**Are the Tropics Different?**

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Ever since my OTS Fundamentals Course in Costa Rica and subsequent generous support of my dissertation field work there, I've wanted to know more about Latin America and the Caribbean region; and many of my interests, e.g., in Conservation Biology, are informed by the history and politics of the region. However, I feel conflicted—an impostor—as a Latin-Americanist because my world view as a biologist encompasses greater scales in space and time. I am similarly conflicted about the question of whether the tropics are "different," motivating the following ruminations. A lot of research and diverse scholars have influenced my thinking, providing the *masa* for whatever *empanadas* may have come out of the oil.

One answer: who cares? I doubt that Jay Savage, Dan Janzen, and others who pioneered Tropical Fundamentals courses in Costa Rica cared about whether or not the tropics are "different." It was vision enough to recognize the tropics as a biological frontier, and the importance of training a generation of scientists to kick-start tropical science. Their efforts were wildly successful by any criteria, although the complexity of tropical biology remains daunting.

A second answer: the tropics are clearly different. Janzen himself argued that mountain passes are higher in the tropics—metaphorically, because of relatively poor dispersal by tropical organisms. Costa Rica, roughly the size of West Virginia, has more bird species than all North America north of Mexico, we tell students, while launching into descriptions of, and explanations for the Latitudinal Diversity Gradient (LDG). The dozens of plausible hypotheses to explain this gradient suggest we are still pretty clueless. Doesn't this diversity of species and species interactions distinguish the tropics? Traversing Holdridge's Costa Rican Life Zones by OTS Land Rover while an OTS student left me gaga over the differences from anything I'd encountered further north—no manakins or ant-acacias in New England. I chose to explore tropical diversity of insectivorous flycatchers for my dissertation (with Henry Hespenheide, who also coordinated my 1976 OTS course), motivated by predictions from niche theory of resource partitioning via narrow niches.

A third answer: there's no difference in the kinds of species interactions in the tropics, and the very idea of differences is a zombie idea that just won't die. If correct, then why have so many past studies, and plenty of recent ones, documented a difference?

A fourth answer: a goal of science is to transcend the particulars with unifying theories, such as can incorporate tropical diversity and ecology within global patterns and mechanisms. Many scientists wouldn't even ask whether the tropics are different while seeking broadly unifying principles—like evolution by natural selection, or niche theory. Gordon Orians' sabbatical study in 1964, including La Selva birds, was an exemplary niche approach, in which he concluded that, instead of narrow niches, "the greater range of resource types permanently above threshold values in tropical forests is the major cause of increased bird species diversity." Although many other studies echoed Orians' conclusions, my own dissertation research identified striking diet specializations that did not sit well with niche theory because they didn't look anything like resource "partitioning." I needed to try and figure out why.

Identifying unifying biological principles that are broadly applicable, from tropical rainforests to high elevations and latitudes, and from birds to plants, is no easy task. Our classes typically include how to do science, including the hypothetico-deductive method. OTS courses couple this method with ample opportunities to generate and test hypotheses with field data (and sleep deprivation). However, we learn by experience about a lot more to science than the hypothetico-deductive method, including the value of expanding one's natural history base beyond just birds or trees, devising better methods to measure relevant variables, and—serendipity.

I experienced serendipity while a graduate student at La Selva, on a side project with Lucinda McDade, the station manager at the time. We captured diverse insects—including a mega-cockroach that fell on my bed one evening—and presented them in the La Selva Arboretum to a large-insect predator, the Costa Rican Nunbird. When nunbirds arrived with their flockmates, we released an insect to document the response, and the birds quickly learned to associate easy food with our whistled imitations of their calls, coming on cue and following us like cattle egrets after cows. The serendipity was our discovery of several previously unreported traits of the insects that were particularly effective, and arguably adapted, to defend against avian predators like nunbirds. We were glimpsing an arms race, whose starting gun was the asteroid impact 65 million years ago that triggered the spectacular Cenozoic adaptive radiations of birds and lots more. Henceforth, I considered insects' perspective more attentively.

Many other scientists have documented coevolution of diverse organisms, including who eats whom or cooperates with whom, a natural history pillar of broader ecological and evolutionary theories. A few La Selva examples include Tim Moermond's and Julie Denslow's studies of fruit-eating birds, Gary Stiles' monumental body of work on hummingbird-plant relationships, Johel Chaves-Campos' radio-tracked and genotyped Ocellated Antbirds to reveal mechanisms of exploiting insects fleeing army ants, and Lee Dyer's and colleagues' work on tri-trophic interactions of plants, caterpillars, and parasitoids.

Early studies of arms races involved plants and their natural enemies, especially herbivores. In 1964, before I was even graduated from high school, Paul Ehrlich and Peter Raven proposed a radical idea for their time. They looked at butterfly and plant communities through an evolutionary lens, and suggested possible links with plant speciation, a driver of tropical diversity. Coevolution of plants with herbivores, and other flavors of coevolution, have become a major research focus, another widely applicable paradigm.

These evolutionary approaches to tropical plant communities provided a compelling alternative to niche theory. For example, how could so many coexisting tropical tree species divvy up (aka "partition") the few plant essentials, like nitrogen, phosphorus, water, and light? In 2001 Steve Hubbell provided another alternative, his Unified Neutral Theory of Biodiversity and Biogeography, in which individual plants colonize newly available sites, such as treefall gaps, randomly, assuming equivalent (neutral) demographic rates among species. He argued that the coexistence of extraordinarily diverse tropical tree species is possible without any niche specializations.

Hubbell’s theory stimulated a lot of tropical research—and controversy. One argument against it was that many tropical plants are extraordinarily specialized, just not so much trophically, as once argued based on niche theory, as in how they defend themselves against their natural enemies. Diverse seed predators and herbivores attack tropical plants relentlessly. Phyllis Coley, whom I first met on my OTS Fundamentals Course, addresses tropical tree coexistence, including adaptations to natural enemies, using the >300 species of Neotropical *Inga* species; and other labs are studying other plant taxa similarly. Increasingly, plant ecologists are compiling detailed natural history records of herbivores and other plant enemies, as well as how plants hurl an arsenal of costly biochemical, physical, phenological, and other defenses at their foes. Anticipating these ideas, Dan Janzen and Joseph Connell independently proposed in the early 1970s how plants’ natural enemies could contribute to coexistence, and not just in the tropics. Maybe the tropics are not so different after all!

My own studies of insectivorous tropical birds also started to make far more sense when I abandoned resource partitioning in favor of an evolutionary arms race. It has been eye-opening to recognize a variety of parallels of insect-bird coevolution with that of plants and their natural enemies. Convergence suggests generality. Eureka…a unifying approach to tropical diversity! The tropics are just like higher latitudes, only more so in terms of adaptive struggles with the biological more than physical environment, and more time for arms races to evolve!

Well, not so fast. We have lots to learn about the generality of these ideas, which is a stretch considering the immense variety of tropical organisms and ecosystems, and considering the difficulty of even defining the tropics. Besides latitudinal comparisons, are the Neotropics anything like the Paleotropics, the lowlands like higher elevations nearby, and perennially wet forests like seasonal forests and savannas? What about disturbances, and mainland areas versus islands, even large islands like New Guinea or Madagascar? How important or unique was the tropical climate of Gondwanan remnants that comprised South America when the Chicxulub asteroid struck, or the tradewind-drenched Andes that stoked speciation rates by swelling the Amazon River and tributaries?

I remain conflicted about whether or not the tropics are different, but an excursion into the LDG informs the issue considerably. Broadly applicable theories, and the prospect of rapid advances using powerful new evolutionary tools, emphasize the continuity of the tropics with other, less species-rich, environments. On the other hand, I am increasingly impressed by the extraordinary evolutionary legacy of the Neotropics, whose unique history and geography have accumulated so many species as to nurture novel species relationships and processes. The Neotropics, and the tropics generally, are also proving extraordinarily fragile ecologically, and the question of tropical distinctiveness withers in importance next to the crises precipitated by the Anthropocene “asteroid.” Essentially all biological diversity is threatened by humans, and the impending loss of tropical biological diversity raises the stakes dramatically, which brings me back to Latin American Studies programs. Any broadly applicable theories of economics, politics, and history, just as in Science, must confront Latin American particulars, including how best to inspire humans to recognize our indigenous—and indeed global—threats, and thereby inspire action commensurate with the challenges.