy imply *Apis* provides more reliable outcrossing services than small Meliponini?

In summary, consider the pollinators that allow mega-events like the general burst of plant reproduction to occur, and then consider the general rarity of the flowers and plants that are involved. Like the dipterocarp trees that now dominate the forest, there is an intrinsic difference in tropical ecology where General Flowering occurs. Pollinators range from the very large to the very small, with high abundance being roughly compensatory for relatively poor ability to reach a rare or distant target. Fig wasps are extraordinarily small, most less than 1.5 mm; thrips are similar; and the smallest meliponine bees and beetles are slightly larger. Those groups can, however, be spectacularly numerous. Being the only pollinators of many plants, they and other small animals will often determine which plants and animals survive in tropical forests. In contrast, the long-distance bat, bird, or certain insect pollinators, while never very abundant, are equipped, instead, to reach distant flowers and to locate them efficiently (Gribel and Griggs 2002). Both are master chefs of gene combinations. Frugivores, although often not as specialized as pollinators in their interactions, must provide mutualistic services for seeds, virtually all of which need transport away from the parent. Ecology in the rain forest of Southeast Asia functions as it does because the flowers are as rare as their pollinators are scarce, opportunistic, tiny, or specialized. The Borneo forest at Lambir Hills, Sarawak, demonstrates loose niches and limited coevolution, side by side with highly diverse and specific relationships that derive only from extensive coevolution, in a usually benign yet dynamic physical environment that will persist as long as we allow it to do so.

2. The Canopy Biology Program in Sarawak: Scope, Methods, and Merit

Takakazu Yumoto and Tohru Nakashizuka

The mixed dipterocarp forests in Sarawak are among the richest tropical rain forests in the world with almost 1200 species of trees known in an area of only 52 hectares (see Condit et al. 2000). We can easily imagine that the reproductive system, from flowering through pollination and seed dispersal, plays a crucial role in maintaining the rich diversity of plants. However, relatively little study has explored this topic at the community level in the tropical rain forests of Southeast Asia.

Tropical rain forests in this region are also known for the *general flowering* or *mass-flowering* phenomenon in the community (Ashton et al. 1988; Appanah 1993). More than 80% of the canopy trees species bloom during a period of up to 6 months at irregular intervals of 2 to 10 years, with a mean of once every 4 to 5 years. In a general flowering, or GF, so many species bloom in such a short period that a pollinator shortage inevitably occurs for some length of time. Effective pollinators must provide populations that can quickly meet the needs of millions of flowers and hundreds of species.

Previously, tropical rain forests in Southeast Asia were believed to exist in a stable, warm, humid climate throughout the year. However, it has recently been found that rainfall in this region changes from month to month, and with various long-term rhythms (Inoue and Nakamura 1990; Inoue et al. 1993). Among these repeated cycles, the most dominant occurs every 4 to 5 years. Its cause is known as the El Niño-Southern Oscillation (ENSO). This relatively dry period may last for a few to 10 months. An early hypothesis was that drought triggered general

flowering in mixed dipterocarp forests in the Malay Peninsula and Borneo Island (Ashton et al. 1988; Ashton 1993; Appanah 1993), but the physiological mechanism that produces flower induction in spite of little environmental change is still under study. How the insects that are the predominant pollinators, and others that consume flowers or seeds, respond to such an unpredictable and drastic change of food availability is one of a number of topics currently being investigated. To understand patterns of community dynamics in a changing environment, a systematic program to monitor plant phenology and insect abundance for at least one episode, from one general flowering event to another, was founded in Sarawak.

The Canopy Biology Program in Sarawak (CBPS), led by the late Professor Tamiji Inoue, Kyoto University (see Plate 1A), began as part of an international cooperative project known as the Long-Term Forest Ecology Research Project at Lambir Hills National Park, Sarawak, organized in 1992 by the Forest Department of Sarawak, Harvard University, Ehime University, Osaka City University, and Kyoto University, and financially supported by the Japanese Ministry of Culture, Sports, Science, and Technology, and by other sources.

The first goal of CBPS was to clarify how unpredictable environmental changes at the global level influence phenology and reproductive systems of forest plants, from flowering through pollination and flower/seed-predation by herbivores to seed dispersal, in the mixed dipterocarp forest. A second aim was to understand how the animals that build mutualistic relationships with plants (pollinators, seed dispersers, and ant-mutualists) as well as antagonistic relationships (flower or seed predators, and herbivores) are affected by the same environmental changes, directly or indirectly, mediated by plant phenology.

The importance of such studies is increasingly clear, but technical difficulties tend to inhibit their progress. The canopy of the mixed dipterocarp forests reaches up to 75 meters aboveground, making any sustained work there quite difficult. Nonetheless, forest tree reproduction occurs mostly in the canopy; CBPS therefore established a canopy observation system that consisted of tree towers and walkways. Using this canopy access system, we conducted bimonthly continuous censuses of both plants and insects along a fixed route in the canopy, aimed at a period long enough to securely encompass at least one GF.

2.1 Location and Vegetation

Lambir Hills National Park is located about 30 kilometers south of Miri, the capital of the Fourth Division, Sarawak, Malaysia, at 4°20'N, 113°50'E (see Fig. 2.1A). The park covers an area of approximately 6,949 hectares. The highest peak in the park is Bukit Lambir, at 465 meters (see Plate 1A). The vegetation can be classified as typical *lowland mixed dipterocarp* forest (Ashton and Hall 1992), dominated by Dipterocarpaceae in the emergent canopy layer. The habitat is further typified by an extraordinarily rich diversity of tree species (Lee et al. 2002).

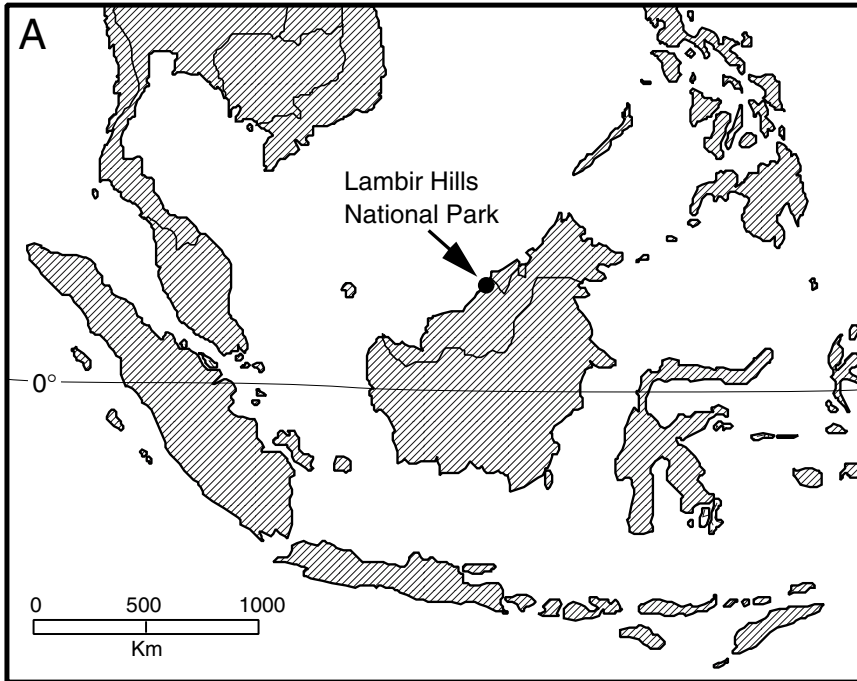


Figure 2.1A. The location of Lambir Hills National Park.

In 1992 and 1993, we established an 8 hectare (200 by 400 m) plot, or Canopy Biology Plot (CBP), at an elevation of 150 meters to 200 meters above sea level (see Fig. 2.1B). The plot includes *humult* and *udult* soils (sandy clay, light clay, or heavy clay in texture), several ridges and valleys, a closed stand (mature-stage forest), and canopy gaps. At the central part of the plot we made two tree towers on neighboring ridges and connected them by walkways of approximately 300 meters long.

In March 2000, a canopy crane was installed in a nearby forest with comparatively flat topography. A permanent plot, or Crane Plot (CP), was established at 400 meters to 500 meters northeast of the CBP. The soil in CP is poorer and trees are lower than at CBP; together, these facilities greatly increase the accessibility of the forest canopy.

2.2 The Canopy Observation System

In the early 1980s, pioneer work in tropical rain forests revealed that the canopy is the center of most plant activities (Sutton et al. 1983; Whitmore 1984), both in production and reproduction. Animal abundance (mainly insects) also displays

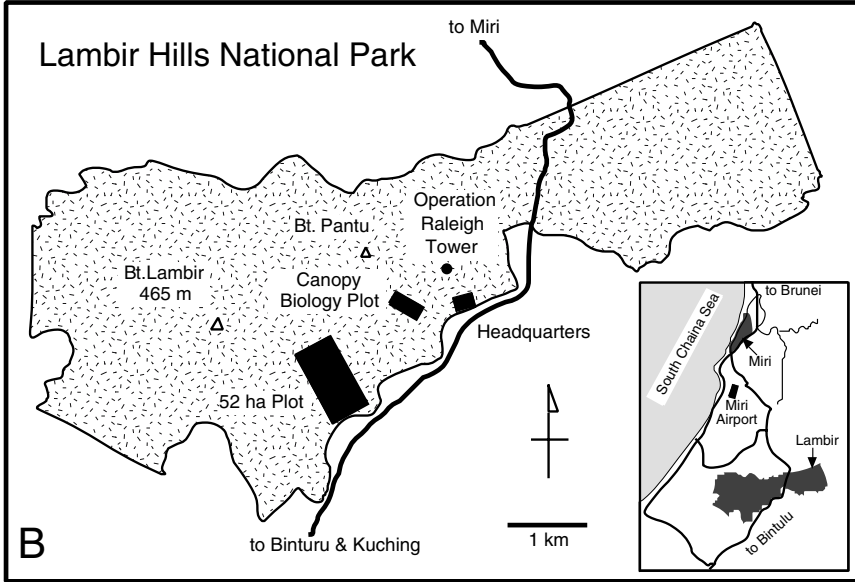


Figure 2.1B. The site of the canopy biology plots in Lambir Hills National Park (*inset* Miri and surrounding area).

its peaks there (Erwin 1983, 1988; Stork 1987a, 1987b, 1988a, 1988b; Rees 1983), regulated by factors such as distribution of food and shelter. These findings necessitated a concerted effort to approach the high canopy, at least 40 meters aboveground. Several access methods to the canopy have been developed: for example, ascent by tower and walkway (see Plate 3A, C-E, G; Mitchell 1982), by crane (see Plate 3B, F; Illueca and Smith 1993; Joyce 1991), by rope (see Plate 4D; Mitchell 1982; Perry 1978, 1984; Dial and Tobin 1994), and by raft (Hallé and Pascal 1992).

In CBP, we combined tree towers and aerial walkways for the long-term observation described above. An existing technology, such towers and walkways are constructed in various places in Southeast Asia (Pasoh, Peninsular Malaya; Poring, Sabah; Semengoh, Sarawak among others). We modified previous methods to accommodate long-term use and integrated devices in order to cover a wide area of canopy. We constructed two tree towers with heights of 50 meters and connected them by nine spans of aerial walkway that pass through various canopy layers. The total length of walkways spanned 300 meters, making the total system one of the largest in the world.

Tree tower 1 (T1) was constructed around an emergent tree of *Dryobalanops lanceolata* (Dipterocarpaceae), 70 meters in height and 1.5 meters in diameter at breast height on a gently sloping ridge (see Plate 3A). Eleven wooden platforms and 11 flights of stairs are set around the trunk of the tree, and observers walk in a spiral up to the top wooden platform 33 meters above the ground.