SPECIAL FEATURE

Fungal Symbionts of Tropical Trees[1]

The lush green vegetation of moist tropical forest is not what it appears. Dissolve away all the plant matter from the dense foliage, giant buttressed trunks, tangled lianas, and sinuous roots, and a ghostly fungal shadow of the forest will remain. These fungi—diverse symbionts that include mutualists, commensals, and parasites—play critical roles in the dynamics, diversity, structure, and functions of tropical forests. The last two decades have led to an appreciation for the ubiquity and diversity of fungal symbionts, and to much speculation about their impacts. Understanding the nature and scope of their impacts on tropical diversity, plant growth and recruitment, and species interactions requires untangling the connections that fungi establish between their host plant and other species and the environment. This Special Feature explores these themes through analysis of the patterns and roles of tropical fungal symbionts along several dimensions: from mutualists to commensals to pathogens; from the forest canopy to the dark understory to the soil; from a postage-stamp sized piece of leaf to ecosystems; from seeds to leaves to roots. Through studies of an array of endophytes, epiphytes, and pathogens, we are better able to see tropical vegetation as a plant–fungus chimera and to critically explore the complex roles of fungi in tropical forests.

Nearly all plants form symbioses with a diversity of endophytic (within the plant) fungi. These endophytes colonize leaves (foliar endophytes), roots (mycorrhizal fungi), or other plant parts. Arnold and Lutzoni used molecular sequence data to compare foliar endophyte communities along a latitudinal gradient from the Canadian arctic to lowland tropical forests in Panama. They found that foliar endophytes increase in incidence, diversity, and host breadth from arctic to tropical environments. Arctic fungal assemblages comprised a low number of fungal species from a broad diversity of higher taxonomic groups, whereas tropical assemblages included a broad diversity of species from a narrower subset of higher taxa. The nature of the interaction between endophytes and their hosts varied from mutualistic to parasitic, depending on species and abiotic conditions. Experiments by Herre et al. show that both foliar endophytes and arbuscular mycorrhizae in *Theobroma cacao* (chocolate) reduce disease caused by the foliar pathogen *Phytophthora palmivora*. They demonstrate both the importance and the feasibility of incorporating endophytic fungi into studies on plant defense, physiology, and genetics of plants in tropical forests.

Most plant roots are linked in symbiosis with mycorrhizal fungi, which receive a significant fraction of fixed carbon from the host plant in exchange for critical services in resource foraging in the soil. The degree of host specificity for these fungi is important in the amount of ecological connectivity they may mediate. Trees in species-rich tropical forests are mostly associated with arbuscular mycorrhizal (AM) fungi, which are traditionally thought to lack host specificity. Aldrich-Wolfe used terminal-restriction fragment length polymorphism (T-RFLP) to analyze the AM assemblages associated with the canopy tree *Terminalia amazonia* in both forest habitat and pastures undergoing reforestation. Seedlings planted into the pasture developed mycorrhizal associations different from those in forest habitat, but neither did they share the AM community of the dominant pasture grasses. These results suggest that host specificity is not likely to be a prime determinant of the AM assemblage that develops on forest plants, but that neither is there great opportunity for establishing a common mycorrhizal network. In contrast, McGuire studied the importance of common mycorrhizal networks formed by ectomycorrhizal fungi (ECM), which are common in monodominant tropical rain forests but rare in species-rich forests. Seedlings with access to a common mycorrhizal network had significantly greater growth and survivorship than did seedlings excluded from the network. Seedlings showed positive survivorship effects of being near to conspecific adults, suggesting that the negative density-dependent effects thought to help maintain

[1] Reprints of this 58-page Special Feature are available for $10.00 each, either as PDF files or as hard copy. Prepayment is required. Order reprints from the Ecological Society of America, Attention: Reprint Department, 1707 H Street, N.W., Suite 400, Washington, DC 20006 (esaHQ@esa.org).

diversity in species-rich tropical forests may be reversed for species that form ectomycorrhizal associations.

Tropical forests have strong vertical structure, with much of the leaf biomass and fruit production in the brightly lit canopy, and seed germination, seedling growth, and juvenile recruitment in the dark understory. A connection between fungal symbionts of adult trees and juvenile recruitment is an underlying assumption of the Janzen-Connell hypothesis for pest-driven maintenance of plant diversity. Leaf surfaces in wet tropical forests are commonly colonized by a suite of epifoliar fungi, commensals whose life cycles are obligately tied to living leaves. Gilbert et al. used canopy access cranes to evaluate the host- and habitat-specificity of these fungi in two rain forests, finding that environmental conditions, rather than host range, governed both vertical and horizontal fungal distribution patterns. In contrast to Janzen-Connell expectations that adult trees act as reservoirs for fungi that infect their offspring in the understory, canopy trees were unlikely to be the sources of inoculum for understory juveniles. Similarly, Gallery et al. found that fresh seeds of pioneer trees were seldom colonized by fungi, but that most seeds were colonized quickly once in contact with the soil. Fungal infection of seeds of tropical pioneer species reduces seed survival in soil and can influence recruitment patterns. Within the broad diversity of fungi that colonized seeds, the more common fungi showed host affinities at the scale of individual tree crowns, rather than at smaller scales within crown shadows. These studies suggest that the dynamics of plant–fungus symbiosis may occur primarily in the understory and may be influenced by the locations of mature trees, but that the trees may not act directly as fungal reservoirs.

Finally, García-Guzmán and Morales took a broad synthetic look at life-history strategies of plant pathogenic fungi. Drawing on a wide variety of sources, they present a framework for looking at how life-history traits of pathogens and their host plants affect the distribution of plant pathogens in different tropical habitats and evaluate the importance of host phylogeny in determining the habitat associations of obligate fungal pathogens.

Together, the papers in this Special Feature highlight the commonalities across a diversity of plant–fungal symbiosis in tropical forests, and the context-driven complexity of the outcomes of the interactions. The relative importance of host ranges and abiotic factors in determining the spatial structure and impacts of plant–fungal symbioses are key to understanding the ecological roles of symbionts from mutualists to pathogens in tropical forests. The large effects of even "asymptomatic" endophytes suggest that plant–fungal symbioses need to be considered in the full range of evolutionary ecology of tropical plants.

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