

Research in large, long-term tropical forest plots

Richard Condit

It all began in 1975 with a 13 ha plot in Costa Rican dry forest that has since been invaded by fire and abandoned¹. Steve Hubbell¹ contended that adequate evaluation of dispersion patterns, density dependence and the production and sustainable extraction of tropical tree species would require large-scale studies. Most work had been done in single hectare or smaller plots, or on one or two adult trees and the seedlings around them, but the relative rarity of many species in tropical forests necessitated large-scale census plots. Thus began the study of forest dynamics plots: complete maps of saplings and trees in large areas of tropical forest.

Following the initial study in Costa Rica, Hubbell and Robin Foster established a 50 ha plot on Barro Colorado Island (BCI) in Panama at the Smithsonian Tropical Research Institute's field station in moist seasonal old-growth forest². BCI has a 70-year history of forest research and the best-known flora in the tropics³, and was thus ideal for such a large and long-term project. The 50 ha plot has now been fully censused three times (in 1981–1983, 1985 and 1990). The 1990 count included 244 000 stems and 303 species ≥ 1 cm in diameter⁴. Several early publications on the plot championed the view that the composition of the BCI forest drifts randomly, that is, that most species are effectively equivalent competitors whose abundances fluctuate stochastically^{5,6}. This view got Hubbell into many arguments, but one in an English pub in 1983 led to the second forest dynamics plot. Peter Ashton insisted that Hubbell's drift model would not apply to Southeast Asian forests, where tree diversity is very high and many congeneric species co-exist. To settle the matter, the Forest Research Institute of Malaysia established a 50 ha plot in moist aseasonal old-growth forest at the Pasoh Forest in Peninsular Malaysia, following the BCI protocol exactly⁷. The initial census at Pasoh included somewhat more stems (335 000) than BCI and many more species (814); the genus *Eugenia* (Myrtaceae) alone had 45 species^{8,9}. Distribution maps of all 814 species have been published¹⁰.

A third 50 ha plot was established by the Indian Institute of Science in southern India in 1987 in a forest selected to contrast with BCI and Pasoh. Mudumalai is a dry deciduous open-canopy forest where fires often burn the grassy understorey. The plot has 26 000 stems (less than one-tenth

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 density at Pasoh) and 71 species¹¹. Additional 50 ha plots are now completely mapped at Lambir National Park in Sarawak, Malaysia and at the Huai Kha Khaeng Wildlife Sanctuary in Thailand, but data are not yet analysed. Both are in moist evergreen forest, but the Thai site is seasonal and at the fringes of deciduous forest. The Lambir plot may have more tree species than any other forest in the world – early projections include 1100 species, with 86 in the Dipterocarpaceae alone. At the Thai site, the main research issue is what factors control the boundary between deciduous and evergreen forest¹².

A forest dynamics plot of 16 ha was established in the Luquillo Experimental Forest in Puerto Rico immediately after Hurricane Hugo in 1989, with trees ≥ 10 cm diameter included¹³; stems of 1–10 cm diameter were recently added to the census. Additional large-scale plots are now under way in Sri Lanka, the Philippines, Cameroon, Zaire and Ecuador. Stems ≥ 1 cm diameter will be

mapped in at least 16 ha at each site.

The goal of the network of forest dynamics plots has expanded from the original focus on community ecology and the maintenance of diversity to include management-oriented analyses as well: economics of forest resources, dynamics of sustainable extraction, and the change of tree communities with changing climates. Governments and forest managers need a solid base of data to make sensible decisions about managing forests, and the scientists involved with the network realized that permanent, large-scale census plots are one important tool for generating that database. Forest dynamics plots are thus now seen as centrepieces for multi-disciplinary research, and the plots in native forest will eventually serve as controls for large-scale plots in harvested forests where models for the extraction of goods can be carefully tested.

It is crucial that the results of the plots are comparable, so that broad-reaching hypotheses about tropical forest dynamics can be tested. This requires standardized data-gathering techniques as well as communication and collaboration between workers in different disciplines and at different sites. To achieve a cohesive network and to foster communication among investigators at different forest dynamics plots, the Smithsonian Tropical Research Institute created the Center for Tropical Forest Science, or CTFS.

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 by Asian scientists at a 1989 workshop in Bangkok (sites in India, China, Indonesia and Papua New Guinea have not yet been implemented). In 1994, CTFS hosted a similar meeting in Panama to identify Latin American sites.

Census methods and database management

Initial censuses of 50 ha plots have taken two years with a field crew of about 12 people and a cost of about \$150 000. Recensuses have taken half the time with the same crew and a cost of \$100 000 (but costs vary greatly 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 and the duration of the studies. Would the scientist who originally mapped a large plot maintain publication rights on the plot 30 years later? 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 ≥ 1 cm dbh in 50 ha^{14–16}, and at Mudumalai, 25% of the species do¹¹. 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's¹ 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 Foster⁵, Hubbell *et al.*¹⁷ and Condit *et al.*^{4,18,19} were able to evaluate the Janzen–Connell hypothesis^{20,21} (see Box 1) in more than 80 species. A few 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 effects¹⁷. 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.*²² showed that a defoliating caterpillar did more damage to saplings beneath adults in one tree species in the plot than to saplings far from adults, and Gilbert *et al.*²³ implicated a canker-causing fungus in density-dependent mortality for another species.

The BCI plot has also provided tests of the hypothesis that diversity is maintained by species differences in the regeneration niche²⁴ (see Box 1); again, the data set allowed detailed analysis of a large fraction of the community. Welden *et al.*⁶ analysed growth, survival and recruitment responses of individual species to light gaps in the BCI plot but found little evidence to support the hypothesis. Most mature-phase species displayed a similar response to canopy openings: moderate increases in growth and mortality but no tendency to recruit preferentially in gaps. Hubbell and Foster^{5,15,25} 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-responding 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). The

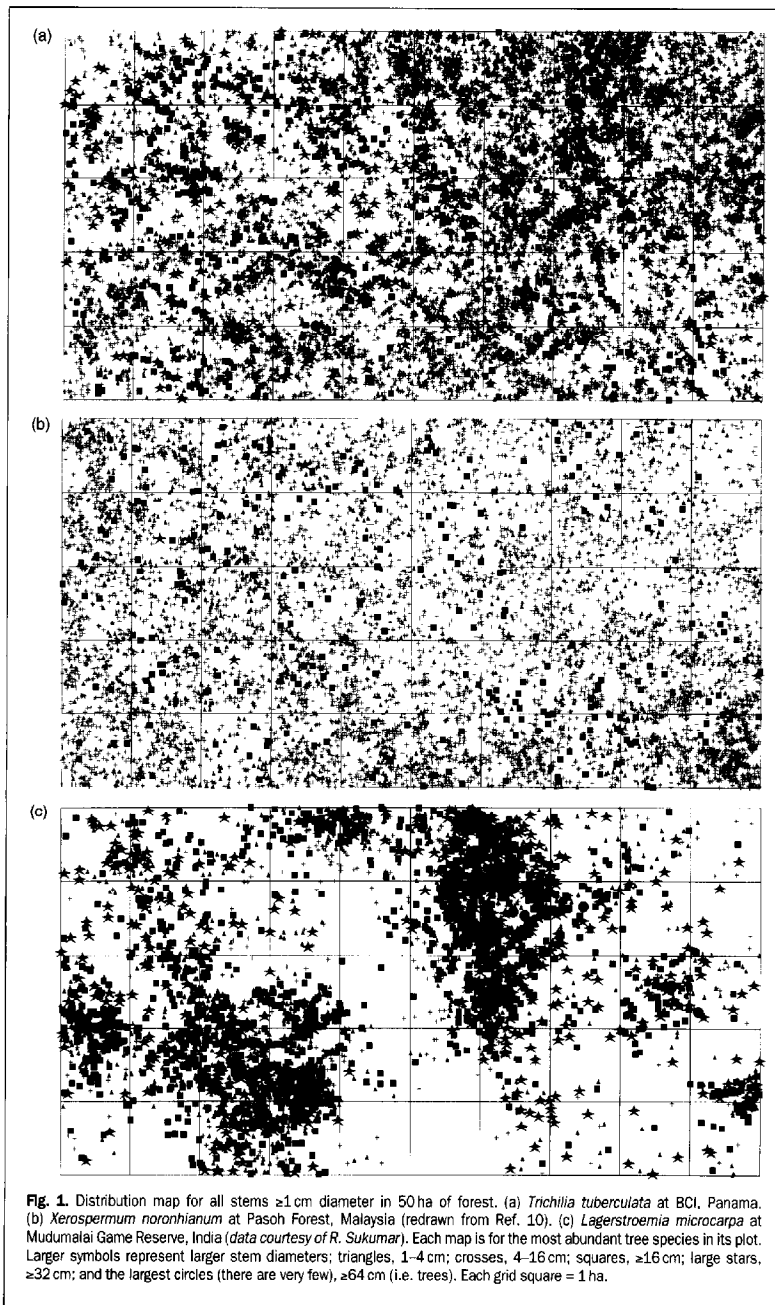


Fig. 1. Distribution map for all stems ≥ 1 cm diameter in 50 ha of forest. (a) *Trichilia tuberculata* at BCI, Panama. (b) *Xerospermum noronhianum* at Pasoh Forest, Malaysia (redrawn from Ref. 10). (c) *Lagerstroemia microcarpa* at Mudumalai Game Reserve, India (data courtesy of R. Sukumar). Each map 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 shift^{2,4,28,29}. Forest-wide mortality was 50% higher during 1982–1985 compared to 1985–1990, and mortality rates of some canopy tree species have been very high^{2,30}. Many species are declining rapidly in abundance, mostly those of moist microhabitats within the plot^{4,29}.

The composition of the Indian 50 ha plot has been changing as well, but for much different reasons. This forest

is subject to heavy browsing by elephants (*Elephas maximus*), which have a tremendous impact on forest composition³¹. 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 tree 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 \leq 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.*³² 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.*³³ 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 storehouse³⁴.

Forest dynamics plots have also provided information on growth rates and mortality rates of more than 200

Box 1. The Janzen–Connell effect

Janzen²⁰ and Connell²¹ noticed that seedlings of tropical trees found close to conspecific adults often suffer higher mortality than seedlings further away, and they explained how this pattern can maintain diversity in a community. This phenomenon, often called the Janzen–Connell effect, can lead to density dependence in population growth, because as a population increases, more of the forest will be in the zone of high mortality close to adults¹⁸. Therefore, seedling survival will decrease as the population increases, and this can regulate the population. The Janzen–Connell hypothesis is a special case of the more general theory that predators can enhance diversity among prey by preferentially attacking more abundant species.

Another often-cited explanation for the high diversity of tropical forests is the regeneration-niche hypothesis²⁴. According to this, different species have different requirements for seed germination and seedling production, segregating an otherwise uniform habitat by variation in the light environment associated with gaps in the forest canopy.

individual tree species. Hurricane-induced mortality was evaluated in 26 species on the 16 ha plot in Puerto Rico¹³. 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 year³⁰. 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.*³⁵ 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. LaFrankie³⁶ estimated the economic productivity of two tree species in the Pasoh forest that provide non-timber goods – cinnamon (from *Cinnamomum mollissimum*) and gharu (a spice made from reaction wood that surrounds a fungal infection in the trunk of *Aquilaria malaccensis*). Because both were rare in the 50 ha plot, profits would be low, as is typical for many non-timber products analysed³⁷. Given the large number of non-timber products, however, the value of the whole forest might be reasonably high³⁴. Condit *et al.*^{38,39} 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 50 ha 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 50 ha area, and so must be studied using smaller plots (at BCI, seedlings are now being mapped in subsections of the plot). Moreover, a 50 ha 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 50 ha 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 ecosystems⁴⁰. 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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Closely 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^{1,2}, 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 studies³. 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 geographically varying predation³. Subsequent work has shown that the color patterns of each population do indeed represent this balance^{4–8}, and a similar pattern is

Guppies show geographical variation in many different kinds of traits. Traits covary with each other, with predation and with other environmental factors. Phenotypic correlations are often assumed to result from genetic correlations, but may also result from covariation among different sources of natural selection and interactions among the traits' functions. This network of interactions could bias the direction of evolution in characteristic ways, and suggests how intraspecific variation may give rise to interspecific variation.

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also found in guppies living in different predator faunas^{6,8}. 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^{3,4}. Seghers^{9–11} 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 covary with each other and with predation intensity (Table 1). Increased predation is usually associated with less conspicuous color patterns, a smaller and more fusiform body (larger length/height