

Tropical Forest Diversity—The Plot Thickens

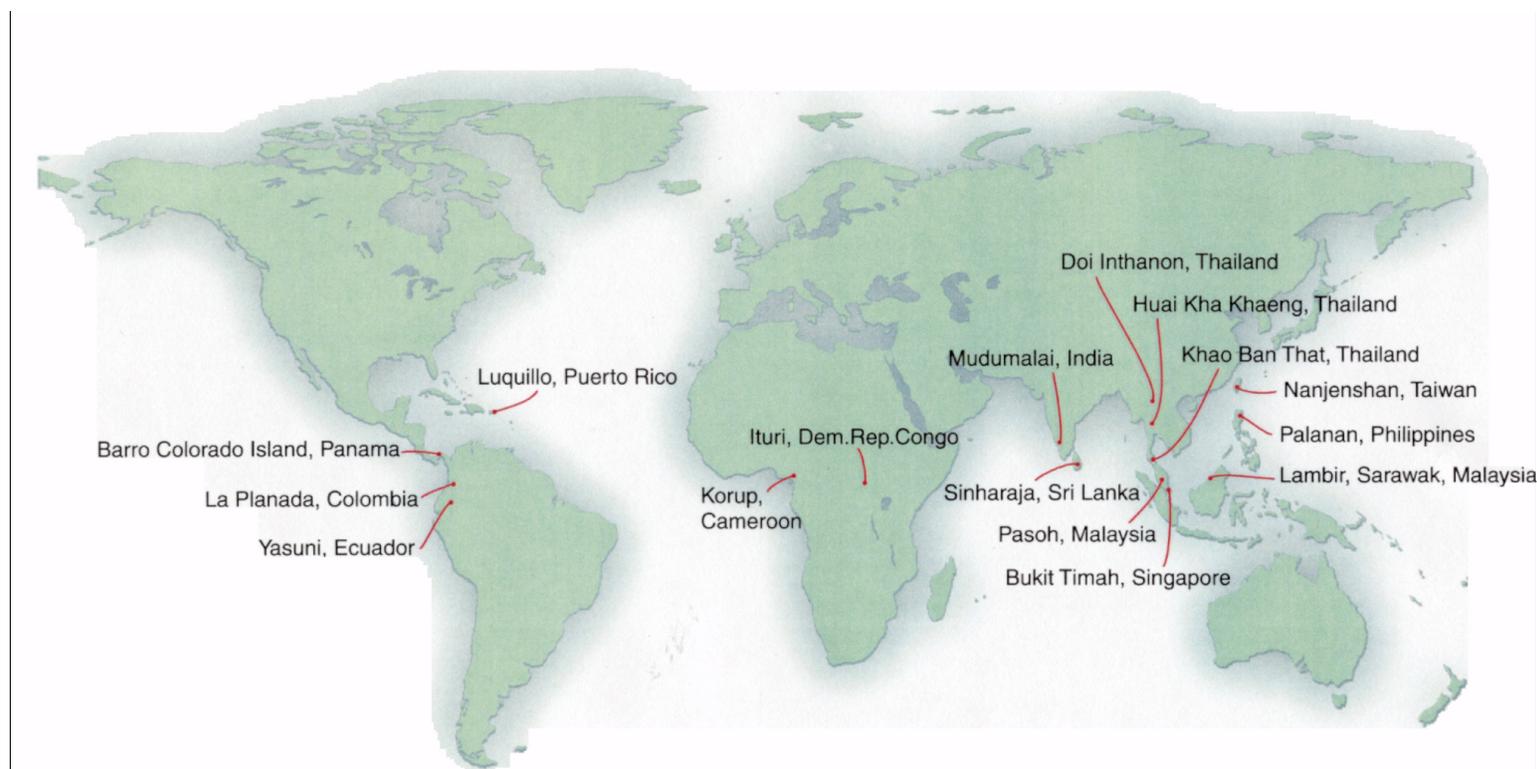
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The tropical forests of the world support a huge number of tree species—more tree species are found in 0.5 km² of some tropical forests than in all of North America or Europe. Although tropical ecologists have put forward a number of hypotheses to explain this species diversity, testing these hypotheses has been hampered by the lack of field studies with sufficiently large long-term data sets.

species. The physical, demographic, and taxonomic information accumulated for each site has also catalyzed research on, for example, the dynamics of soil seed banks (3), photosynthesis (4), the economics of nontimber forest products (5), and molecular analyses of gene flow within tree populations (6).

marked, mapped, identified, and measured at 5-year intervals. This global data set includes over 3 million trees comprising 6500 different species (about 10% of the total tropical tree flora). Two or more censuses have been completed in 8 of the 16 plots; a second census will start soon in two more plots.

Two decades' worth of results from the 16 FDP sites were discussed at a workshop on tropical forest diversity in Singapore (7). One goal of the workshop was to determine from the FDP data sets the factors that are most crucial for maintaining species diversity in tropical forests. Factors that are thought to be important for species coexistence include: habitat disturbance (different regeneration



To fill this void, the Center for Tropical Forest Science (CTFS) of the Smithsonian Tropical Research Institute has formed a network of permanent forest sites in the tropics—the forest dynamics plot (FDP) network—that are between 15 and 52 ha in size (see the figure, below) (1). By counting, identifying, and measuring all trees greater than 1 cm in diameter in the FDP sites at 5-year intervals—with a standardized protocol (2) to facilitate comparisons between sites—CTFS has obtained a unique and comprehensive data set. This data set provides valuable insight into the distribution, abundance, and dynamics of tropical tree

Forest dynamics and FDP plots. The forest dynamics plot (FDP) network has grown from the original 50-ha site established in 1980 in Panama to include more than 16 sites in 13 countries. In each FDP site, all trees greater than 1 cm in diameter are individually

requirements); natural enemies (different susceptibilities to pests, predators, and pathogens); limitations on seed dispersal; variation in nutrient availability; niche differentiation (different requirements for limiting resources); competitive equivalence (inability of a species to outcompete similar species); and fluctuating recruitment (which, together with juvenile persistence, may result in a species "storage effect"). Hubbell (USA) (8) concluded that evidence from the FDP sites supports the contribution of at least four factors—niche differentiation, natural enemies, seed dispersal limitation, and competitive equivalence—to the maintenance

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of tropical forest diversity. Data did not show, however, that habitat disturbance or fluctuating recruitment were important factors.

Although debate continues, the FDP data suggest that no single factor is likely to be sufficient to account for tropical tree diversity. The historical polarization of this debate into camps favoring different theories of how species coexist may be an artifact of the limited data available to earlier workers, and the tendency for individual researchers to work on a narrow range of tropical forest sites. The network approach advocated by CTFS erodes these constraints, as illustrated by the emerging trend to compare FDP data sets from two or more tropical forest sites (9).

There are two strategies for comparing FDP sites. The first is to examine the effects of the biophysical environment on ecological processes at FDP sites that differ in climate, soils, or topography. The second is to investigate the stability of ecological processes in sites that are far apart and that have different floras (and faunas) but similar environmental characteristics, such as rainfall and soils. An example of the first approach was provided by Debski (UK), who compared the lowland dipterocarp forests of a hilly site straddling two major soil types in Sarawak, Borneo, with a more uniform site in the Malay Peninsula. He found that soil type was consistently more important than topographic position in dictating the distribution of tree species. Garwood (UK) described the effect of climate on the phenology of seed germination and dispersal in a seasonally dry site in Panama compared with a permanently wet site in Ecuador. Thomas and Makana (Canada) presented the workshop's only intercontinental comparison, an examination of commercial timber trees in FDP sites in Malaysia and the Democratic Republic of the Congo. They found differences in the distribution of stem sizes and in the biomechanical properties of wood between the two sites, which may reflect variations in disturbance due to climatic factors such as wind.

Although early workers commonly assumed that the greater tree diversity of tropical forests was accompanied by an even spatial distribution of species, recent studies (10) indicate that tropical trees nearly always show a marked degree of clumping. Such clumping could be caused either by limited dispersal of seeds or by the association of species with habitat variables such as canopy openings or soil type. Distinguishing between these two alternatives is akin to the problem

of deciding whether habitat differentiation or dispersal limitation is the more important factor in maintaining species diversity. Investigators have examined clumping in FDP sites in several different ways—by analyzing tree spatial distribution data with randomization methods (Valencia, Ecuador; John, India; Gunatilleke, Sri Lanka; Kenfack, Cameroon; Ahmad, UK); by directly measuring seed dispersal and combining these data with simulations of microsite occupancy (Dalling, Panama; Seidler, USA); and by reciprocal transfer of tree seedlings between habitats (Palmiotto, USA; Kuo, Taiwan). Taken together, these studies emphasize that both habitat specificity and dispersal limitation contribute to clumping of tree species, with their relative importance being determined by dispersal mode, site history, and habitat complexity.

Workshop presentations—ranging from discussion of the species composition and biogeographical relationships of flora in recently established FDP sites (Hara, Japan) to long-term tree mortality in well-established FDP sites (Sukumar, India—illustrated how FDP research has evolved during the last two decades. Early FDP studies were usually descriptions of species composition, diversity, and distribution. It is only with the accumulation of more census data that the emphasis has switched to seeking the underlying causes of these patterns.

The FDP sites are becoming focal points for local networks of smaller plots. Dattaraja (India) reported on the relationship between species diversity and local rainfall and soil type derived from data from small plots surrounding the Mudumalai FDP site in India; Ohkubo (Japan) discussed the effects of forest fragmentation on the area surrounding the Lambir FDP site in Sarawak, Borneo.

The flood of new information from the expanding network of FDP sites has resulted in a rapid evolution in how ecologists think about the forces that shape tropical tree diversity. One area for future research is to expand theoretical models so that they incorporate more than one factor important for maintaining tree diversity. A second pressing concern is to apply what we have learned about the maintenance of diversity in relatively pristine tropical forests to a more accurate prediction of how tropical forests respond to the impact of humans through logging and forest fragmentation. Existing tropical FDP sites will surely provide a platform for future advances in both the theory and practice of tropical forest management and conservation.

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Forest dynamics and FDP plots. The forest dynamics plots (FOP) network has grown from the original 50-ha site established in 1980 in Panama to include more than 16 sites in 13 countries. In each FOP site, all trees greater than 1 cm in diameter are individually marked, mapped, identified and measured at 5-year intervals. This global dataset includes over 3 million trees comprising 6500 different species (about 10% of the total tropical tree flora). Two or more censuses have been completed in 8 of the 16 plots; a second census will start soon in two more plots.

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