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New Perspectives in Comparative Ecology of Neotropical Rain Forests: Reflections on the Past, Present, and Future[1]

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ABSTRACT

In an effort to understand variations in ecological patterns among lowland tropical rain forests, Alwyn Gentry and colleagues synthesized data sets from four of the premier Neotropical field stations—La Selva (Costa Rica), Barro Colorado Island (Panama), Cocha Cashu (Peru), and the Biological Dynamics of Forest Fragmentation Project (Brazil). To promote the kind of geographically comparative tropical ecology advocated in the 1990 Gentry book, the Organization for Tropical Studies and the Smithsonian Tropical Research Institute organized a course in 2001 that visited each of these field stations. Papers from some of the studies resulting from this course are highlighted in this special section. These studies are notable for the consistent methods applied across forests, and they underscore the acute need and bright future for comparative tropical ecology. Key site characteristics for each of the field stations are summarized here.

RESUMEN

En un esfuerzo de entender las variaciones en patrones ecológicos entre selvas tropicales de bajura, Alwyn Gentry y colegas sintetizaron bases de datos en las cuatro principales estaciones biológicos del Neotrópico: La Selva (Costa Rica), Barro Colorado Island (Panamá), Cocha Cashu (Perú), y el Proyecto de Dinámica Biológica de Fragmentación de Bosque (Brasil). Con el fin de promover el estudio ecológico tropical comparativa a nivel geográfico recomendada por Gentry en 1990 la Organización para Estudios Tropicales y el Smithsonian Tropical Research Institution organizaron un curso en el año 2001, el cual visitó cada una de éstas estaciones. Los artículos científicos de algunos de los estudios producto de este curso se presentan en esta sección especial. Estos estudios son notables debido a la consistencia en los metodología aplicada a través de los cuatro sitios. Asimismo, estos estudios denotan la necesidad y el potencial de llevar a cabo más investigación a nivel de ecología tropical comparativa. Características importantes para cada una de las estaciones de campo son resumidos en esta sección.

Key words: *Brazil; Costa Rica; French Guiana; Panama; Peru; rain forest.*

IN 1990, ALWYN GENTRY AND COLLEAGUES COLLATED AND SYNTHESIZED INFORMATION from four of the most extensively studied Neotropical field stations: La Selva (Costa Rica), Barro Colorado Island (Panama), Cocha Cashu (Peru), and the Biological Dynamics of Forest Fragmentation Project (Brazil; Fig. 1). This book provided benchmark data sets for understanding how ecological processes (*e.g.*, forest dynamics) and patterns (*e.g.*, species presence) varied across lowland Neotropical rain forests (Gentry 1990). This book challenged tropical biologists to think outside the boundaries of their local field sites, at broader geographic scales.

In 2001, a group of 13 young scientists was given the unique opportunity to conduct truly comparative research at a continental scale in the field stations highlighted in Four Neotropical Rainforests. This course was cosponsored by the Organization for Tropical Studies (OTS) and the Smithsonian Tropical Research Institute (STRI) with funding from the Andrew W. Mellon Foundation and was led by Gordon Orians and Erika Deinert (OTS course 2001–25, Advanced Comparative Neotropical Ecology). The ten-week course visited each of the four sites, and the participants conducted both group and individual research projects in which standardized methods were applied at all sites. The studies contained in this special section are among those that resulted from this course and are focused on comparing and contrasting forest structure and biomass, the distribution of life history traits, the landscape-level context of woody plant regeneration in both gaps and shaded understories, and resource availability among the four forests. These studies complement previously published studies on flower color and pollination (Altshuler 2003) and root architecture in seedlings (Paz 2003). Through additional funding

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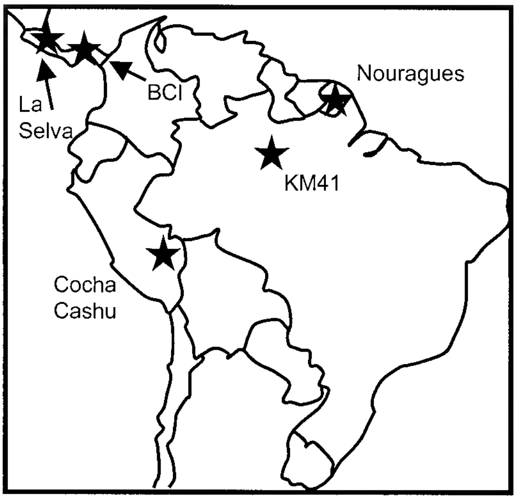

FIGURE 1. Map with locations of the five Neotropical field stations.

from OTS and Centre National de la Recherche Scientifique, some of the studies in this special section were extended to a fifth field station, Nouragues, French Guiana, in 2002 (Bongers *et al.* 2001).

As highlighted by the papers in this special section, one of the powers of comparative studies lies in their ability to identify ecological, environmental, and evolutionary forces that link and differentiate tropical forest ecosystems. Geographically comparative studies can be more powerful than *post hoc* literature reviews or meta-analyses, which are often hampered by inconsistent data collection methods (Vogt *et al.* 1998). A major strength of the papers in this special section is that consistent methods were applied across all sites. On a more personal level, the experience of working in different sites sharpens the individual researcher's ability to see how a local field site may be particular or generalizable.

What lessons have we learned and what is the outlook for comparative tropical ecology? A synthesis of key physical variables and results from some of the studies in this special section suggests large variations in ecosystem state factors (*e.g.*, precipitation, seasonality and soil fertility) and community responses to these environmental components (Table 1). For example, the density of tree, palm, and liana stems is inversely correlated to soil fertility across the forests, but aboveground biomass is not. Data such as these are needed to inform our understanding of the differences and similarities among tropical forests and refine our hypotheses about the processes that generate and maintain this diversity. The comparative framework and patterns established in the studies contained in this special section will likely provide the impetus for future research.

Despite the considerable logistical and financial challenges of conducting geographically comparative research, a number of recent developments in resources, conceptual approaches and technologies make the future for such studies bright. First, programs such as the International Long Term Eco-

TABLE 1. *Ranked differences in the physical environment, resource levels, and forest structure of four Neotropical forests (values of each variable are shown in parentheses). The four forests are ranked for each variable, without implying statistical significance among sites that differ in rank. Dry season length is defined as the number of months with rainfall of less than 100 mm. All variables were measured in common transects using standardized methods.*

Characteristic	Site rankings in increasing order	Reference
Physical environment		
Mean annual precipitation (mm)	CC (2165) $<$ BCI (2600) $<$ KM41 (2650) $\ll$ LS (4000)	1, 2, 3, 4, 5
Dry season length (mo)	LS (0) $=$ KM41 (0) $\ll$ CC (3) $<$ BCI (4)	1, 2, 3, 4, 5
Mean annual temperature (°C)	CC (24.2) $<$ LS (25.8) $<$ KM41 (26.7) $<$ BCI (27)	1, 2, 3, 4, 5
Soil fertility index§	KM41 (0.66) $\ll$ CC (1.47) $<$ BCI (1.54) $<$ LS (1.72)	6
Light (% canopy openness)	KM41 (3.8) $<$ BCI (3.9) $=$ LS (3.9) $<$ CC (4.5)	7
Forest structure		
Individuals/ha*	LS (3360) $\ll$ BCI (4910) $<$ CC (5377) $\ll$ KM41 (6150)	8
Aboveground biomass (Mg/ha)*	BCI (214) $<$ LS (234) $<$ KM41 (269) $\ll$ CC (392)	8
Root biomass (g/m^2), 0–40 cm	LS (237) $<$ BCI (278) $\ll$ CC (497) $\ll$ KM41 (800)	6
Small sapling density (no./m^2)	LS (1.1) $\ll$ KM41 (5.6) $<$ BCI (6.1) $<$ CC (6.4)	9

* Including trees, palms, and lianas.
§ Based on extractable P, base cations, and total N.
[1] Sanford *et al.* (1994); [2] Dietrich *et al.* (1982); [3] Wilf (1997); [4] Orians & Deinert (2001); [5] Laurance (2001); [6] Powers & Lerdau (pers. obs.); [7] Montgomery (2004); [8] DeWalt & Chave (2004); [9] Harms *et al.* (2004).

logical Research Network, NASA's Large-Scale Biosphere–Atmosphere Ecology Program in Amazonia, and OTS-STRI Fellowships in Comparative Tropical Research have brought new financial, administrative, and organizational resources to bear on geographically comparative studies in the tropics. Second, new conceptual approaches, such as networks of collaborators who use common methods and sampling techniques but are distributed at field sites scattered across the tropics, can overcome some of the logistic problems associated with large-scale ecology. This approach has recently been used to study beta-diversity (Condit *et al.* 2002), forest biomass and dynamics (Malhi *et al.* 2002), and litter decomposition (Powers 2003) across tropical forests. Last, developments in technology such as global positioning systems, geographical information systems, and remote sensing have led to dramatic improvements in our ability to visualize variations in properties such as vegetation cover and net primary productivity across large spatial scales and in our ability to map ecological attributes within that matrix.

Responding to the threats facing tropical ecosystems due to global environmental changes such as land-use change and habitat fragmentation, nitrogen deposition, and increasing temperatures requires detailed understanding of site-specific factors on one hand and an appreciation of large-scale patterns and geographic variation on the other. The studies that resulted from the Advanced Comparative Neotropical Ecology course speak to both of these needs and will serve as an important framework for future work in comparative tropical ecology.

STUDY SITES

Important aspects of the physical conditions and climate of all five sites are summarized below and in Table 1. Most of the studies included in this section used a common set of transects that were stratified within two habitat types defined by soil orders to provide an intra-site contrast among four of the forests. Although there are no comparative soil fertility data sets for the five forests in the literature, unpublished data collected with common methods suggest that the forests can be ranked along a soil fertility gradient as follows: KM41 < Nouragues < Cocha Cashu ≤ BCI < La Selva (J. Powers & M. Lerdau, pers. obs). All of the forest stands studied are mature, with little or no documented human use within the past 500 years (except for the Grau study).

La Selva Biological Station (Costa Rica), 10°26′n, 83°59′w.—The soils at La Selva derive from volcanic parent materials and the main contrasts among soil types result from differences in geomorphology and soil age (Sollins *et al.* 1994). Two main soil types are recognized at La Selva: more fertile alluvial Inceptisols that have been deposited along river corridors and less fertile residual Ultisols that have weathered in place from volcanic lava and mud flows (Sollins *et al.* 1994).

Barro Colorado Island (Panama), 9°09′n, 79°51′w.—The bedrock underlying the soils on BCI is of two main types, basalt and marine sediments (Dietrich *et al.* 1982). Andesite predominates on the highest elevation plateaus of the island, while sedimentary rock underlies the flanks or slopes that descend to Gatun Lake (Leigh 1999). The andesite-derived soils are Oxisols and are considered to be of lower fertility than the sedimentary rock-derived Alfisols, although there are few differences in some soil chemical properties between these soil orders on BCI (Yavitt 2000).

Cocha Cashu Research Station, Manu National Park (Peru), 11°54′s, 71°22′w.—Located at the foot of the Andes in the Western Amazon, the geomorphology and soils of Cocha Cashu are controlled by the dynamics of the meandering Manu River, which creates levee–backwater topography (Rasanen *et al.* 1987). *Terra firme* upland sites (Ultisols) are old, weathered river bars and the nutrient-rich floodplain soils, classified as Entisols, are relatively recent deposits of alluvium (Terborgh *et al.* 1996).

Kilometer 41 field camp of the Biological Dynamics of Forest Fragments Project (Brazil), 2°30′s, 60°0′w.—KM41 is located on ancient sedimentary materials bounded by the Brazilian and Guianan Shields (Fearnside & Filho 2001). Topography strongly influences hydrology and edaphic conditions at KM41. Ridgetop plateaus are characterized by clay-rich Oxisols, while "baixios" are lower-lying, streamside areas classified as sandy Spodosols (Chauvel *et al.* 1987). The Oxisols have slightly higher concentrations of extractable P and cations than the Spodosols (J. Powers, pers. obs.).

Nouragues Research Station (French Guiana), 4°05′n, 52°42′w.—Nouragues receives *ca* 2990 mm precipitation in an average year, with a two- to three-month dry season and a mean annual temperature of 26.3°C (Grimaldi & Riera (2001). The station is located on the Guiana Shield and has protruding, granite inselbergs and lower elevation plateaus. Plant community composition and stature varies across this topographic gradient; our studies were restricted to the "Grand Plateau," where the soils are classified as Oxisols. These soils, derived from volcanic and sedimentary parent materials, are highly weathered, acidic, rich in clays, and contain abundant lateritic nodules (Grimaldi & Riera 2001).

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