

Short-term dynamics of a neotropical forest: why ecological research matters to tropical conservation and management

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Arguments that ecological research on species-rich tropical forests is too little, too late, an irrelevancy, and a luxury we can ill afford when time is running out to save tropical forests are wrong. Focused basic and applied ecological research has a vital and cost-effective role to play in tropical forest conservation and management. Sustainable management of natural tropical forests is not possible without a better holistic understanding of how such forests actually work ecologically and interact with humans. Because time is short, however, we must learn "on-the-job" by conducting research as we implement management plans. We base our argument on experience with a large-scale study of the tropical forest on Barro Colorado Island (BCI), Panama. In the space of 5 years, it was possible to collect essential silvics data on stocking levels, growth, yield, survival rates, and microhabitat requirements of a large fraction of the BCI tree community of more than 300 native species. We conclude that a program of comparable studies of representative natural and managed tropical forests at key sites throughout the tropics would rapidly improve the global fund of knowledge on which to base better decisions for the conservation and management of tropical forests. International agencies and foundations should increase their support of mission-oriented, holistic research on the community ecology of tropical forests far beyond the present emphasis on basic inventories of biodiversity.

On one point there is no argument: tropical forests are indeed in big trouble.

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Even as international agencies, policymakers, and the general public express concern and call for action, the world-wide destruction of tropical forests continues to accelerate world-wide, as the 1990 tropical deforestation figures released by the World Resources Institute show. Tropical deforestation is causing large-scale and long-term environmental damage and the irreversible loss of tens to hundreds of thousands of plants and animals. Only a tiny fraction of land is being reforested. In Panama, for example, reforestation efforts of all kinds replaced a scant 4 500 ha of lost forest between 1980 and 1990. During the same period, deforestation obliterated about 865 000 ha of forest, a loss rate nearly

200 times greater than the replacement rate. Moreover, virtually all of these replacement "forests" consist of monocultures of multi-purpose exotic trees such as eucalyptus, acacia, and gmelina in plantations that are biodiversity deserts. Conservation of biodiversity is not on the agenda of these reforestation programs.

It is easy to understand why this is so. Developing countries generally depend more heavily on agricultural and forest production for income than do countries of the developed world. The loss of this production capacity and the associated environmental degradation threatens tropical countries with imminent economic catastrophe. These countries are in a hurry. Rightly or

wrongly, they see their native forests as far too complex and slow-growing to understand and manage for sufficiently high economic return to solve their near-term economic problems. They urgently need fuelwood and other wood products, and a restored forest cover of any sort to rejuvenate soils and protect watersheds. The "debt-for-nature" swaps proposed by conservation groups do not solve these problems, and in any event such swaps would be seriously inflationary if they ever amounted to a large fraction of their debt. Tropical forest countries are also skeptical about extractive reserves as a general model of forest management, the so-called "fruits and nuts" approach. Extractive reserves may only work at unrealistically low population densities and, even if they can be managed sustainably, may condemn their rural populations to perpetual subsistence-level poverty. Finally, they point to the hypocrisy of the developed world, which demands that tropical forests be protected but at the same time seems unwilling to pay its fair share of the opportunity costs for conserving the biodiversity it claims to cherish so highly.

The truth is, much of the debate on both sides is political and ideological, with little basis in proven fact. There have been almost no rigorous, long-term tests of the ecology and economics of alternative models of sustainable tropical forests management. In the few cases where sustainable forest management systems seem to have worked, as in Ghana, they have mostly been abandoned with the postcolonial breakdown of government enforcement of forestry regulations, so it is no longer possible to analyze their long-term performance. Five years after FAO put forth its ambitious Tropical Forestry Action Plan, a negligible 1% or less of tropical forests are being managed sustainably, and the TFAP is itself undergoing extensive revision. At present "sustainable tropical forestry" is little more than a slogan and the subject of heated scientific and economic debate (Poore et al. 1989). Recently, strong public pressure has been brought to bear on the international development agencies, demanding that their policies be more consistent with the sustainable management of tropical forests and with the conservation of biodiversity. Ironically, no one knows what this means except in the broadest sense; scientific and economic guidelines simply do not exist.

The importance of ecological research on tropical forests

How should ecologists respond to this crisis of ignorance? There are those who declaim that it is too late for research, that research is not the limiting factor, and that only action will suffice. We reject this argument. In twenty years, when the remaining tropical forests will have become even more threatened than now, we will

need a far better understanding of how they work than we have today. Current policies to manage tropical forests are largely ad hoc. The fate of tropical forests is determined more often by default than by design, by the vagaries of market fluctuations and political changes, and - on the ethereal plan of GATT negotiations and national income accounts - by policy analysts and accountants with no ecological grasp of how tropical forests work nor how local people actually use the forest. Such policies seem unlikely to have much chance of lasting success. But in our present ignorance, ecologists are ill-prepared to tell policymakers what to do instead.

It must be also said that so far the ecological sciences have offered little to tropical forest policymakers and managers beyond theoretical generalities. Ecologists have much to offer, but to be effective, the discipline needs to adopt a more balanced program of basic and applied research on tropical forests - more balanced than the current *laissez-faire*, largely curiosity-driven approach. We need a program guided to a greater extent by goals, priorities, and timetables, and informed by social and economic needs (Hubbell 1990). Ecologists are unaccustomed to such a pragmatic or "clinical" research mentality, but we need such a perspective if we are to be taken seriously in the effort to solve tropical forest conservation and management problems. We need to ask ourselves: What do we really need to know about the ecology of tropical forests and their interactions with man, and what are the policy implications of this knowledge?

There seem to be two general needs for greater understanding of tropical forests that can be grouped under the rubrics of biogeography and community ecology. In the case of biogeography, we need better knowledge about what species and resources tropical forests actually contain. It is pointless to devise management plans for unknown resources. Recognizing this need, many international agencies and conservation organizations have begun supporting tropical biodiversity inventory programs. Unfortunately, a complete inventory of the earth's bio-diversity is not a realistic goal. Recent estimates peg the possible number of species on Earth in the tens of millions of species-ranging up to 50 million - most of which are insects and other arthropods living in tropical forests. This would mean that only 2% to 10% of extant species have been named by all the taxonomists who have ever lived. Unless there is an unforeseen technological revolution in taxonomic methods, limited resources will force us to choose, either by design or by accident, which groups of organisms will be cataloged. At the moment this choice is guided almost entirely by historical accident - which taxonomists and biogeographers are alive who have interests in which group of organisms. There is virtually no discussion of whether we should consciously focus funding and training priorities on groups that have the greatest ecological and economic importance, and if so, how to decide which groups merit this attention. It is on the second

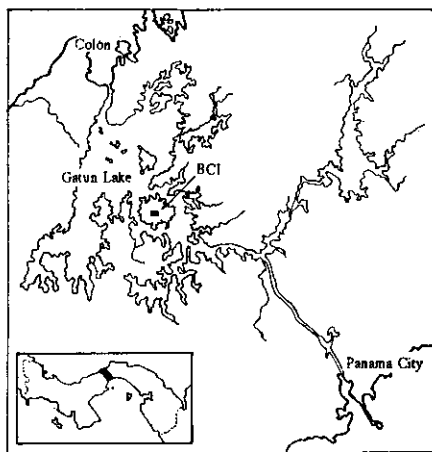


Fig. 1. Central Panama, showing the Panama canal area with Gatun Lake, and Barro Colorado Island. The small black rectangle on BCI is the 50 ha plot, measuring 1 km in the east-west direction, by 500 m in the north-south direction. Insert: The Republic of Panama.

question that community ecology can be of greatest assistance.

Our ignorance of how tropical forests work is profound. If tropical forest countries decided tomorrow to restore their degraded or destroyed native forests, it could not be done. The basic ecology and interdependencies of the vast majority of tropical forest plants and animals are simply unknown. For most tropical trees, we don't know basic things like what animals pollinate their flowers or disperse their seeds, what light, water, soil, and mycorrhizal conditions they need to survive and grow, what pests and diseases they carry, and which animals critically depend on them for food. On the human side, natural and social scientists know little about how indigenous peoples actually use the good and services of tropical forests. We don't know how useful these and other as yet undiscovered natural resources are, what level of exploitation they can sustain, or what impact exploitation has on tropical forest diversity and stability. These represent serious, even debilitating gaps in our understanding of the ecology and economics of tropical forest management. But just as it is impossible to inventory all tropical biodiversity, we cannot study the detailed community ecology of all tropical forests. However, we do need a program to study a set of tropical forests carefully chosen to represent the major tropical forest types of the world.

These two approaches, biogeography and community ecology, are mutually complementary. Neither approach alone is sufficient. The program in community ecology is locally intensive and regionally superficial. It provides great depth in understanding the function of

particular forest communities. The program in biogeography is regionally extensive and locally superficial. The community ecology studies inform the biogeographic surveys of what key elements should be included in regional inventories. In return, the biogeographic inventories inform the community ecological studies of their degree of generality.

Questions in tropical forest community ecology

Our own approach has focused primarily on locally detailed studies of the community ecology of tropical forests, with special emphasis on trees. Along with our colleagues, we have described the structure, species composition, and short-term dynamics of the tree communities in three large permanent forest plots located in the new and old world tropics. Each research site represents a major regional forest type. The longest running of these studies and the flagship of the program is the BCI forest dynamics project, begun in 1980 (Hubbell and Foster 1983). The other current projects in the program are located in peninsular Malaysia and India.

Through these studies, we have been able to answer a number of fundamental questions about the structure and dynamics of tropical forests. This paper highlights some of the recent discoveries from the BCI forest dynamics project in particular that have conservation and management implications. To focus present discussion, we address the following questions: How species-rich is the tree community? How variable is tree species abundance, and why are some tree species common and others rare? Is the tree species assemblage in equilibrium? If not, what are the rates of change in species composition, and what are the factors that appear to be driving this change? How strong are the stabilizing forces in the forest tending to restore equilibrium in the face of these changes?

To the hands-on forest manager, the question of whether a tropical forest is in equilibrium may seem esoteric, but the answer to this question is important for sustainable management. If tropical forests are non-equilibrium assemblages continually turning over in species and change rapidly in response to climate change and anthropogenic disturbances, then conservation and management strategies will be different than if forests are strongly stabilized by biotic interactions. But apart from answering questions at the community level, we can also address specific practical questions about individual tree species, such as: What are their stocking levels and recruitment rates? Can these stocking levels be increased? What factors prevent stand densities of a given species from becoming higher in the natural forest, and can these factors be controlled? How fast do the trees grow? What are their survival rates, and how are these and growth rates related to shade tolerance or

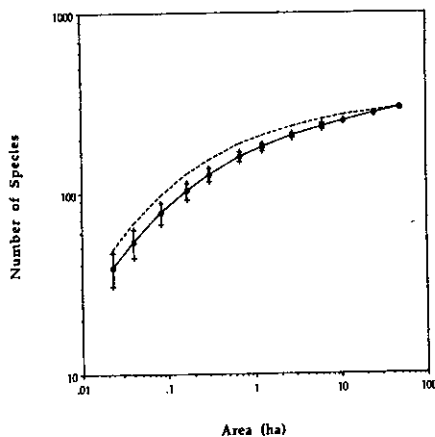


Fig. 2. Species-area curve for the BCI 50 ha plot. The dotted line is the theoretical curve that would be obtained if all species were randomly mixed. The solid curve is the actual species area curve, indicating incomplete mixing of the species. The error bars indicate one standard deviation of the mean number of species for the given sample area. Variation was generated by starting the species accumulation from different starting points (subsamples) within the plot.

intolerance? How do the tree species influence each other's performance? To present all of this information is beyond the scope of the present paper, but we can refer readers to recent publications for the details (Foster and Hubbell 1990a, b, Hubbell and Foster 1990a, b, c, Hubbell et al. 1990, Welden et al. 1990).

Barro Colorado Island and the forest dynamics project

Barro Colorado Island is a 11500 ha former hilltop in central Panama that became an island when the Chagres River was dammed, creating the main reservoir of water for the Panama Canal, Gatun Lake (Fig. 1). The climate of BCI is strongly seasonal, with a four and a half month dry season from late December until late April. The forest is semi-evergreen and, at 2500 mm annual rainfall, is classified as tropical moist forest by the Holdridge system (Leigh et al. 1982). Since 1923 BCI has been a biological reserve and laboratory, administered after 1946 by the Smithsonian Tropical Research Institute (STRI). Over BCI's 70 year history, the flora and fauna of the island have become the best known of any tropical forest of comparable size in the world. Over 1500 scientific papers have been written on the biota, climate, and geology of BCI. The publication of The

Flora of Barro Colorado Island (Croat 1978) capped six decades of research on the flora of the island. This wealth of background information and the facilities and research staff of STRI, made BCI an excellent site to launch a long-term program on tropical forest ecology.

The BCI forest dynamics project began as a study in basic community ecology. The organizing objective was to understand the maintenance of tree diversity in the BCI forest and the factors that determine relative tree species abundance. Because we wanted a community-level approach, the project had to have sufficient scope, scale, and permanence. We reasoned that understanding the tree community would minimally require detailed demographic studies and life histories of individual species. To understand species interactions, this demographic information would have to be collected in a community setting, so we would need to map and tag all plants individually. Also many tropical tree species are infrequent or rare, so we would have to have a large plot to obtain adequate population samples for statistical analyses of the rare as well as the common species. Finally, since trees grow relatively slowly, we would need a long-term study.

Accordingly, a 50 ha permanent plot was established on the central plateau of the island, and all free-standing woody plants with a stem diameter of 1 cm dbh (diameter at breast height) were individually tagged, identified to species, measured, and mapped (Hubbell and Foster 1983). The first census was completed in 1982; subsequent censuses were undertaken in 1985 and 1990. Long-term changes in the forest will be monitored by recensusing the plot regularly every 5 years. The history of the forest on BCI and elsewhere in Panama has been revealed by the extensive paleoecological studies of Piperno (1990) and colleagues. The phytolith and artifact record from plot site on BCI indicates that the forest never sustained slash-and-burn maize agriculture, but small seasonal hunting camps were made in the forest between 550 and 1500 AD.

In addition to the demographic data on trees, measurements on light environments, soils and soil moisture regime have been taken, so that differences in plant performance could be interpreted in relation to micro-site conditions. An annual census of canopy structure and treefall gaps has been conducted throughout the plot since 1983 (Hubbell and Foster 1986b). With this information we have been able to quantify the degree of gap dependence among the BCI tree species (Welden et al. 1990). Information on soils and soil water regimes enabled us to assess the degree of edaphic or habitat specialization among the species as well (Hubbell and Foster 1986c). We also have examined how patterns of abundance and specialization are related to plant growth form. We defined four categories of form based on the height of the adult plant. Shrubs were plants with an adult height of less than 4 m; understory treelets were between 4 and 10 m; midstory trees were between 10 and 20 m; and canopy trees were over 20 m tall.

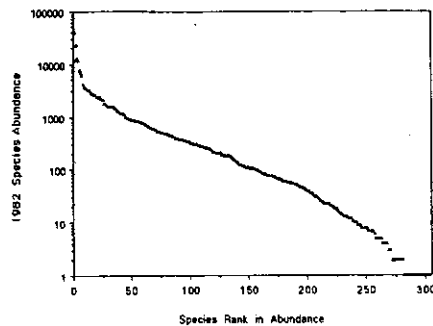


Fig. 3. Dominance diversity curve for the 50 ha plot for all stems greater than 1 cm dbh. Note the asymmetry of the curve, and the relatively high dominance of the rank-1 species (*Hybanthus prunifolius*).

Other collaborative research has included studies of the reproductive phenology and breeding systems of the trees (e.g., Murawski et al. 1990).

Results of the BCI forest dynamics project

We can conveniently divide what we have learned about the BCI forest into three topics for discussion: (1) species composition and relative species abundance, based on the primary census data (forest statics), (2) forest dynamics, based on the 1985 recensus data, and (3) research design and methodology. The results of the 1990 recensus will not be known until next year, so our

conclusions on forest dynamics are based on the three-year interval between the first and second censuses, 1982. The implications of these findings for conservation and management are discussed following the results.

Forest statics: results of the primary census

There were 303 species among the 235 895 free-standing woody plants > 1 cm dbh in the BCI plot in 1982. This is a moderately species-rich forest by tropical moist forest standards (Foster and Hubbell 1990a, b). These species were quite thoroughly intermixed spatially, as the species-area curve for the plot shows (Fig. 2). The theoretical species-area curve that would be expected if the plants were randomly intermingled (dotted line) can be calculated exactly if the abundances of species are known (Coleman 1979). The solid line is the observed species-area curve (± 1 SD) obtained by repeated samplings of the plot. The observed number of species per unit area was only slightly below the random expectation. Not only were species well mixed on the spatial scale of 50 ha, but also on larger spatial scales as well. Although the 50 ha plot represents only 3% of the area of BCI, it nevertheless contained 75% of all free-standing woody species > 1 cm dbh known from the entire island (409 species).

This high degree of intermixing is a general indication of the capacity of most BCI tree species to regenerate beneath themselves and amongst one another, a capacity that we have formally tested quantitatively elsewhere (Hubbell and Foster 1987a). While this was generally true, we found significantly depressed numbers of saplings beneath conspecific adults in some species, es-

Table 1. The eighteen BCI species that constitute approximately half the total number of individuals within their respective growth forms. Because the analysis is within growth form, these include some but not all of the 18 most common species in the 50 ha plot.

Species	Family	Growth form	Abundance in:		1982-85 % change
			1982	1985	
<i>Alseis blackiana</i>	Rubiaceae	Canopy	7587	8055	6.17
<i>Cordia lasiocalyx</i>	Boraginaceae	Midstory	1703	1665	-2.23
<i>Desmopsis panamensis</i>	Annonaceae	Understory	11752	12145	3.34
<i>Eugenia oerstediana</i>	Myrtaceae	Midstory	2079	2202	5.92
<i>Faramea occidentalis</i>	Rubiaceae	Understory	23465	25121	7.06
<i>Guarea guidonia</i>	Meliaceae	Midstory	1784	1827	2.41
<i>Guarea sp. nov.</i>	Meliaceae	Midstory	1558	1493	-4.17
<i>Hirtella triandra</i>	Chrysobalanaceae	Midstory	4142	4652	12.31
<i>Hybanthus prunifolius</i>	Violaceae	Shrub	39911	41106	2.99
<i>Oenocarpus mapouira</i>	Palmae	Midstory	1807	1731	-4.21
<i>Poulsenia armata</i>	Moraceae	Canopy	3437	2838	-21.97
<i>Protium panamense</i>	Burseraceae	Canopy	2713	2838	4.61
<i>Protium tenuifolium</i>	Burseraceae	Midstory	2671	2919	9.28
<i>Rhedia edulis</i>	Guttiferae	Midstory	3654	4028	10.24
<i>Tachigali versicolor</i>	Legum.: Caesalp.	Canopy	2922	2971	1.68
<i>Tetragastris panamensis</i>	Burseraceae	Canopy	3233	3682	13.89
<i>Trichilia tuberculata</i>	Meliaceae	Canopy	12942	13164	1.72
<i>Virola sebifera</i>	Myristicaceae	Midstory	2404	2273	-5.45

Table 2. Various measures of relative species abundance, and commonness and rarity, within the four categories of growth form: shrubs, understory treelets, midstory trees, and canopy trees. Abundances are for all stems > 1 cm dbh. The "percentage rank-1 species" is the fraction of all stems made up by the single most abundant species within the given growth form. The "number of species constituting 50%, 90%, and the bottom 1%" give the count of species that collectively make up half, ninety percent, or the rarest 1% of the total stems in the given growth form. The figures in parentheses are the percentages of species in the particular growth form. The rightmost column gives the number and percentage of "rare" species, defined for present purposes as any species with fewer than one individual per hectare (< 50 individuals in total).

Growth form	No. of species	Median sp. abundance	% Rank-1 species	No. of spp. constituting			No. of "rare" species
				50%	90%	bottom 1%	
Shrub	56	40	53.4	1 (1.8)	9 (16.0)	34 (60.7)	29 (51.8)
Treelet	60	156	41.6	2 (3.3)	16 (26.7)	25 (41.7)	21 (35.0)
Midstory	80	175	10.0	9 (11.3)	32 (40.0)	21 (26.3)	20 (25.0)
Canopy	107	80	20.4	6 (5.6)	29 (27.1)	44 (41.1)	41 (38.3)

pecially in the two most abundant canopy trees, *Trichilia tuberculata* (Meliaceae) and *Alseis blackiana* (Rubiaceae). In the recensus this sapling deficit was found to result from lower sapling survival, growth, and recruitment near adults, relative to the performance of saplings of competing species in the same microsites (see below).

In addition to being well mixed in the forest, the 303 species exhibited very unequal abundances, as the dominance-diversity curve for the 50 ha plot reveals (Fig. 3). One shrub species, a woody violet, *Hybanthus prunifolius*, had 39 911 individuals, almost 1 in 6 plants (16.9%) out of the total of 235 895 recorded in 1982. *Hybanthus* was 1.7 times more abundant than the second most common species, *Faramea occidentalis* (Rubiaceae), an understory small tree with 23 465 individuals, and 3 times more abundant than the most common canopy tree species, *Trichilia tuberculata*, with 12 942 individuals > 1 cm dbh. At the other extreme of abundance, there were 22 species having a single individual apiece in half a square kilometer of forest. The very common

species raised the mean abundance of species in the plot to 779 individuals (SD = 2950); but the median species abundance was much lower (102 individuals), corresponding to a density of only 2 individuals per ha.

One consequence of this very unequal species abundance is that the BCI forest is taxonomically rather simple if one ignores rare species. If we break the community down by growth form and ask how many species constitute half of the individuals, one species (*Hybanthus*) constitutes more than half of the shrubs, 2 species more than half of the understory treelets, 9 species more than half of the midstory trees, and 6 species more than half of the canopy trees - 18 species in all (Table 1). If we ask how many species make up 90% of the individuals of each growth form, there are 9 shrubs, 16 treelets, 32 midstory trees, and 29 canopy trees - only 78 species, or one quarter (25.7%) of the total species in the plot. Conversely, if we focus on the rarest species and ask how many species of each growth form collectively make up the last 1% of the individuals of their respective growth form, then there are 34 shrubs, 25 treelets, 21 midstory trees, and 44 canopy trees (Table 2). Thus, there are almost seven times as many species in the last 1% of individuals than there are in the first 50%.

Further inspection reveals that the patterns of relative species abundance were not the same among plants of different growth form in the BCI forest. There was greater dominance in the shrub and understory treelet communities than in the midstory and canopy tree communities (Fig. 4). However, the shrub and canopy tree communities had a greater number and percentage of rare species. There was no relationship between dominance by common species and species richness or percentage of rare species (Table 2). Among shrubs and understory treelets, the single most abundant species constituted 53% and 42% of their respective communities, whereas among midstory and canopy trees, the rank-1 species were only 10% and 20%, respectively (Table 2). In spite of greater dominance in shrubs, the highest fraction of rare species - those averaging fewer than one individual per ha - occurred in shrubs as well

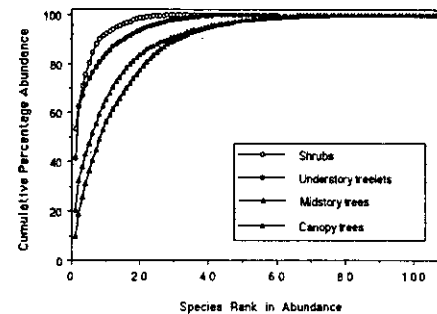


Fig. 4. Cumulative percentage abundance curves separated for the shrub, understory tree, midstory tree, and canopy tree communities. The fastest rising curve was in the shrub community, indicating the greatest level of dominance. The lowest dominance was found in the midstory tree community.

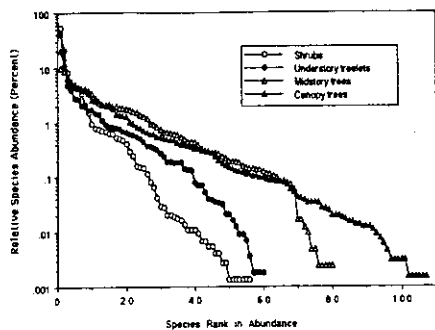


Fig. 5. Dominance-diversity curves for the shrub, understory tree, midstory tree, and canopy tree communities. Note the truncation of the understory and midstory tree curves, reflecting the relatively low numbers of rare understory and sub-canopy tree species. In contrast, there were more rare shrubs and canopy tree species.

(52%). The next highest fraction of rare species was among the canopy trees (38%), and the lowest was among midstory trees (25%). These differences produced quite different dominance-diversity profiles among the four growth forms (Fig. 5).

The explanation for these huge differences in relative species abundance – ranging over 4.7 orders of magnitude – is only partially understood. On the one hand, we can say that no canopy tree species can become as abundant as *Hybanthus* simply because of its size: there are only about 20,000 trees of all species > 10 cm dbh in the entire 50 ha plot. On the other hand, we still do not know why *Hybanthus* is so common; the other woody violet shrub in the BCI plot, *Rinorea sylvatica*, is only 1/15th as common. We have been able to show, however, that common species, more often than rare species, tend to be habitat and regeneration niche generalists (Hubbell and Foster 1986b, c, Welden et al. 1990). The association commonness with habitat and regeneration niche generalists, and rarity with specialists, was especially apparent after the dynamic data on growth, survival, and recruitment became available after the recensus (see below).

Before turning to the dynamics of the BCI forest, we consider a final question about species densities or "stocking levels" that is of practical importance in silviculture. The lower diameter cutoff for forestry inventories to measure stocking levels is usually 10 cm dbh. Smaller stems of saplings and subadult trees are often termed "advance regeneration". The question is often asked: is there a general relationship between the stocking level of tree species, i. e., densities > 10 cm dbh, and the amount of advance regeneration? Under some selective logging regimes, such as the Malayan Uniform System, the decision to log is based on levels of advance regeneration. If sufficient sapling regeneration is pre-

sent, then logging is permitted. The relationship between abundance of trees > 10 cm dbh and those 1–10 cm dbh is shown in Fig. 6 for all BCI midstory and canopy tree species. Although there is a significant positive relationship between the two abundances ($p < 0.0001$, $R^2 = 0.674$), the ability to predict levels of advance regeneration from the abundance of large trees is weak. The stocking level of plants > 10 cm dbh predicts advance regeneration with an error of about plus or minus one order of magnitude (Fig. 6).

Forest dynamics: results of the recensus

Probably the most unexpected discovery of the recensus was the remarkable dynamism and instability of the old-growth forest on BCI (Hubbell and Foster 1990b, c). This instability should have been anticipated from the primary census. We noticed that many tree species, whether gap specialists or shade-tolerant, mature-phase generalists, exhibited very different densities and population size structures from one hectare to the next (Hubbell and Foster 1987b). This variability indicates that the recent population history of a given species must have been different in different parts of the forest. However, we were unprepared for the magnitude of the change and instability that we found in 1985. Over just a 3-year period, 40% of the 300 BCI species changed by more than 10% in total abundance (Hubbell and Foster 1990b).

Large changes were not limited to one growth form, but occurred in all growth forms, from shrubs to trees. A majority of species experienced population declines,

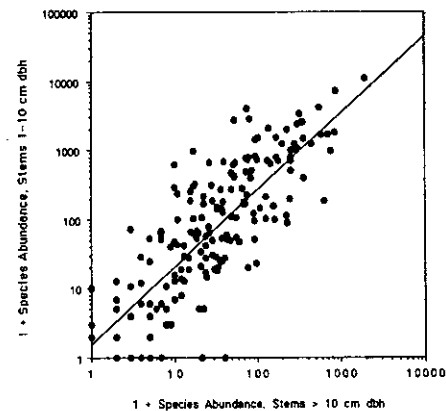
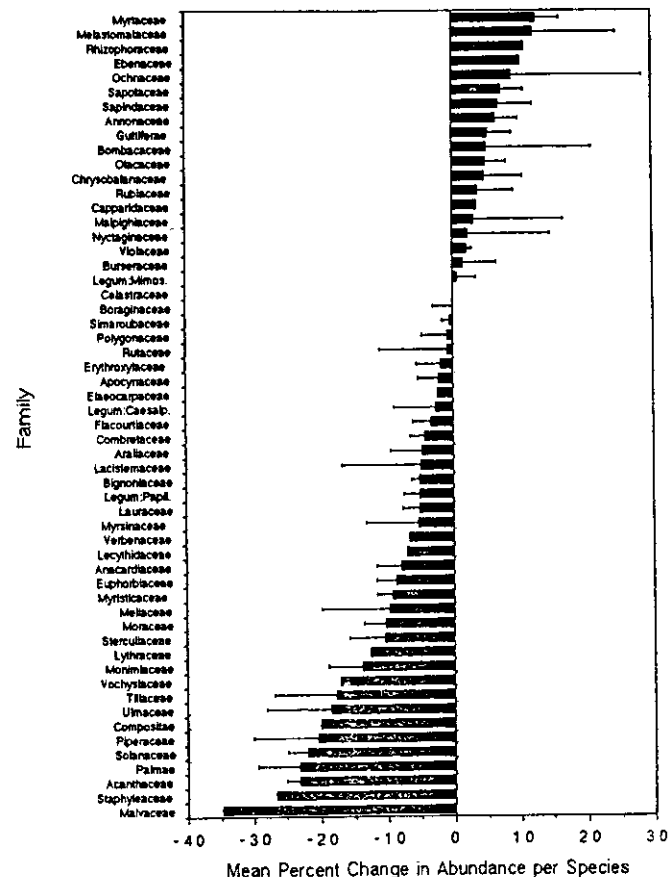


Fig. 6. Relationship between the number of trees of large size (> 10 cm dbh), and the number of saplings and pole-size trees between 1 and 10 cm dbh ("advance regeneration"). For all canopy and midstory tree species in the BCI plot. The R^2 value for the regression is 0.674.

Fig. 7. Patterns of average percent change in total abundance among species of different plant families in the BCI plot over the period covering the El Niño drought of 1982–1983, ranked by percentage change. The error bars represent one SE of the mean percentage change in abundance of the species in the given family. Families without error bars were generally monospecific.



some of which were catastrophic. Some species increased. Closely related species, congeners and congeneric species, were much more likely to have similar trajectories of population change, both in direction and magnitude, than expected by chance (Hubbell and Foster 1990c). When families were ranked by the average percent change in abundance of their member species, strong differences were apparent (Fig. 7). For example, all 8 species of palm declined, and the average percentage change in total abundance per species was -23%. However, all 6 species in the family Myrtaceae increased, for a mean change per species of +12%.

Increases in population size were particularly characteristic of common species, and decreases of occasional or rare species (Hubbell and Foster 1990c). Of the 44 species with more than 1,000 individuals apiece in 1982, three-quarters (34 species, 77%) registered increases. Among the 18 very common species making up half of

the individuals of their respective growth form (Table 1), only 5 species exhibited declines ($p < 0.05$), and only 1 of these experienced a serious decline (-22.0%), the moisture-loving species, *Poulsenia armata* (Moraceae). Conversely, of the 63 species with fewer than 10 individuals in 1982, 50 species (79%) were decreasing or stayed the same. This is strong evidence of the nonequilibrium status of the BCI forest. Instead of finding that rare species have a frequency dependent per-capita advantage over common species, which would tend to maintain the current species assemblage, the rare species are heading toward local extinction. Indeed, three rare species present in 1982 were no longer there in 1985 (Hubbell and Foster 1990c). Many of the rare species in decline appear to be ruderal species that are common roadside and pasture-edge trees and shrubs. Small populations of these species may have been sustained in old-growth forest by immigration from nearby pastures

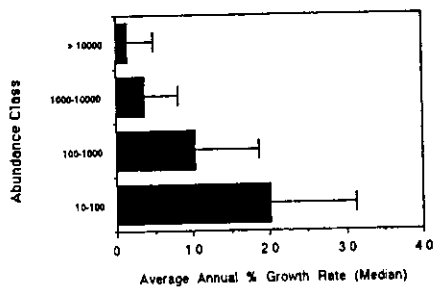


Fig. 8. Mean annual percent growth rate for species of different orders of magnitude in abundance. Growth rates are averages of the median growth rates of saplings 1-4 cm dbh for midstory and canopy tree species. Very common species (> 1000 individuals apiece) grew 10 times more slowly on average than rare species (10-100 individuals apiece). Error bars are one standard deviation.

in precanal days, and are now in permanent decline due to the succession of these adjacent pastures to forest.

Mortality rates were high in all size classes, but were especially elevated in large trees. Nearly 15% of all canopy trees over 32 cm dbh died between 1982 and 1985 (Hubbell and Foster 1990a). This is more than 300% higher than the rate of tree mortality previously reported from BCI (Putz and Milton 1982). The apparent cause of this heavy mortality was a severe El Niño drought which began in the wet season of 1982 and extended through the dry season of 1983. In that year, dry season rainfall was 85% below normal, and the dry season was 6 weeks longer than usual (Windsor 1990). As might be expected, the species that were hardest hit tended to be moisture-loving species found in normally wetter habitats within the plot (Hubbell and Foster 1990c).

The directional change in forest composition may also be due to long-term climate change in central Panama. Many of the increasing species appear to be species with greater drought tolerance. Windsor (1990) had documented a decrease of more than a 20% in the mean annual rainfall on BCI over the past 70 years. Although definitive proof is lacking, there is reason to suspect that this drop in precipitation has been caused by the progressive deforestation of central Panama over the past 50 years. Deviations in rainfall decrements can be traced to historical differences in when local deforestation took place.

The data on patterns of survival, growth, and recruitment confirmed the overall association of commonness with generalist and rarity with specialist regeneration strategies (Welden et al. 1990). Common species tended to be slow-growing species and rare species faster growing (Fig. 8). Common species were generally more shade-tolerant, and recruited in gaps as well as in the understory, and had high survival in both gaps and understory shade. Across species, there was a strong

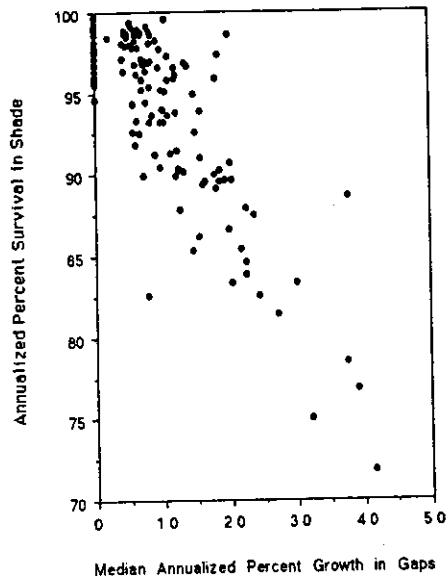


Fig. 9. Negative correlation between annual survival rate of saplings 1-4 cm dbh in understory shade vs median annual percent growth in the sun in treefall gaps, for canopy and midstory tree species. There were many slow-growing, shade-tolerant species for which the median growth rate was "zero". In the first census, we measured diameter in half-centimeter increments, so the actual growth rate in these species was too slow to detect.

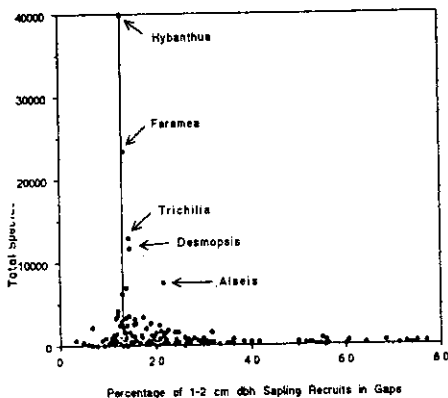


Fig. 10. Relationship between the percentage of 1-2 cm dbh new sapling recruits in gaps (the "index of heliophily") and the total abundance of the species in 1982. Note that species with high indices of heliophily were all occasional or rare, never common. The vertical bar at 13% represents the expected percentage of saplings in gaps based on the percentage of total plot area in gaps in 1983. Four out of 5 of the most common species cluster about this line. These species were statistically indifferent to whether they recruited in gaps or in the understory shade.

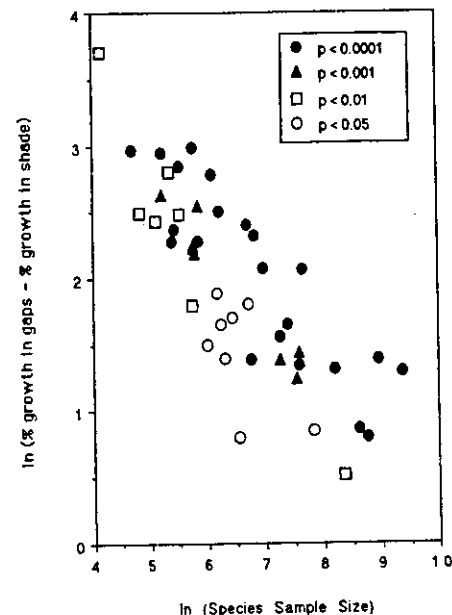


Fig. 11. The effect of sample size on the ability to detect statistical significance between annual percent growth rates of BCI tree species in light gaps vs understory shade. The points represent individual tree species with particular values of growth rate difference and population size. The legend (box) indicates the level of statistical significance achieved by the difference in growth rates.

negative association between sapling survival rate in understory shade, and median sapling growth rate in gaps, suggesting strong life-history tradeoffs between shade-tolerance and gap specialization. For BCI trees, a decrease in mean annual survival of about 5% accompanies each 10% increase in median annual growth rate (Fig. 9). One measure of gap specialization is the percentage of new sapling recruitment that occurs in gaps. We have proposed using this percentage as an "index of heliophily" (Hubbell and Foster 1986b). Species with high indices of heliophily were occasional or rare, never very common in the BCI forest (Fig. 10). This can be explained by the gap disturbance regime on BCI, which seldom generates the large gaps suitable for regeneration in very light-demanding species (Hubbell and Foster 1986b).

The results of the census also shed light on the factors limiting population size in BCI tree species and regulating tree species diversity in the BCI forest. Using natural variation in local population density, we were able to test for the existence and strength of density- and frequency-dependence contributing to the maintenance of diversity in the tree community. As mentioned

above, we found strong density dependence in the two most abundant canopy tree species, but not in the remaining majority of tree or shrub species. By modeling population growth in an explicit spatial context, we could demonstrate that the observed density dependence was sufficient to limit population size at current abundances in *Trichilia*, the most abundant canopy species, but not in *Quararibea asterolepis* (Bombacaceae), the fifth most common canopy tree (Hubbell et al. 1990). For most of the remaining tree and shrub species, however, we concluded that populations are far below the conspecific densities at which strong density-dependent effects would noticeably affect their dynamics (Hubbell and Foster 1986a, 1987a, unpubl., Condit et al., unpubl., Hubbell et al. 1990). As for frequency dependence, we found evidence, not of stabilizing effects due to rare species advantage, but destabilizing rare species disadvantage, which predicts the progressive loss of rare species.

Research design and methodology

The details of the field methodology, data entry, and database management for establishing and maintaining 50 ha plot studies in species-rich tropical forest are now published (Manokaran et al. 1990). The detection, correction, and management of errors for a database of this magnitude (20 to 30 megabytes of primary raw data, and increasing with each census by 5 to 10 megabytes) is a topic in its own right, and will be discussed separately (Hubbell et al. unpubl.). There are also many important gaps in the BCI research program that have not yet been filled due in part to insufficient funding. For example, the animal communities and human uses of the forest have been studied only intermittently or not at all, and no thorough program of research on the reproductive biology of the BCI tree community has been undertaken to date. Elsewhere we outline a complete program for priority research on the community ecology of tropical tree communities to meet conservation and management needs (Hubbell 1990).

The main point we wish to emphasize here is the critical importance of having adequate sample sizes for understanding the community ecology of species-rich tropical forests. The decision to choose a 50 ha sample or some other plot size is dictated by the biology of the rarest species of interest and by the questions to be answered. If the question is how species-rich is a particular forest, a smaller sample may suffice than if one wants to know the relative abundance of the species. As we have seen above, the rarest 40% of the species in the BCI forest collectively constituted just 1% of the total individuals, making them hard to catch without large samples. Very accurate relative abundance information, particularly of rare species, requires a total stand enumeration. If one further wants to understand the population dynamics of the tree species, then one needs

even larger population sizes for demographic analyses. As a rule of thumb, 500 individuals of all size classes gives a reasonable number for estimates of size-specific growth and survival rates. By this criterion, only one quarter of the BCI species (77, 25.2%) are sufficiently abundant to be analyzed. If we relax this criterion to a smaller sample size, say 100 individuals, then we can analyze up to half of the BCI species (157 species, 51.3%).

We need especially large samples to discern habitat preferences and regeneration requirements of tropical trees – perhaps the ecological information most valuable to silviculturalists and forest managers. To illustrate this problem, we show how sample size affects our power to detect significant differences in growth rate between plants growing in gaps vs in the shade (Fig. 11). This difference is an important ecological indicator of whether a species is light demanding or shade tolerant. For example, given observed growth rate variation, a 12% difference in mean growth rate between gaps and shade could be picked up at $p < 0.05$ with a total sample size of about 150 individuals. However, a 2% difference in growth rate, to be detected at $p < 0.0001$ would require a sample size on the order of 5 000 individuals (Fig. 11). In many closed-canopy tropical forests there is likely to be a correlation between shade intolerance and rarity. In such tropical forests, small plot sizes are to be especially avoided if one goal is to quantify, compare, and contrast the gap requirements of individual tree species.

Implications for conservation and management

There are still many important questions that remain unanswered, but we have made substantial progress toward understanding the structure and dynamics of tropical moist forest in Panama, as represented by the BCI forest. We have endeavored to show that a great deal of practically useful ecological information about a species-rich tropical forest can be obtained in a reasonably short amount of time (3–5 years). Perhaps this is the single most important result of the BCI study, to demonstrate the feasibility of gathering essential life history data on growth, survival, and recruitment rates, and regeneration requirements, simultaneously on a substantial fraction of the tree community. The large-plot approach is quite cost-effective on a per-species basis (see below).

The results showing the very thorough spatial mixing of tree species is potentially good news for tropical forest conservation. Much has been made of the high levels of point endemism, particularly in tropical montane forests, and the difficulty of conserving all these endemics. In some Andean forests, for example, large numbers of endemics may be restricted to the sides of a

single mountain, with total ranges under a few tens of square kilometers (Gentry 1986). However, such extremes of point endemism may not be common for trees in lowland tropical forests. We have seen that the BCI plot contains three-quarters of all the known tree species from BCI in 3% of the island area. Unfortunately, we cannot extend this analysis to a regional scale until the tree flora in Central America is better known. But we can do so in peninsular Malaysia, where the tree flora is very well known. The 50 ha plot at Pasoh forest Reserve, one of the two parallel studies to the BCI plot, contains 802 species, one-quarter of the 3 197 tree and shrub species in Malaya (Kochummen et al. 1990). This is quite remarkable given the fact that the Pasoh plot represents only 0.00038% of the original lowland forest estate (131 600 km²) of Malaya. In fact, the Pasoh plot contains almost half of all species that might be expected to be there based on ecological considerations of similar forests on the peninsula.

The BCI forest dynamics study has confirmed the extraordinary rarity of large numbers of tree species in tropical forests. However, we were surprised by the fact that in spite of relatively high species richness, there was also moderately high dominance by a few species, particularly in the BCI shrub and understorey tree communities. This may not be a general result. There was comparatively much less dominance in the Pasoh forest, which also had over two and a half times the number of species that BCI had. The commonest species at Pasoh constituted only 2.7% of the stand vs 16.9% for *Hybanthus* in the BCI plot.

Many of the rare species seem to be so because they are adapted to regenerate only under high-light conditions in large gaps, which are created only infrequently in the BCI forest. Many of these species are also light hardwoods of commercial value. To increase their stand densities in natural forest may require opening the canopy to a greater extent than is desirable for the undisturbed maintenance of other plants and animals in the forest. Enrichment planting of saplings in gaps left by logging may be a viable alternative to increase their representation in the next generation. Some of these species may also take well to plantation.

A variety of static and dynamic tests were conducted to search for self-limiting density dependence in BCI tree species. These tests failed to discover strong density dependence except in the two most common canopy tree species, where it was demonstrably sufficient to regulate densities at or near current abundances and prevent total dominance. While we do not know the mechanism behind this density dependence, we suspect that it may be pathogenic heart-rot fungi, at least in the case of *Trichilia* (Hubbell et al. 1990). For the remaining species, our current hypothesis is that there are few density-dependent brakes on further population growth. Many of these less common species may coexist in drifting relative abundance for long periods of time driven by time-varying, density-independent factors af-

fecting mortality and recruitment rates. To manage a forest with such dynamics, the best strategy is a large reserve that can buffer the local fluctuations of tree populations.

We were especially surprised by the rapid and directional change in the old-growth forest on BCI in such a short period of time (3 years). The forest has not sustained heavy impact from humans within the past several centuries. Admittedly, change was accelerated by the stress of the extreme drought of 1982–83. Nevertheless, the results show the speed with which a forest can respond to climate change if stressed. In view of predictions that global change in the tropics will bring increased droughtiness and seasonal unpredictability, it seems a safe bet to anticipate that tropical forests will continue to show disequilibrium behavior for the foreseeable future. Our results also suggest that regional deforestation may provoke major changes in moisture regimes in neighboring forest reserves that could in turn trigger major changes in forest structure and composition.

Toward a global network of tropical forest research sites

As an isolated study, the BCI forest dynamics project can be easily justified on both basic and applied research grounds, but it would gain far more value as part of a global network of tropical forest research sites and comparable research projects. In a real sense each one of these studies is a single data point in the effort to understand the community ecology of tropical forests. We need the comparative perspective to separate general results from local ones. It is hoped that international development agencies and foundations will increasingly recognize the importance of community ecology to the long-term success of their own mission to promote the conservation and sustainable management of tropical forests.

The Smithsonian Tropical Research Institute has recently established a Center for Tropical Forest Science (CTFS) to help coordinate this global research program on the community ecology of natural tropical forests. The program is different from most other tropical forestry programs in focus, scale, scope, and standardization:

Focus. The CTFS research program has adopted a holistic approach to understanding how natural tropical forests work as ecological communities. In contrast, most tropical forestry today is focused on evaluating the performance of a small number of multiple-use tropical tree species, typically exotics grown in plantations apart from and ignoring the natural ecological setting in which they evolved. Such efforts are and will continue to remain crucial to satisfying the increasing wood and fuel

wood requirements of heavily deforested tropical countries, and they may also help to lessen pressures to cut the last remaining forests. However, international development agencies are also committed to reducing rates of deforestation, managing tropical forests sustainably, and conserving biodiversity. With the new emphasis on natural forest management, the holistic, community-ecology approach is needed to understand the mutual interactions and dependencies among the species, and therefore the conservation and management needs of natural tropical forests.

Scale. In collaboration with institutions in host countries, the CTFS promotes long-term tropical forest research projects. At the three current sites in Panama, peninsular Malaysia, and India, more than half a million individual trees are under continuous, long-term study. This represents more than 1 000 native tropical tree species, over twenty times the number of tropical tree species currently under intensive development for plantation forestry by international development agencies. Three more research sites, in Thailand, Sarawak, and Indonesia, are being added, and others in Africa, Madagascar, and South America are in the planning stage. The database is expected to grow to include several million trees and several thousand tree species by the mid 1990's. Within the next decade, the goal is to obtain forestry-relevant data on tree species representing as many of the major tree groups (genera) and forest types in the tropics as possible.

Apart from scientific merits, there are major economies of scale that occur in large-plot studies. The most important economy is that data can be gathered on the fundamental ecology of hundreds of species simultaneously. How much does it cost? The first and second censuses of the BCI plot in constant 1980 dollars cost approximately \$620 000 for equipment, supplies, travel, about 15 field assistants and data entry personnel during census years, and computer costs. By the end of the second census, there were records on about 242 000 plants. Thus, the cost was about \$2.56 per plant, not including the salaries of the principal investigators, Hubbell and Foster. This cost may sound high, but on a per-species basis it is good value for the money. Thus, for the 303 BCI species, the average cost was only about \$2 000 per species. Even if we restrict the valuation to the roughly 50% of the species for which we obtained reasonably good data on life history and regeneration requirements, the average cost is only \$4 000 per species. It is doubtful that separate studies on the ecology of 150 tropical tree species would cost a little as \$4 000 per species. Separate studies of species would cost more if they each had to establish the community setting independently, whereas such costs are borne collectively by all species in the-plot approach. Even this cost estimate is probably high for repeating such a study today in most other tropical countries. BCI costs were high in part because it was the pilot project on which many of the logistics and methods were developed and

debugged. In addition, wages for field assistants are lower in many tropical countries than in Panama.

Scope. The goal of the CTFs research program is to extend considerably beyond the boundaries of traditional forestry, to include research on animal populations and human uses of the forest. Plant-animal interactions will be a major research focus, particularly the plant food requirements of threatened vertebrates, and the long-term security and predictability of food availability in the forest to support animals. Also important to include are the animal agents essential to plant reproduction (pollination and seed dispersal), especially in trees.

In regard to management, a goal of the Center will be to foster new economic approaches to tropical forest management that have greater ecological validity and incorporate critical biological and social tradeoffs. The program will include research to assess such tradeoffs, for example, the impact of logging and other extractive uses of the natural forest on conservation of biodiversity and sustainability. The permanent plots in natural forest serve as essential scientific control plots for experiments in silviculture and extractive reserve design, and for assessments for the ecological and economic tradeoffs among alternative exploitation and management systems.

Standardization. A special strength of the program is the high degree of standardization of research methods and database management protocols across all sites, so that the data and results can be rigorously compared around the world. In the case of trees, this international standardization has helped to cope with the enormous number of species in tropical forests. By comparing the ecology of closely related trees in diverse tropical forests simultaneously using standard methods, we can more easily and quickly generalize the results to cover a broad fraction of the world's tropical tree species, thereby sidestepping the nearly impossible task of studying them all – a task for which there are neither sufficient time nor resources.

Summary

We propose a global program of comparative research on the community ecology of natural tropical forests, the beginnings of which are already in place. The applied objectives of this program are threefold: first, to provide basic data of practical value on the ecological performance (growth, survival, reproduction, yield, stocking, and regeneration requirements) of a large fraction of the local tree flora in the natural forest; second, to monitor long-term forest dynamics and changes in species composition in response to natural and anthropogenic disturbance; and third, to serve as essential scientific control plots for experiments in silviculture and extractive reserve management. The results

from these long-term plot studies will enable the development of ecologically more valid economic approaches to tropical forest conservation and sustainable management.

The main results of the BCI forest dynamics project so far can be summarized as follows: In the first census in 1985, unexpectedly large changes in absolute abundance (greater than 10%) were observed in 40% of all species even though the inter-census interval was just 3 years. The stabilizing effects of density dependent factors were generally weak in the face of these changes, except in the most abundant canopy tree species. Large changes in abundance were not limited to species of one growth form, but occurred in all growth forms, from shrubs to trees. The main cause for these changes was the severe drought of the 1982–1983 El Niño year, the most severe in Panama in this century. Catastrophic declines exceeded 20–40% in some moisture-loving species. Palms were especially hard hit by the drought, but other groups weathered the drought well. Related taxa (e. g. congeneric species and confamilial genera) were much more similar in population trajectory than expected by chance.

In addition, rare species experienced more declines, and common species more increases, than could be explained by chance. Very rare species, with fewer than 10 individuals apiece in the half-square kilometer plot, were 3 times as likely to decrease than increase. Conversely, species with more than 1000 individuals each were 3 times more likely to increase than decrease. We concluded that the current species mix is not an equilibrium one, due in part to late-stage successional changes that appear to be eliminating currently rare secondary forest species, and in part to episodic climatic disturbances such as El Niño droughts that differentially affect BCI tree species. Seasonal tropical forests may be more often hit by periodic severe droughts than wet tropical forests and therefore may be especially vulnerable to climate change.

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