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# Short-Term Dynamics of a Neotropical Forest

*Change within limits*

Richard Condit, Stephen P. Hubbell, and Robin B. Foster

Since the mid-1970s, community ecology has undergone a slow shift away from a long preoccupation with questions of community equilibrium and stability. This shift has occurred not because these questions are unimportant; rather, it has occurred largely because current theory poses the questions too naively and in a manner that cannot be tested (Connell and Sousa 1983). Moreover, most ecologists now recognize that the stability and equilibrium status of ecological communities cannot be meaningfully discussed without reference to a defined spatial and temporal scale, because community change is inevitably continuous and scale dependent. No community of species achieves, let alone remains in, static equilibrium. Species continually wax and wane in relative abundance; they even go extinct locally and re-immigrate. These changes are due to exogenous (e.g., climatic, geological, and anthropogenic) forcing of the community and to endogenous ecological and evolutionary change. As with climate, the longer one monitors a com-

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## Tropical forest diversity is only weakly self-preserving

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munity, the more change one expects to observe (Davis 1986, Pimm 1991).

But how much change do we, in fact, expect? Current community theory is not much help in answering this question, because it focuses on equilibrium conditions. The empiricist is faced with community dynamics far from, or at least away from, equilibrium (if indeed the concept of equilibrium has much meaning for communities). Therefore, the empirical problem of community dynamics must be recast as testing for change within limits on a given scale of observation.

How rapidly do communities change over time and space? Do factors exist that resist change in the community, such as density- and frequency-dependent factors that regulate the growth of member species? How rapidly do communities respond to and rebound from exogenous perturbation? This question has assumed growing importance with the rise of concern about global climate change.

These questions are difficult enough to answer in simple communities, let alone in complex communities such as tropical forests. Species-rich tropical forests contain more tree species than can be identified by even well-trained botanists, not to mention the average field ecologist. Unlike associa-

tions such as beech-hemlock or oak-hickory that often typify temperate forests, there are no simple characterizations of tropical forests based on dominance, because the most abundant species generally account for only a few percent of the tree individuals. First-time exposure to the diversity of a species-rich tropical forest such as that found on Barro Colorado Island in Panama can produce a kind of intellectual vertigo in temperate-trained ecologists accustomed to simple, heuristic community-assembly rules.

High species diversity in tropical tree communities does not necessarily imply complex assembly rules and dynamics. It is possible that such communities can be described by a reduced dimensionality of some number less than the total number of species. However, the extent to which the functional dimensionality of a tropical forest is reducible is still not known, and it depends on the question asked. Similarly, expectations for rates of change in tropical tree communities remain uncertain. To address such questions for a particular species-rich tropical forest, we launched a long-term study, now in its twelfth year, of the structure and dynamics of old-growth forest on Barro Colorado Island.

## The setting

Barro Colorado Island is a former hilltop that became an island 75 years ago when the Chagres River was dammed to create Gatun Lake in the Panama Canal. No forest in Central Panama has escaped human influence,

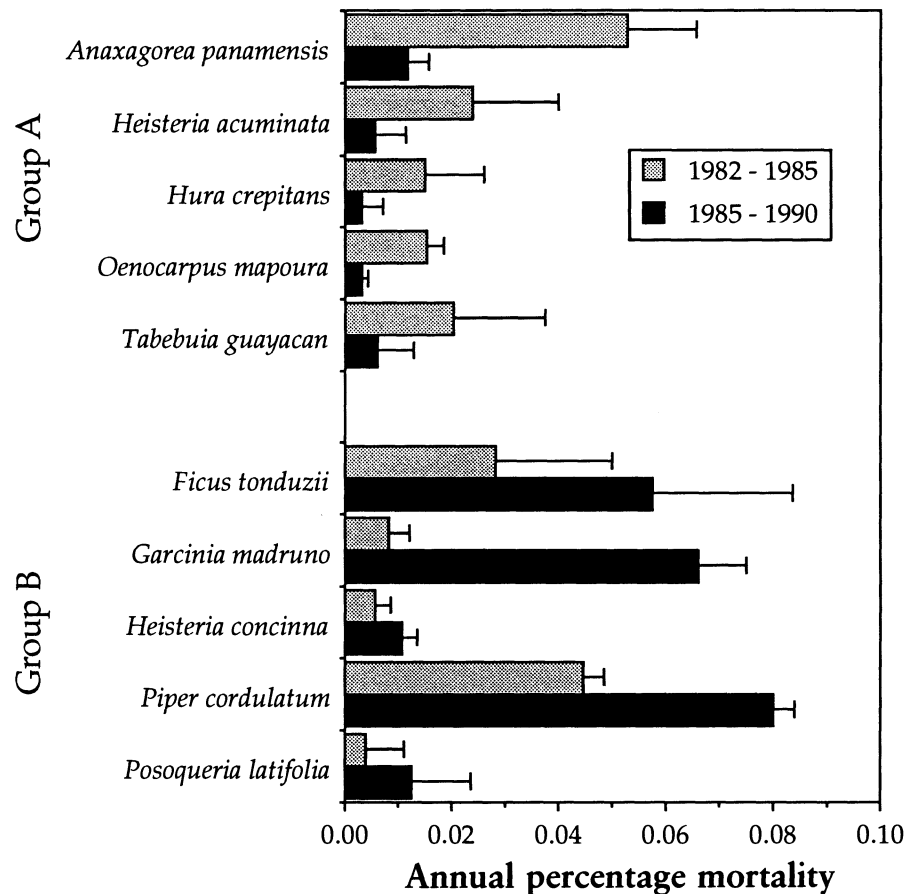
and thus Barro Colorado Island is not the place for studies of pristine tropical forest dynamics. River valleys in this area were densely populated in precolumbian times, and remains of the small seasonal camps that have been found indicate that hunters and gatherers exploited the forest.

However, there is no indication that the hilltop forest on Barro Colorado Island was subjected to precolumbian swidden agriculture. Thorough paleoecological surveys of Barro Colorado Island have failed to turn up maize phytoliths in the forest soil, which would be present had maize ever been planted there. Fossil remains of maize are abundant in other sites a few kilometers away (Piperno 1990). Shortly after the Spanish arrived, central Panama became depopulated by European-introduced diseases, and there is no evidence of human impact on the Barro Colorado Island old-growth forest during the past 500 years. For the past 70 years, Barro Colorado Island has been a protected biological reserve.

The climate of Barro Colorado Island is seasonal, with a 4- to 5-month dry season from December through March or April. At supraannual time scales, a significant decline of approximately 14% in annual precipitation has occurred over the past 70 years, dropping from approximately 2.7 m in 1925 to 2.4 m at present. The cause for this drying trend has not been proven, but it has been attributed to progressive large-scale deforestation on either side of the zone of the Panama Canal over the same period (Windsor 1990, Windsor et al. 1990). Drought and, at long intervals, fire are the factors that could potentially cause the greatest exogenously forced changes in the Barro Colorado Island tree community (Wright 1992).

A severe drought occurred on Barro Colorado Island in 1983, an unusually long and hot dry season (Leigh et al. 1989). The drought accompanied a strong El Niño event in the eastern Pacific, and in 1992 another El Niño brought a less severe drought to central Panama and Barro Colorado Island. Unlike Puerto Rico and further north in Central America, however, central Panama is not subject to such disturbances as hurricanes (Crow 1980, Walker et al. 1991).

In 1980, a 50-hectare permanent



**Figure 1.** Mortality rates for the ten species that showed the most extreme changes in mortality over the two census intervals, excluding species with fewer than 50 individuals in 1982. Species in group A had higher mortality during the census interval containing the drought, whereas species in group B had lower mortality during the drought interval. Families for species in group A are: *Anaxagorea* (Annonaceae), *Heisteria* (Olacaceae), *Hura* (Euphorbiaceae), *Oenocarpus* (Palmae), and *Tabebuia* (Bignoniaceae). Families for species in group B are: *Ficus* (Moraceae), *Garcinia* (Guttiferae), *Piper* (Piperaceae), and *Posoqueria* (Rubiaceae). Vertical lines show 95% confidence limits. Differences in mortality between census intervals were statistically significant in *Oenocarpus*, *Anaxagorea*, *Piper*, and *Garcinia*.

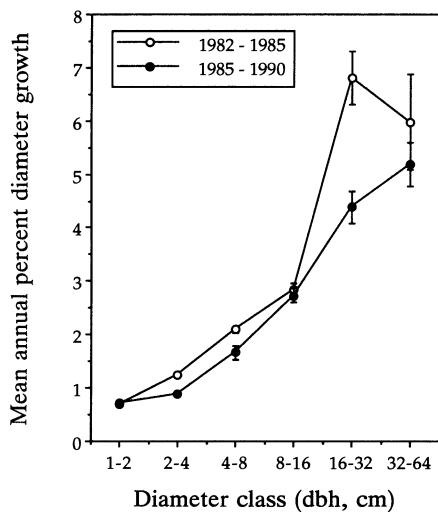
forest plot was established on the relatively flat plateau on top of Barro Colorado Island. All free-standing woody plants that were at least 1 cm dbh (diameter at breast height) were identified to species, measured, and mapped (Hubbell and Foster 1983, 1985, 1986a,b,c, 1990, 1992). The first census was completed in 1982; since then, two more total censuses were completed in 1985 and 1990, and all plants have been remeasured for growth, mortality, and new sapling recruitment. Over the three censuses, 310 species were recorded in the plot, with data on 306,620 individual stems.

For some analyses, species were grouped into four physiognomic classes based on the height of adult plants (shrubs less than 4 m, understory trees less than 10 m, medium subcanopy trees less than 20 m, and

large canopy trees at least 20 m). To interpret patterns of growth and mortality in relation to light in canopy gaps versus the understory, we have also recorded changes in vegetation height and layering on a 5-meter grid over the entire plot every year since 1983 (Hubbell and Foster 1986b, Welden et al. 1991).

In this article, we address two principal questions. First, on the spatial scale of a half-square kilometer, how much change actually occurred in this tropical tree community over almost a decade? Second, can evidence be found that these changes are bounded or limited and that the population sizes of trees are regulated in the community?

Answering the first question is a straightforward empirical matter of describing changes in numbers of stems



**Figure 2.** Mean annual percent growth rates for all individuals of canopy tree species in the 50-hectare plot. These means are unweighted: the total growth increments divided by the total number of individuals. Some plants decreased in diameter due to stem breakage; these plants were excluded. Vertical lines indicate 95% confidence limits. Limits for the 1–2 and 2–4 centimeter dbh classes are too close to the circles to be visible (sample sizes were more than 17,000 individuals in these size classes).

and species and of the abundance of individual species. Answering the second question requires a deeper look at the spatial dynamics of tree populations in the Barro Colorado Island forest to test for and measure the strength of stabilizing density- and frequency-dependent factors. We examine an old hypothesis advanced more than two decades ago by Janzen (1970) and Connell (1971) to explain the density-dependent regulation of tropical tree populations by herbivores and pathogens.

### Forest-wide patterns of constancy and change

We were surprised by the dynamism of the Barro Colorado Island forest in some aspects and the relative constancy of the forest in others. One feature of the forest that changed markedly between the two census intervals was mortality rate. Compared with mortality during the interval 1985 to 1990, annualized forest-wide mortality from 1982 to 1985 was elevated 10.5% in shrubs, 18.6% in understory trees, 19.3% in subcanopy trees, and 31.8% in canopy trees. The difference in mortality was more than 50% in trees

more than 16 cm dbh.<sup>1</sup>

The mortality increase was probably due to the extreme dry season of 1983, during which substantial wilting occurred. Large numbers of dead or dying trees were present in the forest at the height of the drought in April 1983 (Leigh et al. 1989). Many species had dramatically increased mortality during and immediately after the drought, particularly palms such as *Oenocarpus mapouira* (Figure 1). Overall, approximately two-thirds of the species in the plot had higher mortality during 1982–1985 than during 1985–1990.<sup>2</sup> There were interesting exceptions, however: species with dramatically lower mortality during the drought interval than during the subsequent nondrought interval. *Garcinia madruno* (Guttiferae), for example, had an unexplained six-fold increase in mortality rate after 1985 (based on sample of more than 650 stems).

Forestwide growth rates were also different between census intervals. A priori, one might have anticipated lower growth rates would accompany the higher mortality rates during the interval containing the 1983 drought, but the reverse was true. Growth rates were higher during the interval containing the drought for a broad range of plant sizes, from 2 to 32 cm dbh. Figure 2 shows mean annual percent diameter growth rates for canopy tree species. Shrubs, understory trees, and midsized trees also exhibited qualitatively similar patterns, with the same size classes (where they occurred) showing elevated growth during 1982–1985. Some differences in growth were remarkably high; for example, growth of 16–32 cm trees was more than 60% faster in 1982–1985 than in 1985–1990. We can suggest no bias in our field techniques that would account for the differences.<sup>3</sup>

We hypothesize that trees surviving the drought achieved faster growth rates due to high mortality in the canopy tree layer, which presumably reduced root competition for water and nutrients, opened the canopy, and allowed more light into the understory. After the drought, there was a gradual increase in

the percentage of low-canopy (gap) area in the plot (canopy more than 10 m high), rising from approximately 9% at the time of the drought to a peak of more than 15% by 1987. By 1991, the percent gap area had returned to pre-drought levels.<sup>4</sup> We are now analyzing in more detail our data on changes in vegetation height and layering between 1983 and 1990 to test this possibility further.

Similar synchronous, parallel variation in mean annual growth rates among unrelated tree species of diverse life history has been reported by Clark and Clark<sup>5</sup> over an eight-year period at La Selva, Costa Rica. The Clarks found that growth rates were higher in years having greater insolation and lower in rainier, cloudier years. The pattern was the same in species having high and low mean rates of growth. Their results and ours raise the possibility that growth rates in tropical tree communities as a whole, canopy trees included, may actually become light limited during years of persistently overcast skies. Such a possibility is not unreasonable. Physiological and morphological changes in leaves and crown geometries better suited for tolerating the high-light, high-thermal stress environment of the canopy may increase the likelihood of light limitation on dark, cloudy days.

Despite large changes in community-wide mortality and growth rates in the Barro Colorado forest, there was near constancy in overall forest structure and species composition. The number of species in the plot remained virtually unchanged over the decade: 301, 303, and 300 species in 1982, 1985, and 1990, respectively. This constancy occurred despite some species turnover; ten species dropped out of the census between 1982 and 1990, and nine species were added, all rare. Constancy in species richness is not surprising because a decade is a short time to measure species turnover in a community of long-lived organisms such as trees. It will be interesting to find out whether species number remains constant over longer periods.

Perhaps more surprising was that the number of individuals in the plot

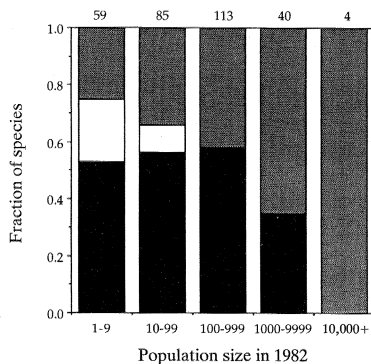
<sup>1</sup>R. Condit, S. P. Hubbell, and R. B. Foster, 1992, manuscript in preparation.

<sup>2</sup>See footnote 1.

<sup>3</sup>R. Condit, S. P. Hubbell, and R. B. Foster, 1992, manuscripts submitted.

<sup>4</sup>S. P. Hubbell, 1992, unpublished data.

<sup>5</sup>D. A. Clark and D. B. Clark, 1992, unpublished manuscript.



**Figure 3.** Fraction of species that increased (shaded bar), decreased (black), or remained the same (white) in abundance over the 1982–1990 interval, as a function of initial 1982 abundance. The total number of species in each abundance class is given at the top of each bar. This figure updates data reported by Hubbell and Foster (1992).

remained nearly as constant as the number of species. For example, the total count of trees occupying the canopy layer has been remarkably stable: 4032, 4021, and 4107 individuals in each respective census—a change of only 2%. This constancy is all the more remarkable given the large increase in mortality rates caused by the 1983 drought. The total individuals in the canopy remained almost the same because increased growth rates elevated equal numbers of new recruits into the canopy layer, balancing the increased losses of canopy trees from the drought (Table 1). It is not surprising that canopy trees were replaced; the surprise is that replacement occurred so quickly and with such precision.

### Constancy and change in individual tree species

In contrast to the relative constancy of numbers of species and trees in the canopy layer, populations of many individual species in the 50-hectare plot underwent sizeable changes in absolute and relative abundance. We were impressed by the magnitudes of change in some species in just a few years. Forty percent of the species changed in abundance by more than 10% in the first three years of the census (Hubbell and Foster 1992). Over both census intervals, more species declined in abundance than increased, and changes were generally

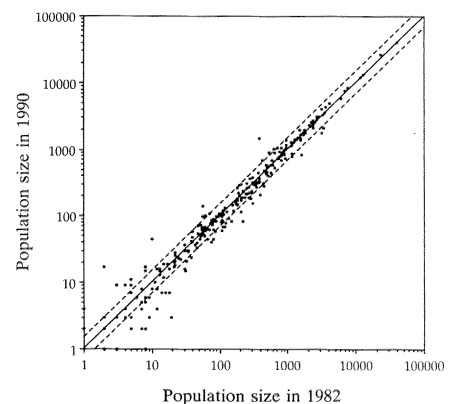
monotonic: declining species in the first census interval continued declining in the second, and increasing species continued increasing. Three-quarters (68 of the 88 populations) of the species that decreased by more than 10% in the first census interval declined further during the second interval. Similarly, three-quarters (34 of 46) of the species that increased by more than 10% during the first interval increased again in the second. Particularly noticeable was that rare species were more likely to decline than common ones (Hubbell and Foster 1992; Figure 3), suggesting that the community is undergoing directional change, with the currently more dominant species gaining further in dominance.

Part of this directional change in species composition may be due to shifts in climate, trends accelerated by events such as the 1983 El Niño drought. Most of the species whose populations declined rapidly between 1982 and 1990 were species of moist soils.<sup>6</sup> These species suffered high mortality rates, far higher than their recruitment rates. A group of 20–30 moisture-loving species, perhaps more, appear headed for local extinction in the plot because of the long-term drying trend on Barro Colorado Island. Another group of declining species appear to be ruderal species that by immigration were sustained as sink populations in the old-growth forest. This immigration subsidy has been cut off because neighboring areas have regenerated from pre-canal pastures into mature forest.

Conversely, almost all the species whose populations grew rapidly from 1982 to 1990 were light-demanding species (nonruderal species characteristic of mature-forest gaps). These species benefited from the opening of the canopy, which took place after the 1983 drought, when more light reached low levels in the forest, improving their recruitment.<sup>7</sup> The elevated abundance of these species is expected to be transient if the canopy returns to its original structure, unless droughts become more frequent and permanently force a more open canopy. In that case, pioneer species are expected to increase and persist at higher densities. Three-quarters of the shade-tolerant,

<sup>6</sup>See footnote 3.

<sup>7</sup>See footnote 3.



**Figure 4.** Changes in total abundance of 287 species in the 50-hectare plot. All these species were represented by at least one individual in both 1982 and 1990. Four species of shrubby palms in the genus *Bactris* were omitted because these palms grow in clumps with multiple stems and census methods for them were changed midway through the study. The solid line represents the line of equality for the 1982 and 1990 abundances. Dots below this line represent declining species and points above represent increasing species. On this logarithmic plot, distance from the line indicates percent population change regardless of density; the two dashed lines show where a population that increased or decreased by 5% per year would fall on the graph. An annual 5% change is substantial: after eight years it yields a 47% increase or a 33% decline. Any point falling outside those dashed lines indicates a rapidly changing population. The coefficient of determination,  $r^2$ , for the simple linear regression of the log-transformed 1990 abundances on 1982 abundances was 0.965.

mature-phase species having high abundances of more than 1000 individuals also increased but more slowly.

Although many species showed marked changes in abundance, there were nonetheless species whose populations changed little. *Picramnia latifolia* (Simaroubaceae), a small understory tree, provides an illustration: its population size was 1170 individuals in 1982, 1176 in 1985, and 1173 in 1990. Mortality claimed more than 200 *P. latifolia* plants during the eight-year period (2.5% per year), but new sapling recruitment almost perfectly balanced mortality.

The overall changes in species abundances in the Barro Colorado Island forest can be conveniently summarized by plotting the population size of species in 1990 against the population size in 1982 for all species present

**Table 1.** Turnover of individuals in the forest canopy. Tree density is the total number of trees in each hectare more than 30 cm dbh. Mortality is the mean annualized percent mortality rate of trees of this size during the two census intervals. Recruitment is the number of trees entering the 30-centimeter class each year divided by the number present at the start of the year and then multiplied by 100.

Census year or interval	Tree density	Mortality	Recruitment
1982	80.6		
1982–1985	—	3.6	3.3
1985	80.4		
1985–1990	—	2.1	2.5
1990	82.1		

in both censuses (Figure 4). Although some species changed greatly, most species did not change much in abundance over the eight years: a third of the species (96 out of 286) changed by less than 1% per year, and three-quarters (223 of 286 species) changed by less than 5% per year. To compare rates of change in tropical forests in a more rigorous way and with better chances of predicting how tropical forests are likely to respond to exogenous forcing, we suggest using the coefficient of determination,  $r^2$ , as a convenient quantitative measure of the degree to which the community composition has changed: the lower the  $r^2$ , the greater the change in the community. From a regression of the data in Figure 4, we calculated an  $r^2$  of 0.965 for the Barro Colorado Island forest, but comparable data are not yet available for other tropical tree communities.

### Forces that regulate species abundance

Change is occurring in the Barro Colorado Island forest, and this change is directional, with increasing abundances of already abundant species and the loss of species of the moister soils. Is there any indication of whether and when this trend will end? What, if anything, prevents a few competitively dominant species from taking over the forest and excluding all others? Is there evidence for population stabilizing factors within and among species?

Elsewhere, based on data from the 50-hectare plot, we have published a test of one of the major hypotheses for equilibrating forces in tropical forests (Condit et al. 1992, Hubbell et al. 1990),<sup>8,9</sup>. The hypothesis is the Janzen-

Connell model for population regulation and maintenance of species diversity in tropical tree communities. Janzen (1970) and Connell (1971, 1978) postulated that the mortality of seeds, seedlings, and saplings is higher when the offspring is close to the parents than it is farther away from them; this pattern is called a neighborhood effect because plants perform poorly in the neighborhood of adults of their species (Antonovics and Levin 1980, Silander and Pacala 1990). Neighborhood effects can regulate a population because they create negative density-dependence in population performance. As a species becomes more abundant, mean plant performance (growth and survival) declines because fewer plants escape the neighborhood of adults. The Janzen-Connell hypothesis is a special case of a more general hypothesis of density-dependent population regulation in plants (Antonovics and Levin 1980, Harper 1977).

There are two aspects of any test for density-dependent population regulation in tropical trees. First, the prevalence of density dependence among species in the community must be ascertained. What proportion of the species show negative density-dependence? Second, it must be determined whether observed density-dependence is strong enough to regulate populations. How strong are the effects? Will they restrain population growth below densities that result in complete dominance?

Previous tests for neighborhood effects in tropical trees have focused entirely on the first aspect (Augspurger 1983a,b, 1984, Clark and Clark 1984, Connell et al. 1984, Howe et al. 1985, Howe and Smallwood 1982, Schupp 1988, Wright 1983). Few studies of any plants, let alone tropical trees,

have included the population modeling necessary to address the second issue (Pacala and Silander 1990, Silander and Pacala 1990, Watkinson and Harper 1978). Our goal with the 50-hectare plot has been to determine the extent of density-dependence on a community-wide scale and subsequently to test whether the observed density dependence can be regulating tree populations.

Addressing the first aspect, there is detectable density-dependence in the Barro Colorado Island tree community. Of 80 species ranging from shrubs to canopy trees whose recruitment patterns we examined, 15 species showed evidence of reduced recruitment in the neighborhood of conspecific adults (Condit et al. 1992). In 12 of these species, we studied the performance of juvenile plants as a function of local conspecific density (Hubbell et al. 1990).<sup>10</sup> Six species showed significant neighborhood effects (Table 2). In some common species, notably *Trichilia tuberculata*, plants as large as 8 cm dbh were negatively affected in growth and survival by increases in local conspecific density. In a few species, especially *Alseis blackiana* and *Trichilia*, performance was inhibited by juvenile neighbors as well as by adult neighbors (Table 1).

These data make it clear that there is significant density-dependence in some species of trees in the Barro Colorado Island forest. But some species show only weak neighborhood effects, and others show none. The more difficult issue is whether the neighborhood effects, when observed, are strong enough to regulate tree populations at their current densities, and whether they are pervasive enough to play a role in structuring the community.

We used two approaches to address this issue. In the first, we developed a spatially explicit population model that incorporated neighborhood effects on growth, mortality, and recruitment (Hubbell et al. 1990). A simulated population of *Trichilia* was regulated near its observed density on Barro Colorado Island. Simulations based on data from *Alseis* suggested that the population could increase to a carrying capacity approximately three times higher than its current

<sup>8</sup>See footnote 3.  
<sup>9</sup>See footnote 3.

<sup>10</sup>See footnote 3.

density. Simulations with the other species listed in Table 2 revealed either a carrying capacity much higher than the observed density or no carrying capacity short of complete dominance. Thus, it appears plausible that only 2 of 12 species studied have populations regulated by density-dependent factors.

In the second approach, we calculated separate life tables for individual species in regions of high and low conspecific density in the 50-hectare plot.<sup>11</sup> From these life tables, we calculated region-specific finite rates of population increase,  $\lambda$ . *Trichilia* and *Alseis* had strongly reduced  $\lambda$ s in regions of high density, but the remaining species showed no relationship between population growth and local density. These results supported the earlier conclusion from the simulation studies that there are two common species in the plot whose populations appear to be regulated by neighborhood effects, but that many less-common species appear not to be regulated.

Overall, the analyses of density dependence suggest that many tropical forest trees have populations that are unregulated in the classical sense, with densities well below any carrying capacity set by density-dependent factors. Their abundances appear to be free to drift up or down, fluctuating with climatic anomalies, with changes in populations of interacting plants or animals, or randomly (Hubbell and Foster 1986c). However, it is important that the most abundant species are regulated by density-dependent factors. This regulation prevents any one species from taking over the forest, and thus it limits the extent to which the community can drift. Here at last we find evidence for limits to community change: a cap on the level of dominance that any one species can achieve.

A caveat needs to be made about these conclusions. Our data pertain to trees and their saplings 1 cm dbh and larger. Density-dependent processes occurring earlier in ontogeny may be missed because the spatial signature of earlier density-dependence and neighborhood effects might be lost by the time saplings reach 1 cm dbh (Crawley 1990). Recent work suggests that 1 cm dbh saplings of many of the mature-phase

**Table 2.** Neighborhood effects in 12 tree species on Barro Colorado Island.

Species	Family	Size classes affected* (cm dbh)	Distance of effect† (meters)	Sizes causing effects‡ (cm dbh)
<i>Alseis blackiana</i>	Rubiaceae	1–2	15	1–4, 4–16, 16+
<i>Beilschmiedia pendula</i>	Lauraceae	None	—	—
<i>Desmopsis panamensis</i>	Annonaceae	None	—	—
<i>Faramea occidentalis</i>	Rubiaceae	1–2, 2–4, 4–8	30	4–16
<i>Hirtella triandra</i>	Chrysobalanaceae	None	—	—
<i>Poulsenia armata</i>	Moraceae	None	—	—
<i>Prioria copaifera</i>	Leguminosae	1–2, 2–4, 4–8	15	16+
<i>Protium tenuifolium</i>	Burseraceae	1–2, 2–4	10	4–16, 16+
<i>Quararibea asterolepis</i>	Bombacaceae	None	—	—
<i>Tetragastris panamensis</i>	Burseraceae	None	—	—
<i>Trichilia tuberculata</i>	Meliaceae	1–2, 2–4, 4–8	15	4–16, 16+
<i>Virola sebifera</i>	Myristicaceae	1–2	10	16+

\*Sizes of plants whose performance (either growth or survival) was reduced when conspecific neighbors were present.

†The maximal distance between two plants at which a reduction in performance could be detected.

‡Classes whose presence caused a reduction in performance of neighbors.

Barro Colorado Island tree species are probably quite old; the median age of 1 cm dbh saplings in the Barro Colorado Island tree community is estimated to be at least 16.7 years.<sup>12</sup> For example, the mean age of a 1 cm dbh sapling is estimated to be 37.9 years for *Alseis* and 21.9 years for *Trichilia*. These estimates may be biased by slow-growing suppressed individuals that will ultimately die before reaching the canopy, but we reduced this bias by basing our estimated sapling ages on growth rates of only those plants that survived all eight years of the census.

If these sapling ages are confirmed, a potentially sizeable fraction (~25%) of parent trees could have died before their saplings reach 1 cm, making detection of neighborhood effects in 1 cm dbh saplings more difficult. Given the estimated ages of saplings in *Alseis* and *Trichilia*, the detection of strong density dependence and neighborhood effects in these species is remarkable.

## Conclusions

There can be no doubt that the Barro Colorado Island forest is changing. Some species are going locally extinct; perhaps others will invade to replace them. Most of the major changes appear to be directional and associated with a climatic drying trend in central Panama, punctuated by droughts. If this drying trend contin-

ues, major changes in the Barro Colorado Island forest composition and diversity can be expected over the coming decades. If the drying trend is due to regional deforestation, then one lesson from Barro Colorado Island is that residual tropical forests may not have to be cut down to suffer major deforestation-induced changes in composition and loss of diversity from climatic disruptions. On a global level, understanding how rapidly forests change under different climate scenarios will be critical to the development of workable systems of protected forest areas.

Are there stabilizing forces in tropical forest communities that might buffer them against perturbations caused by climate change or other human activities? To some degree, there are. The Barro Colorado Island forest suffered a severe drought, yet the overall structure of the forest bounced back. There is a regulating force at work here: remove a tree and a tree grows back. But this force only preserves the forest as a forest, not the diversity of tree species it contains. At the level of species diversity, we also found some limits, but not many. If we perturb the species mixture, there is a limit to how much it changes, because the most abundant species are at their carrying capacities; under current conditions, the Barro Colorado Island forest will not convert to a monodominant stand (some tropical trees escape this regulation; see Hart 1990). But there do not appear to be regulating factors for the populations

<sup>11</sup>See footnote 3.

<sup>12</sup>S. P. Hubbell, R. B. Foster, and R. Condit, 1992, unpublished manuscript.

of many rare species, and in this sense the forest is fragile—a perturbation that eliminates rare species would be permanent.

It is important to understand these community-level processes when designing programs for tropical forest management, reforestation, and species preservation. Our results suggest that tropical forest diversity is only weakly self-preserving; it is quite fragile when exposed to external threat.

## Acknowledgments

We thank the field workers who contributed to the censuses on Barro Colorado Island, more than 100 people from ten countries. The Smithsonian Tropical Research Institute in Panama provided generous logistical and financial support for the censuses. This project has been supported by grants from the National Science Foundation, the Smithsonian Scholarly Studies Program, the Smithsonian Tropical Research Institute, the John D. and Catherine T. MacArthur Foundation, the World Wildlife Fund, the Earthwatch Center for Field Studies, the Geraldine R. Dodge Foundation, and the Alton Jones Foundation.

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