Research in large, long-term tropical forest plots

Richard Condit

The past 15 years has seen the creation of large (≥16 ha) permanent inventory plots in each of the major tropical forest formations of the world. Currently, six such plots have been fully mapped, and five more are under way. A standardized methodology is used at all sites — a complete census of all trees and saplings down to 1 cm in diameter — thus assuring strict comparability between sites and allowing the development of general models for the dynamics of tropical forests. The inventories aim to gather demographic information on individual tree species, to provide long-term information on forest composition so that future changes can be detected, to estimate the economic value of forest resources, to generate models of sustainable extraction, and to provide data on underused native species for use in reforestation or plantation forestry. The plots also provide data from undisturbed forest to serve as a control for anthropological and management studies of harvested forests.

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The Center facilitates the exchange of databases, software packages, analyses, publications and scientific visits between the research sites. In addition, CTFS assists in the development of new forest dynamics plots, with the goal of forming a network of sites spanning a range of floristic, climatic, geologic, economic and social conditions. The Asian sites were among 10 recommended for long-term research sites. In addition, CTFS assisted in the large number of scientists and institutions involved with local labor costs and support facilities. At each plot, a 5 × 5 m grid is first surveyed and marked with stakes. After the survey, marking and mapping each plant is routine. The greatest challenge in assembling the data sets has been quality control, particularly with respect to species identification. Although the BCI plot has a well-known flora, other sites such as Lambir, Ecuador and Zaire produce many undescribed species. Moreover, specimens must be identified by vegetative characters alone, since the majority of plants in the censuses are immature. For these reasons, well-trained specialists do most identification, while field crews primarily map, tag and measure trees. The field crews clearly have some impact on the seedling layer while moving through the forest, but most of the plots have substantial populations of large mammals, and the human impact probably pales compared to that caused by pigs, okapi or elephant. Moreover, relative to censusing smaller plots, a crew of 12 in 50 ha should have no greater impact than one person in one hectare. Management of the data sets also poses a challenge. For one, the sheer enormity (25–30 megabytes of data per plot) requires reasonably advanced computing power. CTFS has developed a variety of analytical and mapping programs which run on IBM clones with a minimum of a 200-megabyte hard drive and 386 processing chips (these are the kinds of computers most accessible throughout the world). Some work is done on much faster work stations, particularly analyses of spatial patterns, which require enormous numbers of calculations.

A different sort of challenge to the network has been proprietary rights over the data sets, arising because of the large number of scientists and institutions involved in the creation of the data sets. Who owns the data? How are data used? Who gets credit for de novo discoveries? These are the types of questions that need to be answered, and detailed agreements are written among all the institutions involved. Obviously, there are no uniform answers – India might have different requirements from Thailand – but all parties directly responsible for large-scale plots have consistently made the data available to other scientists, although with certain stipulations.

Results

The main results from the large plots can be divided into three categories: (1) studies of factors involved in population regulation and the maintenance of diversity, the original goal of the research; (2) documentation of changes in species composition, particularly with reference to changes in climate; and (3) models on the demography of individual species (Fig. 1), especially with the aim of developing rules for the sustainable extraction of timber or non-timber forest goods, or identifying new species for growth in plantation. Nothing is harvested within the plots, but information on forest productivity can be modeled.

Generating information in each of these areas requires large samples from individual species and, in the tropics, this requires large plots. As a rule of thumb, statistical confidence in population changes, mortality rates or growth rates requires a minimum of approximately 100 stems. At both BCI and Pasoh, 50% of the species have 100 stems & cm dbh in 50 ha; and at Mudumalai, 25% of the species do. Small plots would not serve: at BCI, a one ha plot would provide a sample of 100 stems for just seven species, at Pasoh, six species and at Mudumalai only one. This was Hubbell's original justification for the large plots.

Maintenance of diversity

An original goal of the BCI and Pasoh plots was to test hypotheses for the maintenance of high tree diversity in tropical forests on a community-wide scale. At BCI, Hubbell and Foster showed that most species in the 50 ha plot showed Janzen-Connell recruitment patterns, and some of the most abundant species in the plot may have reached a carrying capacity set by these effects. Results for most species, however, did not support the predictions of the Janzen-Connell hypothesis. Two studies have elucidated mechanisms causing density-dependent performance – Wong et al. showed that a defoliating caterpillar did more damage to saplings beneath adults in one tree species than in another species, while Hubbell and Foster showed that most species in the plot are habitat generalists, and suggested that selection leads to convergence in life history in a diverse community. More-refined analyses that include seedling populations may demonstrate subtle differences in regeneration niches, and further experiments with seedlings are under way in the plots at Lambir, Huai Kha Khaeng and BCI.

Repeating these analyses at the two plots in Malaysia will go a long way towards understanding the role of these hypotheses in maintaining diversity. If the higher diversity in Southeast Asian forests can be attributed to density-respecting pathogens, or to divergence along regeneration axes, then the analyses described above should show markedly different results in the Asian plots. Recensus results will soon be available to test these propositions.

Community change

The BCI 50 ha plot was fortuitously placed for evaluating the impact of climate change on natural ecosystems, thanks to a long-term decline in rainfall on the island and an unusually severe dry season in 1983 (Refs 26, 27).
Fig. 1. Distribution map for all stems ≥1 cm diameter in 50 ha of forest. (a) Trichilia tuberculata at BCI, Panama. (b) Xerocormum nanonionham at Pasoh Forest, Malaysia (redrawn from Ref. 10). (c) Lagerstroemia microcarpa at Mudumalai Game Reserve, India (data courtesy of R. Sukumar). Each map is for the most abundant tree species in its plot. Larger symbols represent larger stem diameters: triangles, 1-4 cm; crosses, 4-16 cm; squares, ≥16 cm; large stars, ≥32 cm; and the largest circles (there are very few), ≥64 cm (i.e., trees). Each grid square = 1 ha.

Forest on BCI has been remarkably sensitive to this climatic shift1-3. Forest-wide mortality was 50% higher during 1982-1985 compared to 1985-1990, and mortality rates of some canopy tree species have been very high3-6. Many species are declining rapidly in abundance, mostly those of moist microhabitats within the plot.8,9

The composition of the Indian 50 ha plot has been changing as well, but for different reasons. This forest is subject to heavy browsing by elephants (Elephas maximus), which have a tremendous impact on forest composition10. Several preferred shrubs declined sharply in abundance between 1987 and 1990, and it is not yet clear how these species are maintained in the forest. One possibility is that elephants shift their feeding range over large scales of time and distance, so that trcc populations can decline sharply for a while but then recover after the elephants move on. This emphasizes the need for studying large spatial and temporal scales in tropical forests11. At any rate, the two forest dynamics plots where multiple censuses are available have not supported the view that tropical forests are stable mixtures of species.

Demography and economic valuation of individual species

Forest dynamics plots have provided the most precise information yet available on the distribution of rare tropical trees. At Pasoh in Malaysia, 273 species had densities < one per ha, and 24 had one individual in 50 ha (Ref. 10). At BCI, 111 species had ≥ one stem per ha and 25 had one per 50 ha (Ref. 15). These calculations can be used to predict reserve sizes needed to maintain viable populations16. Murawski et al. demonstrated that low density limits outcrossing rate in some tree species in the BCI 50 ha plot; an important factor in evaluating population viability.

Information on density can also lead to estimates of the value of forest products. Saw et al. identified 76 species of trees carrying fruit edible to humans in the Pasoh plot, but showed that their densities were mostly low. Thus, while the harvest of any one species could not provide much income, the forest maintains wild populations of large numbers of useful species. Economists are working to quantify this value as a genetic storehouse17.

Forest dynamics plots have also provided information on growth rates and mortality rates of more than 200
individual tree species. Hurricane-induced mortality was evaluated in 26 species on the 16ha plot in Puerto Rico. Many species suffered low mortality despite severe wind damage, but other species had rates as high as 59.7%. At BCI, mortality rates for 205 species were mostly <2% per year, but, for some species, rates were as high as 6% and, for a few pioneers, 10–28% per year. The BCI analysis also showed the impact of the drought in 1983, which raised forest-wide mortality from 2% per year to 3% (Refs 4, 30).

Growth data from all size classes allow projections of lifetime diameter-age relations. Condit et al. used such trajectories from 160 tree species at BCI, in order to identify the most rapidly growing trees, suggesting that these would be good candidates for reforestation projects. Only a handful of species had mean growth rates above 1 cm per year throughout their lifetime, but growth in plantations should be higher. Lifetime growth data are also crucial in developing models of sustainable harvest. LaFrankie estimated the economic productivity of two tree species in the Pasoh forest that provide non-timber goods – cinnamon (from Cinnamomum malabatum) and gaharu (a spice made from reaction wood that surrounds a fungal infection in the trunk of Aquihria malaccensis). Because both were rare in the 50ha plot, profits would be low, as is typical for many non-timber products analysed. Given the large number of non-timber products, however, the value of the whole forest might be reasonably high. Condit et al. estimated growth trajectories and potential profit of several timber species in the BCI plot and found that mean growth rates in the forest were probably too low to support economically viable timber production sustainably. However, growth rates of individual stems were highly variable, suggesting that appropriate management techniques might raise growth rates to an economically viable level.

What 50ha plots do not do

Not all questions in tropical ecology are best answered in single large plots. Seedling demography cannot be evaluated over an entire 50ha area, and so must be studied using smaller plots (at BCI, seedlings are now being mapped in subsections of the plot). Moreover, a 50ha plot may be a full evaluation of a large fraction of one community, but it is only one site. Undoubtedly, there is important variation at wider scales, and such variation will have to be evaluated using different techniques (e.g. widespread smaller plots combined with remote sensing). Finally, the 50ha plots fail to capture much information about rare species, and when their demography is important, it will be necessary to monitor stems over a very wide area without mapping everything in between.

Conclusions

A network of long-term research sites representing a variety of major forest types has been recommended by scientists from a range of disciplines, from taxonomists who seek to rapidly identify the vast number of unknown species in tropical forests, to climatologists who need basic figures on gas exchange and carbon storage in tropical ecosystems. CTFS has advocated the same approach for studies of forest dynamics. Various groups with different research agendas would do well to work together in developing a joint network of long-term sites suitable for the various objectives. There are many species and many communities in the tropics, and a concerted program involving international collaboration will be an effective tool for gathering and disseminating the basic information urgently needed for management and conservation.

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Multiple-trait coevolution and environmental gradients in guppies

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Closer related species are often divergent in many different kinds of traits, and particular suites of traits are characteristic of particular environments. This differentiation is best known in life history traits, but is also found in physiology, morphology and behavior. Guppies (Poecilia reticulata) are one of the few species in which within-species, genetically based, geographical variation is known for many different kinds of traits. Is there any pattern in this variation, and does it have general implications? Guppies are small poeciliid fishes native to small clear streams in northeastern South America and adjacent islands. Haskins et al. were the first to point out their value to evolutionary studies. They noted that predation intensity varies among populations, but females prefer more conspicuous males, so the genetically controlled polymorphic color patterns of any one place could represent a local balance between sexual selection and geographical variation in predation intensity. Subsequent work has shown that the color patterns of each population do indeed represent this balance, and a similar pattern is also found in guppies living in different predator faunas. On average, as one moves from low to high predation intensity, the color patterns become simpler and have less visual contrast than low-predation populations. The changes in visual contrast are achieved with different combinations of genes in different populations, but their phenotypes vary in parallel with predation. Segers was the first to document geographical variation in behavior and morphology, and relate it to predation risk. On average, as one moves from low to high predation intensity, the anti-predator defenses increase. Since this pioneering work, there has been an explosion of interesting work on geographical variation in diverse traits in natural populations of guppies. This is summarized in Table 1.

Covariation between traits and predation

Many different suites of traits coevolve with each other and with predation (Table 1). Increased predation is usually associated with less conspicuous color patterns, a smaller and more fusiform body (larger length/height