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Tallying the Tropics

Seeing the forest through the trees

By ELIZABETH PENNISI

Casual hikers probably don't notice the faded orange and green ribbons lying half buried in the leaf litter of the tropical forest on Barro Colorado Island (BCI) in Panama.

Likewise, visitors to this island reserve probably don't miss the birds that no longer live here or the herds of white-lipped peccaries or the big cats such as puma and jaguar. Those animals seem to have disappeared after this 1,500-hectare (3,700-acre) hilltop was cut off from surrounding land by engineers creating Lake Gatun, part of the Panama Canal.

Only because this reserve has served as a mecca for tropical biologists for the last 70 years do the data exist to reveal the changes in species likely brought about by isolation. And even if one of the ribbons did catch a watchful eye, how could that hiker guess its purpose?

Two ecologists began tying ribbons around tree trunks no bigger than their thumbs more than 12 years ago. At the same time, they tacked metal plaques onto larger trees. Each plant so decorated received a code number. Stephen P. Hubbell, now at Princeton University, and Robin B. Foster, now at Chicago's Field Museum of Natural History, surveyed more than 238,000 trees in this 1 kilometer by 0.5 km rectangle, placing each within a grid marked every 20 meters and again every 5 m. The name, size, and location of each became part of a computer database.

Then considered an ambitious — if not outrageous — undertaking, the Tropical Forest Dynamics Plot now serves as a model for similar study sites being established across the globe (see sidebar).

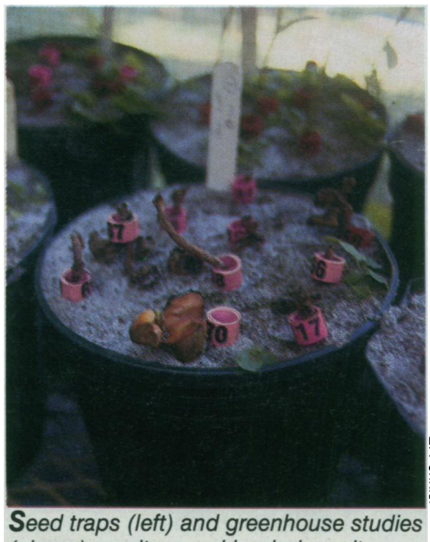
At first, the ribbon-tying scientists just wanted to monitor species diversity: They planned to count the kinds of trees present at regular intervals. But before long, many more people started trekking up to the plot, an hour's walk from BCI's buildings. For more than a decade, senior scientists, students, even amateur researchers have been watching these trees grow and produce fruit and have monitored the seedlings in order to learn what controls the organization of the forest. Hubbell and Foster have led two more censuses on the 50-hectare plot, one in 1985 and another in 1990.

Meanwhile, other investigators have ventured elsewhere on the island and to nearby peninsulas, tracking fauna as well as flora.

Bit by bit, the countless hours of note taking are building a new body of knowledge.

"Tropical ecology has gotten to the point where a lot of the easy things have been done," says Gregory S. Gilbert, a scientist at the Smithsonian Tropical Research Institute (STRI), which runs the island reserve. "Now we must get to the underlying mechanisms."

As Gilbert and others gather nitty-gritty details about how trees come to settle, thrive, and die, they hope to learn how physical constraints, such as weather or the island's isolation from other forests, and biological conditions, such as the presence or absence of certain seed-eating animals,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Seed traps (left) and greenhouse studies (above) monitor seed bank deposits.

affect the composition of tropical forests. "One of the big advantages of the plot is that all the trees are identified and labeled and mapped. So even if a tree dies, and falls over, and doesn't have any leaves left, and is rotting, you can almost always reconstruct what it [was]," says Gilbert.

Plant-animal interactions account for the tropics' diversity.

Like dog tags, the ribbons and plaques identify each surveyed plant. Often, trees will die and rot from one census to the next, leaving nothing except these markers on stumps. If the marker is missing, Gilbert can use his computer to get a list of trees in that small section by size. He can also ask the computer to name the nearest neighbors of a labeled tree still standing near the site of the stump. "More often than not, there's only one tree [that fits]," he says.

Computer programs make possible various analyses of the distributions of species in space and over time. At STRI, Richard Condit and his colleagues have determined that only a few – about 10 percent – of these tropical species seem restricted to specific topographies. Oil palms, for example, grow only in the swamp near the center of the plot. A few other trees stick to the slopes, which remain moist during the dry season because a limestone slab underneath traps a subterranean pool of water. Most, however, don't seem to have any preferences.

The analyses also indicate that different trees colonize forest openings at different rates and in different ways. The researchers group trees into guilds depending on whether a species favors sun or partial sun, tends to reside in shady spots, or is indifferent to where it grows. Trees within a guild thrive under similar environmental conditions and respond similarly when those conditions change.

"What a 50-hectare plot can yield are well-documented theories about the demographics of certain guilds of trees," Condit says. Even if tropical foresters can't save every species, he expects that the maintenance of at least some representatives from each guild can ensure the survival of a forest.

At the same time, the work is yielding information about the growth rates of commercially valuable species of trees, about the effects of climate change on tropical forests, and about biological diversity.

Compared to 1966, the island today is 14 percent drier. In addition, the 1982-1983 El Niño caused an unusually long dry season – 4 months without a drop of rain to settle the dust or calm the breezes that rob trees of precious moisture. This weather took a heavy toll. A species with 19 individuals in the plot is now represented by just three. Another's population has dropped from 219 to 83. By 1986, 16 percent of the trees with diameters over 10 cm had died. Overall, there seems to be quite a large turnover in the plot's plant population.

Condit and his colleagues have recently estimated the lifetime growth histories of 160 species inside the plot's boundaries. Balsa grows fastest: Its trunk broadens to 30 cm in a decade, whereas other trees can take 60 years to grow that much. Altogether, these scientists identified 28 fast-growing species, they report. Condit hopes that foresters trying to reestablish woods in Panama will take notice of these 28 rather than depending, as they have been, on planting non-native seedlings.

By seeking out the trees that have died since the last census and examining their status, the researchers can begin to pin down the decomposition rates of different trees. "That can be really useful for looking for species that are worthwhile growing in secondary forests," says Gilbert. "Some species are important because they grow fast, die fast, and turn over nutrients; others are good because they last."

These ecologists hope the data will one day enable scientists to anticipate the effects of logging on a section of forest or

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One is good; more is better

If all proceeds as hoped, scientists and economists will soon be able to compare data from permanent plots in Puerto Rico, Thailand, Malaysia, Ecuador, Sri Lanka, and the Philippines, as well as Panama. Trees from two sites in Malaysia and one in Puerto Rico will be tagged and cataloged by year's end. Similar projects are about to get under way. The idea is to be able to compare similar forest types in different parts of the world, says Peter Ashton, a tropical ecologist at Harvard University.

This effort began with a barroom argument. Ashton, who works only in Asian forests, had thought that the tropics supported incredible numbers of species because each specialized and thrived in particular conditions. Princeton University's Stephen P. Hubbell thought the opposite. He argued that tropical soils and climate offered little variety and little incentive to species to become specialized for a particular habitat. Instead, he suggested that the array of tree types in a forest arose primarily by chance.

Unable to resolve their differences, they agreed to set up a plot in Malaysia similar to the Tropical Forest Dynamics Plot that Hubbell had just established in Panama.

The first comparisons were shocking. North American botanists marveled at Hubbell's 300 tropical species, but that number pales in comparison to the 800 or so identified thus far in the Malaysian plot. And that study site may wind up a distant second to a second Malaysian site, which may be home to more than 1,000 species, says Richard Condit of the Smithsonian Tropical Research Institute. "It's probably the most diverse forest [in number of tree species] in the world," he says. At the same time, the Asian woods lack the variety of vines and air plants, called epiphytes, found in South and Central America. In that regard, Ecuador probably has the world beat.

In addition to trying to resolve their decade-old debate, Hubbell and Ashton expect data from these plots to help guide the development of environmental policies. "We're talking about global issues that require more than one site," says Condit. "This network – where you really document the species composition – is ideally designed for monitoring the impact of long-term [global] change."

Their observations will help foresters manage their resources – sustaining timber harvests while maintaining biological diversity. Just as important, Ashton has recruited economists who will use the productivity information to develop a way of assessing forests financially – not just for the timber and other goods they yield, but also for the services they perform in creating watersheds, absorbing carbon from the atmosphere, and providing pleasant recreational environments. "No one has valued both the goods and the services of tropical forests at the same time," he says. Once this is done, he expects that conservationists will be able to make a much stronger case for the preservation of these resources. – *E. Pennisi*

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the likelihood that planting certain trees on abandoned land will lead to reforestation. For example, the first census indicated that trees grow naturally in patches. This patchiness could mislead foresters. If they survey too small an area, they could underestimate diversity and thus the acreage needed for a sanctuary.

Also, in a recent compilation of studies done throughout the island reserve, STRI's Egbert Giles Leigh Jr. concluded that the island's isolation was having a detrimental effect on BCI's diversity. Those results forewarn of trouble if the only forests saved are small, isolated "islands" surrounded by pastures or development.

Work on BCI demonstrates the interdependence of plant and animal diversity. The wide variety of flowering and fruiting patterns provides many kinds of foods for local herbivores. But the rhythm of productivity sometimes leads to lean times that keep populations under control. Likewise, animals, in particular a small mammal called an agouti, help ensure that the island sustains a wide variety of plants.

James Dalling has become ever more aware of the close links between the island's plants and animals. An ecologist from the University of Aberdeen in Scotland, he now spends much of his time carting soil and seeds from the Tropical Forest Dynamics Plot to a greenhouse outside his temporary office on the island. His goal is to complete the largest investigation ever of seed "banks," dormant seeds on deposit in soil.

He chose to work on BCI because the plot's database enabled him to find individual trees spaced far enough apart to ensure that the seeds he dug up came from a particular tree. He could even verify that no other tree of that species had existed there within the past decade. For months he has collected seeds, some as they fell from trees and some that he sifted out of soil samples collected at particular distances from parent trees.

Specifically, Dalling wants to determine where seeds from two common trees, *Miconia argentea* and *Cecropia insignus*, wind up and how long they persist. These trees are called pioneer species because they are often the first to appear in open spaces, do best in bright sun, and grow fast. But they germinate only in the right mix of light and temperature conditions. His seed traps show that a tree can drop up to 60,000 seeds per square meter (m^2) during its 2-month fruiting season, yet he has never found more than about 8,000 of them per m^2 on the ground. He doesn't know why this is, but he has begun to suspect ants are responsible.

Dalling had expected to find most of the seeds quite near their parent trees. That proved true shortly after fruiting, but the seeds closest to the tree died or disappeared much more quickly than those farther away. As a result, "After 6 months, there are no more seeds in the top layers of the soil beneath the crown than there are at 20 or 30 m away," he reports.

This work not only confirms another study's finding that most seeds are dead or gone within a year, it also reveals that the deeper a seed winds up in the soil, the greater its chances of survival. "If seeds can immediately get buried, there's a chance they could persist for several years," he says. Some fall into cracks in parched earth; others get eaten by monkeys. If they are intact when they leave the monkey, mixed in dung, then beetles bury them. This underscores animals' roles in structuring the forest.

"But then there's a question of whether the seeds even have a chance of germinating and establishing," Dalling adds. He suspects that only if a tree falls and uproots is this sequestered seed ever likely to see the light of day. Thus when these pioneers appear as seedlings, the seeds they came from were either buried or fell recently from a tree nearby.

"The pioneers are really crucial to the restoration of a tropical forest," Dalling notes. "If you're going to rebuild a tropical forest, the first thing you need to do is get a canopy established. The way to do that is by using fast-growing pioneer species."

So he, too, sees a practical application for his work. "Finding a way to enhance their regeneration will be an important step in forest management." □