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Tropical rainforests as dynamic symbiospheres of life

Douglas Zook

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Abstract The remote Tiputini-Yasuni tropical forest region of the northwest Amazon (eastern Ecuador) represents a rich biodiversity likely unsurpassed anywhere else on earth. The myriad ecosystems, habitats and organisms are embedded in layers of symbiotic expressions. This region and particularly its Tiputini Biodiversity Station operated by the Universidad San Francisco de Quito offer unique and significant opportunities for symbiosis research and needed habitat conservation support. The centrality of symbioses in tropical rainforests is discussed through a review of selected literature and based on recent first-hand field experiences.

Keywords Tropical rainforest ecology · Symbiosis · Tiputini · Biodiversity · Yasuni · Conservation biology · Northwest Amazon ecosystems

The Tiputini River flows east from the Andes of Ecuador as a tributary of the Napo. It is a classic “white river” with quickly changing fluvial levels surrounded by terra firme lowland tropical forest. Approximately 300 hundred km east-southeast of Quito, Ecuador in the northwest Amazon is the Tiputini Biodiversity Station (TBS). Operated by the Universidad San Francisco de Quito with collaboration of Boston University (USA), it is among the more remote and biodiverse tropical forest locations on earth.

The extreme wilderness location of Tiputini Biodiversity Station, within the traditional territory of the Waorani people, means that—until recently—the area has been largely protected from the influence of outside forces. As a consequence, this area offers a unique concentration of endemic wildlife. Its high alpha diversity reflects a combination of several factors, including global location (nearly at the geographical Equator at latitude 0° 38’S); an elevation mean of approximately 220 m above sea level; 3,200 mm of annual rainfall; and, nutrient flow and weather system influences of the nearby Andes. The Tiputini Biodiversity Station is adjacent to the 2.6 million hectare Yasuni Biosphere Reserve (about the size of the State of Vermont, USA). Yasuní/Tiputini is within the “Core Amazon,” a particularly wet region with high annual rainfall and no severe dry season (Bass et al. 2010). Finer et al. (2009) review the recent history and urgent conservation needs of Yasuni.

Excursions to the Tiputini-Yasuni region by the author combined with an examination of the research literature strongly indicate that this remote locale, as well as large tracts of tropical forest biomes globally are dominated by symbiotic systems. The term “symbiosis” here can be defined in the traditional ecological “mutualist” sense or in this author’s definition, which de-values specific categorization in place of concrete, temporal changes: “The acquisition of one organism by another unlike organism and through subsequent long-term intimacy, new structures and metabolism emerge.” Field observations and a review of the literature suggest that remote tropical forest locales represent a vast symbiosis research potential, largely uninvestigated.

Overall ecological field research at Yasuni-Tiputini indicates that several major taxonomic groups (vertebrates, invertebrates, lianas, and trees) are among the most species rich in the Amazon and indeed the world (Bass et al. 2010; Kreft et al. 2004; Pitman et al. 2001). Most studies of this region have focused on diversity and taxonomy of megafauna and megaflora. Orme et al. (2005) indicated that more than 570 species of birds are found in the Yasuni region, second in the world only to southern Peru. More than 270 species or reptile and amphibian species have

D. Zook (✉)
Science Education and Global Ecology, Boston University,
Two Silber Way,
Boston, MA 02215, USA
e-mail: dzook@bu.edu

been recorded at Yasuni, the greatest number ever recorded for an area its size. (Bass et al. 2010) The highest number of bat species in the world have been recorded in that region with 58 species out of a possible total of 117 known species of the Amazon recorded at Tiputini (Rex et al. 2008). Insects are estimated in extremely high species richness, with ants particularly prolific (Wilkie et al., 2007). Camera trap field work as led by John Blake (pers. comm.) of the University of Missouri, St. Louis (USA) and supported in part by the National Geographic Society have visually revealed numerous threatened and endangered species, including a high density of *Panthera onca*.

Fundamentally important organisms such as lichens, protists, liverworts, cyanobacteria, bacteria, fungi and most insects and fish have yet to be studied in the region. Field observations at the Tiputini Biodiversity Station in January, 2008 (Symbiosis International *News*, number 14, 2008) by a small team organized of the International Symbiosis Society, and led by the author, indicated a high density of mycorrhizal and saprobic fungal species in just ten days of exploring. The team included noted symbiotic system mycologists Katarzyna Turnau of Jagiellonian University, Kraków, Poland and Håkan Wallander of Lund University, Uppsala, Sweden.

The Tiputini Biodiversity Station can be traversed via its trails fairly easily in the relatively drier months, such as January and August. In so doing, and at a perfunctory few meters per hour pace, numerous symbiotic systems of the Tiputuni/Yasuni region can be observed, documented, and studied. These include:

- a multitude of folicolous lichens with some individual leaves suggesting over a hundred species;
- prolific termite tree and ground nests with vast gut microbiota;
- both monoecious and dioecious *Ficus* species obligately symbiotic with specific wasps able to enter and ultimately pollinate through the ostioles of the fig synconia.
- *Myrmelachista schumanni* (lemon ant)—*Duroia hirsuta*—dominated clearings (myrmecology) based on formic acid excretions
- *Opisthocomus hoazin* (hoatzin), a unique tree-dwelling, leaf-eating bird in lagoon regions (see cover illustration) which features a series of internal adaptations to house a wide array of fermenting microbiota;
- mycorrhizal fungi which dominate the terra much like most plant-covered regions of the world, but which in these tropical forest regions lie amongst and in close interaction with the leaf litter, very top soil surfaces and even the mid- and upper- strata of the of forest architecture;
- orchids in the mid- and upper-canopy and their specialized mycorrhizae ;
- “guard-ants” with extra-floral plant nectaries;
- leguminous plants which are prolific and in association with nodulating understory root and even aerial root bacteria as important nitrogen fixers.

Numerous other organisms of the Amazon, such as species of flatworms, tapirs, primates. salamanders, frogs, liverworts, protists, and a wide variety of insects, likely feature key symbionts.

Neither these taxonomic groups nor most others of a less conspicuous nature have been studied by researchers within a symbiosis context. Therefore, collective meaning and insight on the above observation-based listing of selected significant symbiotic systems prevalent at Yasuni-Tiputini, necessarily depends on studies conducted thus far at other tropical forest regions. And, there is some research history on symbiotic systems from which to build, albeit it is sporadic and seldom discussed within the single discipline of symbiosis. Among the more studied symbiotic systems in the tropical forest biome have been the lichens. More than thirty years ago, Forman (1975) revealed that lichens, particularly those with cyanobacterial symbionts, are important nitrogen contributors in the rapid-growth requirements of the canopy and understory. Thallus leachate finds its way along branches, bark and buttress roots and may augment the prevalent legume fixation and common lightning strikes.

Definitive lichen n-fixation studies in tropical forests are nevertheless lacking, but more prolific, recent data indicates that lichens may play a similarly significant role as vascular plants in soil biochemistry (Cornelissen, et al. 2007). The weathering, element flux-promotion by lichen-mediated degradation is well documented, and there has been some speculation that epiphytes such as orchids and bromeliads may be able to become established in the canopy due to the action of lichenic acids at bark branching points. With climate change threats well established, Benzing’s (1998) findings that lichens and other epiphytes may be most vulnerable to relatively sudden atmospheric gas and temperature changes requires further more up-to-date analysis. Lichen sensitivity to atmospheric chemistry could also serve as indicators of greenhouse gas effects. Emerging studies of carbon dioxide effects on lichens in polar and arctic regions (Hauck 2009; Lattman et al. 2009) need equal researcher attention in tropical forest biomes.

Yet, is lichen biomass and diversity significant enough to have ecosystem impacts in the tropical forest? Lichens are the most dominant of the epiphylls, especially in the understory and lower canopy. Lichen cover on leaves (Fig. 1)—a very rare lichen habitat in temperate biomes—often exceeds 50% in the tropical forest (Anthony et al. 2002). Two large individual dicotyledonous leaves and one large palm leaf in the Costa Rican and Ecuadorian rainforests showed between 40 and 81 lichens species (Lucking and

Matzer 2001). More than 170 lichenized ascomycetes were documented in studies in Papua New Guinea (Aproot 2001). Lichens colonizing the phyllosphere appear to be enhanced by alternating very wet, highly humid, and low light intensities. Contrary to lichens in other habitats, many folicolous tropical lichens may be short-lived, dependent on the life span of its leaf substrate (Pinoklyo, et al. 2006). Interestingly, there are emerging reports that tropical lichens, such as the common, filamentous macrolichen *Coenogonium* harbor numerous bacillariophytes (diatoms) among the extracellular matrix of the mycobiont and among the thallus filaments (Lakatos et al. 2004). Thus, lichens in tropical forest regions may not only represent important biomass and diversity, but exist as a substrate for other autotrophs that are critical in trophic relationships. Lichens are so prolific well away from sulfur dioxide restrictions that they may foster animal biodiversity by being a common substrate camouflage (Seaward 1988).

There has been relatively little work on lichen work at the Yasuni-Tiputini region itself. For example, Mandl et al. (2010) examined alpha- and beta-diversity comparisons among ferns, mosses, and lichens in a large area of southern Ecuador including a portion of Yasuni. Freiberg and Freiberg (2000) looked at epiphyte biodiversity and biomass including lichens in Yasuni-Tiputini, focused particularly on altitude comparisons. The region suggests very high potential for numerous new discoveries involving lichen physiology, distribution, ecology, and of course new species.

Moreover, due to their fine niches within a very defined community space, many tropical lichens can be thought of as on the cusp of microbial ecology—as a kind multi-taxonomic transitional expression between the vast megaflora and the largely hidden but highly influential microbiota. Thus, it is no surprise that high numbers of observed lichens in the tropical rainforest are often overlooked, unnamed and of course many remain undiscovered.

Fungi are not only dominant in tropical forest symbioses through lichens, but through the ubiquitous mycorrhizal fungi. It is well established that when upper soil layers with embedded mycorrhizae are eroded away or otherwise disturbed in tropical forest rhizospheres, the plants become less viable (Powell 1980) and the soil less recoverable (Janos 1987). Arbuscular (AM) mycorrhizae dominate but with important ectomycorrhizal plants as well. For example, Onguene and Kuyper (2001) reported that all 100 species of plants in a portion of the Biafrean rainforest of Cameroon were mycorrhizal, nearly 75% AM and the remainder ectomycorrhizal. Five of the latter were simultaneously infected with AM mycorrhizae. Opik et al. (2008) conducted a meta-analysis involving twenty-six different studies of mycorrhizae fungal taxa in biomes around the globe. Tropical forest plants showed the most varied and dense plant colonization with a mean of 18.2 AM fungal taxa per plant species. Different avenues of study indicate that there has been a consistent underestimate of mycorrhizal numbers and diversity in the tropical rainforest. A recently discovered specific protein of AM hyphae, glomalin, has been detected in tropical soils at over 60 mg/cm^3 (Rillig et al. 2001). Such high amounts were found to extend deeper into the older soil levels. Their results and later work by Lovelock et al. (2004) indicate that a significant amount of soil carbon that contributes to viable soil organic matter (SOM) may not only be from saprophytic fungi acting on rainforest leaf litter, but from a long and continuing history of vast mycorrhizal mycelia accumulating photosynthate from associated plants. Estimates that tropical forests contain 27% of the global soil carbon pool (Dixon 1994) may, therefore, be too low.

Indeed, a profound question in tropical forest ecology is how do the great varieties of tropical rainforest trees, shrubs and other plants interact with the mycorrhizae? What are common physical and spatial pathways for mycorrhizae reaching the plant roots? Such questions resound forcefully because we know that in most tropical forests the soils are relatively poor in nutrient content, variety and even stability. We know that buttress roots (Fig. 2) are common among many tree species, selection favoring only minimal subterranean root growth. We know, too, that there is a great deal of leaf litter and organic material (fruits, nuts, flowers, animal parts, logs) on the forest floor. The high humidity, very frequent rainfall and consistently high temperatures favor very rapid decomposition by bacteria and fungi. What, then, is the relationship between mycorrhizal fungi and the saprophytic fungi? Is the latter a successional conduit for mycorrhizae colonization as partly suggested by data from Stark and Jordan (1978)? They found that when they artificially presented nutrient combi-

Fig. 1 Folicolous lichens, often numbering in the dozens of species on a single leaf, here in the understory near the Tiputini River. Photo by Douglas Zook

nations to plants in the field, more than 99% of that nutrient supply did not percolate past the relatively shallow, fungal-dominated root mat layer. This lends credence to the emerging notion that limiting nutrients such as phosphorus in many tropical forests transfer directly and rapidly from leaf litter to plant root (Aristizabel et al. 2004). This forest floor-shallow soil fungal interplay is likely not trivial, as Langley and Hungate (2003) also showed that mycorrhizae in many habitats can also alter decomposition rates of roots.

Tropical rainforests are not only defined by high precipitation, humidity and temperature, but by epiphytic growth. AM mycorrhizae have been reported, albeit less commonly, in the mid and upper canopy layers of several large rainforest tracts in five countries (Janos 1993). Lesica and Antibus (1990) report that fourteen orchid species in Costa Rica had typical orchid mycorrhizae and four epiphytic Ericaceae featured ericoid mycorrhizae. An additional fifty plant species were examined. Nine species showed low levels of AM colonization. The pan-tropical orchid genus *Vanilla* was found to be associated with several mycorrhizae species (Porras-Alfaro and Bayman 2007). It remains unclear how mycorrhizal spores become available to epiphytes high in the canopies, but often dispersal is thought to be animal-mediated. Janos et al. (1995) found through repeated fecal analysis that two rodent species were key dispersal agents for AM mycorrhizae in the understory. Scat analysis of 17 mammal species, including tree climbers, in the tropical forest of Queensland indicated extensive mycorrhizal spores (Reddell et al. 1997).

Mycorrhizal symbioses in tropical rainforests show some successional history, also in need of further study. For example, Husband et al. (2002) analyzed small subunit ribosomal RNA genes sequences of fungi found associating with the roots of forty-eight plants. Overall diversity was significantly higher than temperate zone mycorrhizal analyses. Most intriguingly, there were strong shifts in AM mycorrhizae over time. Those symbiotic fungi, which were dominant in the newly germinated seedlings, were replaced by previously rare species the next year. Perhaps, this apparent successional replacement of mycorrhizae and its contributions to the rhizosphere soil has a major impact as well in the succession of tropical flora (Janos 1980).

Fungal-based symbioses have a major impact in tropical forest vitality. Such significance is matched by numerous insect symbioses. Among the most fascinating and quite prevalent in the Tiputini-Yasuni western Amazonia region is the *Myrmelachista—Duroia* symbiosis. Known also as the "lemon" ant because of its citric taste when eaten, *Myrmelachista schumanni* alter rainforest landscapes dramatically. These ants have a high preference for the *Duroia hirsuta* tree as a gall-like nest site ("domatia"). Therefore, the ant workers spend considerable time injecting internally-produced formic acid into leaves of non-*Duroia* plants, effectively acting as a powerful herbicide (Edwards et al. 2009). Plants begin to die off within twenty-four hours and can continue so intensively that a broad patch of rainforest understory can be eliminated in weeks and then maintained for years (Frederickson et al. 2005). One "Devil's Garden" or "Chuyathaqi" as labeled by indigenous peoples originally, has been reported to contain over 300 *Duroia* trees covering 1300 square meters. While the tremendous reduction in biodiversity as a result of the ant behavior can be seen as detrimental to the forest ecosystems, it also causes gaps that bring light to the mid and lower level canopy at the perimeter and eventually can be considered as a secondary successional event. Recent studies (Frederickson and Gordon 2007, 2009) indicate that the spread of such *Myrmelachista* spp. may be limited by the curious finding that *Durioa* is actually *more* of a sustenance plant for herbivores within the "Garden" area than outside of it, which suggests that the lemon ants cannot defend "their" plants so completely; thus their abilities to expand are limited, which, in turn, helps to explain why they do not over-run vast rainforest tracts.

Fig. 2 Buttress roots predominate in many tree species, likely associating with mycorrhizal and saprobic fungi in the detritus and the most upper soil horizons. The roots are often extensively colonized by lichens and bryophytes which in turn are habitats for a variety of symbiont-containing insects. Photo by Douglas Zook

Many ant species have fascinating relationships with myrmecophytes (plants that shelter selected ant species within hollow structures) other than *Durioa*, and often bordering on symbiosis. Solano and Dejean (2004) studied three myrmecophytes in the understory of Guiana rainforests. One of the plants, *Maieta guianensis* features uniquely architectured leaf pouches which serve as waste depositories for specific associated ants. This waste is very nitrogen-rich, containing more N than plant leaves. Radioactive isotope analysis showed that 80% of the *Maieta* nitrogen is derived directly derived from the ant waste. In a related study (Dejean et al. 2005), *Cordia* and *Hirtella* spp. are colonized by the ant *Allomerus decemarticulatus*. These associated ants use hairs from the host plant stems to bind together fungal mycelia which they have collected to build a spongy “platform” to trap larger insects. The ants leave holes in the structure, such that when an insect arrives, the ants pass through the holes from underneath, immobilize the prey, transport it, and then the ant colony consumes it. It is likely that such prey capture involving a host plant may be for N assimilation in an N-limiting environment. Fungi may be more common as a third symbiont than previously thought. Defossez et al. (2009) examined domatia-building ants on their host plants, such as *Leonardoxa sp.* in the Cameroon forest and found fungal cultivars of the ascomycete order Chaetothyriales. It is likely that these numerous domatia-centered tripartite relationships are strongly symbiotic involving new structures and long term intimacy.

Ant-plant symbioses involving extra floral nectaries (Fig. 3) appear quite common, with the first enquiries dating back to 1874 (Bentley 1977). Fiala and Linsenmair (2004) found that in a primary lowland forest of Malaysia, of 741 species examined, 12.3% had extra floral nectaries. Moreover, such nectaries were more frequent among those tropical plants that were more abundant. Research has consistently shown that tropical plants with nectaries attract and maintain ant species, which protect the plant. The nectaries are actually glands that secrete sugary liquids, often with amino acids. Stephenson (1982) fostered branches of a *Catalpa* without ants and found those branches quickly feature colonization of eggs and larvae of attacking herbaceous insects and generally a greater leaf herbivory. This reinforced findings of Keeler (1977) who observed the “ant-as-guard” selection behavior involving a plant petiole.

Extra floral nectar may be expressed within defined regions of the upper canopy ecosystem. For example, extra floral nectaries were a main food source for ants that frequent epiphytes such as philodendron and lianas whereas most trees in the upper canopy featured homopterans tended by honeydew-seeking ants (Blüthgen et al. 2000). Nectar source and quality, the physiological requirements of the ants, and intense competitive interspecies interactions may drive the distribution patterns and impacts of the symbioses (Blüthgen and Fiedler 2004).

With ant-myrmecophyte symbioses so widespread in tropical forests, the question arises as to where ants obtain necessary nutrients that are not within their plant host excretions? Perhaps similar to mycetocyte systems of aphids and other insects, many ant species appear to harbor extensive bacteria colonies, which could in turn supply vitamins or key metabolites. For example the *Acacia* mymecophyte is specifically dependent on its ant symbiont, *Pseudomyrmex ferrugineus*. Thirty different bacteria were found to reside in the ant. These ant colony bacterial taxa were significantly different from the bacteria found on the associated plant leaf surfaces, indicating bacteria specific to the ant. Some of the bacteria discovered belong to known N-fixing groups (Eilmus and Heil 2009).

The dominance of ant-centered symbioses in the tropical forest is most obviously seen in the winding parade of countless active attine leaf-cutter ant workers moving cut leaves from the mid- and upper-vegetation to ground-based nests for fungal food cultivation. The ants collect and supply leaves for specific basidiomycete growth, which in turn is genetically strengthened over time by periodic invasive fungi, *Escovopsis*. Selection has favored those attine ant lineages that have accumulated soil actinobacteria which through its antibiotic production tends to ward off the fungal infection and preserve the nutritional food cache (Currie 2001). The filamentous bacteria, several of the genus *Pseudonocardia*, were present on 3 genera of fungus-growing ants (*Acromyrmex*, *Trachy myrmex*, and *Apterostigma*) and were isolated from 126 colonies (Cafaro and Currie 2005). Zhang et al. (2007) have indicated that some leaf-cutter ants can even differentiate between their native actinobacterium strain and other strains isolated from other leaf-cutter ant species. The authors suggest that this ability may give ants an ecological flexibility in protecting their fungal gardens. More recently, a likely fifth symbiont has been discovered, a prevalent ascomycete black yeast localized with the actinobacteria at the ants’ cuticle (Little and Currie 2008).

The leaf-cutter ant multi-tiered symbiosis emphasizes an alternative and emerging view of symbiosis in which organismal consortia are part of an ever-exchanging and opportunistic continuum rather than locked into strict categories of mutualistic and parasitic. For example, Little and Currie (2007) point out that the “parasitism” which they consistently study as part of their complex symbiotic leaf-cutter system actually appears to promote the stability of the symbiotic system. With a variety of multi-genomic and multi-tiered symbiotic systems such as attine ants, this region may be a strong research platform to further examine

Fig. 3 Extra-floral nectaries maintaining specific guard ant species are a common symbiosis at the Yasuni Reserve. Photo by Douglas Zook

this notion of a shifting continuum of interactions among symbionts rather than the traditional mutualism-parasitism-commensalism "boxes."

In part because it is so prolific, this highly co-evolved symbiosis has profound effects in the tropical rainforest. Often what may seem significant tree damage may translate ecologically into effective pruning, at least within certain temporal scales. This is implied by the work of Vasconcelos and Cherrett (1997), who found that despite leaf-cutter ant tree damage, tree seedling densities were not severely affected over time. Negative effects on the trees were mitigated by the observation that ant attacks did not increase even when greater numbers of seedlings emerged. The net effect of attine herbivory on the seedlings was strongest during the initial years and then stabilized. Leaf-cutter ants appear to often prefer young leaves and tend to abandon those leaves from species that take too long to cut (Cherrett 1972). Moreover, trees tended to be less damaged or pruned when they maintained a dense foliage. Thus, it could be revealing to study mycorrhizal responses to leaf-cutter activity, as the former is implicated in photosynthetic rates. Moutinho et al. (2003) further indicated that attine nest building may enhance the growth of pioneer endemic tropical forest plants such as *Cecropia sp.* after a secondary succession deforestation event. Roots from seedlings tended to retain water and nutrients more within and immediately adjacent to the ant colony nests. Not surprisingly, the important *Cecropia* trees are a complex ant-plant ecosystem in and of itself (Yu and Davidson 1997).

Termites in tropical rainforests play a central role in ecosystem strength and vitality. They have long been known for their decomposition of cellulosic litter and logs. However, there is growing evidence that they play a key role, much like the dung beetle, in recycling animal dung on the forest floor (Freymann et al. 2008). At least 126 species have been reported to feed on dung, the majority of these being non-fungus growing termites. Soil quality itself appears greatly influenced by termites. Donovan et al. (2001) allowed termite colonies to work soils in five different sites for two weeks. Termite activity increased organic carbon, water content, the relative amount of kaolinite (white clay commonly with iron oxides) and raised pH in low pH soils. There are indications as well that soil-feeding termite nests foster AM mycorrhizae growth and thus indirectly enhance plant growth. Diaye et al. (2003) simultaneously discovered an increase in nodules in the legume *Crotalaria ochroleuca* in soils fed by the termite nest. Thus, in some microhabitats of the rainforest, mycorrhizae, legumes and termites form an interdependent symbio-ecozone. Such chimeric landscapes may be more the norm than the exception in tropical rainforests, countering in part the dominant perspective of intense competition as the primary driver of niche expression. Indeed a more comprehensive understanding of tropical rainforest dynamics may necessitate new more Humboldtian research approaches in which, for example, the physiology and ecology of well-established, diverse symbiotic systems are studied together as a symbiotic consortium or even guild.

Moreover, the great varieties of termites in the rainforest are hard to explain in fundamental niche theory, for there is minimal evidence for spatial and temporal separations between species as Bourguignon et al. (2009) has pointed out. Using N isotopic ratios, he found that resource partitioning along a humification gradient occurred amongst many termite groups. Thus, feeding niche differentiation can be strongly implicated in termite species richness and diversity.

The predominance and indeed evolution of differing feeding groups in termite lineages in a macro-ecology analysis mirrors the vast microbial ecology gut expression. As Brauman et al. (1992) discussed, in wood-eating termites, carbon dioxide reducing acetate-processing bacteria dominated over carbon dioxide-reducing methanogens for hydrogen generated by fermentation in the hindgut. In contrast, acetogenesis from hydrogen and carbon dioxide is insignificant in the soil-feeding and fungus-growing termite which have more methane dependent microflora. The authors also suggest that given the large biomass of termites in the tropics, this has implications in greenhouse gas analyses. The termite bottom line is exemplified in a recent International Symbiosis Society (ISS)-sponsored excursion (2008) to Tiputini, wherein colleague and termite specialist Betsey Dyer (Wheaton College, Massachusetts, USA) pointed out the many varieties of termite nesting expressions along and above the trails and later, in the Biodiversity Station laboratory in our examination of paunch microflora, reiterated the fact that some termite species in the tropics have a greater and quite different protistan and bacterial biota with differentiated roles than other species. Nevertheless the *sine quo non* remains that all hindgut termites including the tropical rainforest where they are most dominant, are significantly dependent on internal microflora (Breznak 1982).

Another lynchpin of tropical rainforest health might also be barely noticed, the *Ficus* wasp (Agaoninae, Heminoptera), a symbiont with the prolific *Ficus* spp. (Moraceae). The female fig wasp enters the specific, co-evolved opening (ostiole) of the internally inverted flower encasement known as the "synconium." Within, they pollinate and simultaneously lay eggs via their ovipositor deep within the fig ovules. Once these hatch in the synconium from specialized galls, the offspring mate and the females of these disperse, flying very long distances, carrying pollen to other synconia of other *Ficus* trees, which must be compatible. This obligate symbiosis features remarkably specific adaptations (Weiblen 2002). For example, fig wasps have special cutting edges near the mouth and spikes at the tibia to prevent them from reversing direction when entering the ostiole. Moreover, specific chemical cues from the tree are emitted which not only attract the specific wasp type necessary but maintain its presence (Harrison 2005).

Indeed, the wasp and perhaps even the *Ficus* can be considered "keystone" species. The former fits some definitions in which an organism that is relatively inconspicuous but yet in great numbers has a profound contribution to the biodiversity of a region (Zook 2001). Variations (Libralato et al. 2006; Bush 2000) suggest keystone is more broadly linked to the organisms' overall effect on the ecosystem and not necessarily its influence on diversity or species richness. By whatever measure, efforts to conserve *Ficus* trees and their wasp pollinators are crucial to any conservation strategy involving tropical rainforests. Nearly all *Ficus* plants fruit several times each year and in high fruit abundance, sustaining huge numbers of frugivores (Herre et al. 2008). Harrison (2005) emphasizes that *Ficus* is the only ubiquitously diverse plant genus in the lowland tropical rainforest. In this extensive analysis of studies involving 260 *Ficus* species from 75 countries, more than 1200 bird and mammal species in 523 genera and 92 families were found to eat figs regularly. Janzen (1979) in his classic discussion of the importance of *Ficus* posed the question of "who eats figs?" and he went on to point out that "everybody" does (Shanahan et al. 2001). Figs are tantamount to coral reefs of the rainforest, not only being trophically essential, but promoting important (seed) dispersal (Kaufmann et al. 1991).

Ficus species in and of themselves represent a unique diversity in the tropical forest. Harrison (2005) emphasizes the centrality of the symbiotic aspect. He notes, "Given the importance of outcrossing in tropical rainforests, plants can only be as rare as their pollinators allow them to be...and, hence, pollination is potentially a major limiting factor in plant species richness." Clearly, the highly efficient long range pollination system is a key to their diversity and range, in that wasps that are specific for certain species will use above canopy wind to travel long distances (Harrison 2003) and home in on the particular plants which are emitting chemical attractants.

A second group of strongly symbiotic plants in the tropical rainforest are the legumes (Fabaceae). Legumes are the third largest flowering plant family with nearly 20,000 species (Wojciechowski et al. 2004). Smith et al. (2004) estimate 6700 species of legumes in the western hemisphere tropical forest, most nodulating N-fixers. Legumes are seen as dominant vegetation in neotropical rainforests (Burnham and Johnson 2004). How many of these legume species and indeed un-named or undiscovered ones exist in thr Yasuni-Tiputini region is unclear. However, Yasuni is seen to be among the richest areas for vascular plants in the world with at least 3213 identified thus far (Bass et al. 2010). It may be the richest area in the world for woody plants as evidenced by liana density and mean number of trees species per 25–50 hectare (Valencia et al. 2004). The highest numbers of documented epiphytes as recorded in a 0.1 hectare area are found in Yasuni (Kreft et al. 2004). Data shows that up to 655 tree species and at least 900 vascular plants are found in a typical one hectare plot (Valencia et al. 2004). Given this and other related survey data (Bass et al 2010), significant numbers of these plants are likely nitrogen-fixing legumes.

While N is often a limiting nutrient in temperate forests, it shows a persistent availability in tropical rainforests, largely due to symbiotic n-fixing legumes (Reed et al. 2008). Tropical forest nitrogen fixation appears to be most limited by P access (Hedin et al. 2009; Pons et al. 2007). Interestingly, high rates of atmospheric N assimilation are quite plant specific. For example, three closely related species of *Casuarina* in a semi-deciduous tropical forest region of southeast Brazil were compared and differed significantly for N-fixation, photosynthetic capacity, and responses to shading among other ecophysiological characteristics in during both wet and dry seasonal periods. Unlike temperate and boreal forests, tropical forests tend to maintain high symbiotic N fixation even into mature successional stages. This is in part due to the abundance of N-fixing epiphytes particularly in lowland tropical forests (McKey 1994) like Yasuni/Tiputini. Some important epiphyte n-fixation may not be limited to lianas and vines, as Carpenter (1992) showed nitrogenase activity amongst a variety of cyanobacteria and leafy liverworts associated with the palm *Weldia georgii* at Finca La Selva, Costa Rica. Thus, microbial autotrophs along with cyanolichens may be additional diazotrophs augmenting the legumes.

Leguminous nodule-forming bacteria have also been seldom examined from tropical rainforests. Is the high diversity of Fabaceae in the tropics mirrored by the bacterial symbionts? Moreira et al. (1998) shed some light on this in examining 29 legume species in Brazil and extracting 44 bacterial strains. Nearly all strains showed sequences close to *Rhizobium, Sinorhizobium* and *Mesorhibium* species, with the authors pointing out that the strains were very similar to those described from distant agricultural systems.

Research into symbiotic n-fixing systems such as those in Fabaceae may take on added importance, given the growing data on the impacts and threats of global climate change. In a thought-provoking review, Vitousek et al. (2002) reinforces how initial spikes in plant growth through increased carbon dioxide assimilation are later tempered significantly by either a lack of or less mobile source of N (or other nutrients). The author suggests, however, that under certain conditions N fixation could be enhanced under elevated carbon dioxide levels, and urges further study, particularly on initially understanding the constraints on N-limiting systems in tropical forests as well as other biomes. In this climate change research context, Yasuni may be seen as a unique refuge for Amazon species (Bass et al. 2010). Models indicate that increased drought conditions are seen as major expressions of emerging climate change in many global locations, such as in the eastern Amazon. But, with the direct Andes influence, the western Amazon tropical forest regions such as Yasuni are more likely to continue in its current rainforest characteristics (Malhi et al. 2009).

Amongst this diverse, lush, legume-dominated plant growth at Yasuni/Tiputini, certain lagoon areas house another symbiotic system, the unique bird *Opisthocomus hoazin* (hoatzin) (see cover). This is one of the only folivorous birds in the world and the only one known to be so completely dependent on an internal fermenting microbiota (Dominguez-Bello et al. 1994). The hoatzin crop is essentially a foregut fermentation chamber with predominantly Firmicutes and Bacteroidetes bacteria (Godoy-Vitorino et al. 2008). It would seem that a fully operational fermenting organ in a bird would make it non-functional, for it has meant adaptations such as to the sternum that limit flight capabilities. But, individuals keep in flocks close in to the vegetation and do not travel long distances. Selection for this unique feeding leaf-eater and cellulase-based symbiosis has meant that the hoatzin, as it lives over freshwater tropical lagoons, can exploit habitats and food sources that other birds and most mammals cannot (Grajal 1995).

Further major studies in the Yasuni/Tiputini area—most particularly on symbiotic systems, which of course span the phyla—are greatly needed. The International Symbiosis Society working with Boston University's Science Education Department, sedGreen collective, and the Center for Ecology and Conservation Biology are committed to assisting the Universidad San Francisco de Quito and its supportive friends both in and outside of Ecuador in the struggle to preserve this biological treasure. At Yasuni/Tiputini, there continues to be major habitat threats from petroleum exploration and the various road building and infrastructure development that accompanies it. Thus, not only will an extensive, consistent presence by visiting researchers further the knowledge base of symbiosis and tropical ecology immensely, but the researchers' very presence may help to limit continued encroachment and habitat destruction by emphasizing the extraordinary significance the region has to the scientific community and ultimately the health and future stability of the planet.

(Those interested in visiting Tiputini and being a part of an exploratory research team should contact Douglas Zook, Vice President, International Symbiosis Society, c/o Boston University, Two Silber Way, Boston, MA. 02215 USA, dzook@bu.edu)

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