

The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes, edited by E.G. Leigh, Jr., A.S. Rand and D.M. Windsor. Smithsonian Institution Press, Washington, D.C. 468 p. (1982). \$ 25.00.

In 1914, the Chagres River was dammed to form Gatun Lake, in the Panama Canal Zone. The rising water turned a big hilltop into what is known as Barro Colorado Island, 15 square km in area, which is now covered with primary and late secondary forest. For ecologists, this was the only (inadvertent) beneficial effect of the Panama Canal. The first biological surveys were carried out on the island in 1916, and the island was declared a reserve in 1923. The Smithsonian Institution took over its management in 1946, and in 1966 created the Smithsonian Tropical Research Institute. As this book attests, the island probably contains the best studied tropical forest community in the world.

The book is more aptly titled "The natural history of Barro Colorado." There is not much ecology of the forest vegetation as such, and the ecology in the book generally does not exemplify the most modern experimental and analytical tradition. With the exception of an ecological monitoring program initiated in 1971, to measure some physical variables, plant phenology and selected animal populations, no team effort was organized or funded to study ecology in a systematic way. What is presented in this book is a succession (33 contributions by 37 authors) of mostly descriptive accounts of natural history and population changes through the seasons and years, many of them excellent. Herein lies the strength of the book—one can argue that before we can understand the ecology of a tropical community, we must become intimately familiar with the important species groups and their long-term changes. After reading through the book, one does get a fairly vivid impression of what makes the community tick, as a fascinating kaleidoscope of flowers, falling trees, dropping fruits, monkeys, squirrels, beetles, moths, lizards, army ants, antbirds, coatis, etc., passes by, in monthly and yearly throbbing abundance. Furthermore, the book really does have a strong theme: what are the temporal changes, if any, in the community and what causes them? Chapters by editor E.G. Leigh near the beginning and the end attempt to place this theme in some theoretical perspective. In fact, the succession of studies done on Barro Colorado do seem to represent an informal team effort 'organized' by the intellectual stimulation and leadership of the institute's staff.

The book is divided into six sections, dealing with, respectively, the physical environment, biotic environment (vegetation), seasonal rhythms in plants, frugivores, insects of tree crowns, litter community and long-term changes. The physical setting deals with geology, climate and the water cycle, the last in considerable detail. The forest receives about 2500 mm of rainfall annually and has a marked dry season from January to April, near the end of which the soil dries out. There is some important yearly variation in the times of beginning and end of the dry season, however, which has important consequences for the plant community, which appears to be closely tuned to changes in soil moisture.

The section on the biotic setting is perhaps the weakest, as there is no adequate description of the vegetation presented here. There is a qualitative summary of historical changes, an analysis of tree dispersion (they are generally randomly dispersed or clumped, not surprisingly), tree mortality rates, and tree falls. Large tree falls are most frequent in the mature forest, which maintains opportunities for early successional species.

We begin to pick up the main theme in the seasonal rhythms section. The seasonality of moisture drives changes in the leafing, flowering and fruiting of plants which reverberate through the entire community, shaking populations up and down as their food or predators appear or disappear. Sometimes these changes are unpredictable, as when the dry season is too wet, delaying or preventing flowering and fruiting of some species. This makes it difficult for some animal populations to make it through the year. From rainfall records, Foster finds that such a situation probably happens about once in every 10 years, resulting in "famine". The tropical forest is diverse, but not so diverse that animals enjoy their choice food all year round. The early rainy season is the season of highest abundance of fruit and insects; at other seasons, alternative foods must be found.

The section on frugivores highlights the problems of some species in surviving amidst biotic luxuriance. Reproduction in most species is timed to coincide with maximum availability of fruits and insects. Agoutis bury seeds for use in the off season; pacas switch to browsing when fruits are in short supply. Cebus monkeys eat more shoots when fruits are harder to find late in the rainy season. Howler monkeys, which do maintain a fairly stable population on the island, are nevertheless stressed when the fruit supply declines in the mid-to-late rainy season, as reflected by increased numbers of deaths. Milton considers food an important factor contributing to population regulation in howlers. A study by Froehlich and Thorington on genetics and socioecology of howler monkeys finds a correlation between size and some other morphometric traits and vegetation richness. When famine strikes, spider monkeys invade the researchers' dining hall and snatch bananas and bread from the table.

One species, the moth *Urania fulgens*, defies tropical stability even more and engages in population irruptions and migrations at irregular intervals. Neal G. Smith, that great Sherlock Holmes of natural history, tells an absorbing story of his attempt to track down the causes. He is led to evidence for an unstable interaction between the moth and its facultatively poisonous food plant, a large woody climber. Repeated insect damage to the leaves, simulated by Smith, decreased the plants palatability. One of the most important discoveries of modern natural history is that the plants fight back!

The sections on insects of the tree crowns and the litter present yet more evidence of seasonal and yearly instability, for many taxonomic groups. Here I began to get pangs of indigestion—I do not know what to make of all the trends and zig-zags in abundance, and pages of numbers, but I suppose it is good to have them all in print.

After passing through feverish seasonal droughts and deluges year after year, we come to a chapter on “the significance of population fluctuations.” We draw our breaths. Doctor Egbert Leigh places his hand on the violent pulse of Barro Colorado and attempts his diagnosis. The case is a complex one. Is the community gradually dying, species by species, as more and more populations hit the bottom line? If population changes are largely random, then fluctuations could spell a high extinction rate. Barro Colorado is perhaps an abnormally sick case with its limited area, shortage of large predators, and limited immigration across its borders. Or is the throbbing pulse a normal one, typical of most tropical forest communities? Leigh thinks it probably is, and that fluctuations are not random walks which reflect oversensitivity to the environment. After toying with some mathematical formulas, he comes to the fairly self-evident conclusion that regulatory processes must be constraining fluctuations as large as several times mean population density. The seasonal pulse is not necessarily a symptom of an unhealthy (unstable) community. Leigh suspects that the amount of specialization and evolution is related to the diversity of the community and its response to the seasons. To support this diagnosis we perhaps need more experimental work and refined methods of analysis of trends and fluctuations than we have been offered.

This is one of the best edited and presented collections of papers I have seen; it is more than the sum of its parts. It has particular relevance to the highly seasonal forests of Southeast Asia which would probably show similar fluctuations if studied as intensively.

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