

Barro Colorado Island and Tropical Biology

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Barro Colorado Island (BCI), Panama, the subject of more than fifteen hundred scholarly publications, may be the most studied tract of tropical forest in the world. It is perhaps best known for studies in natural history, ecology, and ethology, centering on vertebrates, insects, plants, and their relationships. Large-scale integrated studies at the community level, now in progress, complement the diversity of projects carried out by graduate students, postdoctoral fellows, and visiting scientists.

The 1,500 ha of BCI (9°9'N, 79°51'W) were isolated from the surrounding mainland after the Chagres River was dammed in 1910 (McCullough 1977, 589) to create Gatun Lake and complete the Panama Canal. BCI is now administered by the Smithsonian Tropical Research Institute (STRI) as part of the Barro Colorado Nature Monument (BCNM). The Panama Canal treaties of 1977 gave STRI custodianship of the BCNM, which was established under the Western Hemisphere Convention on Nature Protection and Wildlife Preservation of 1940. The BCNM also includes five nearby mainland peninsulas (fig. 2.1), three of which adjoin Panama's Parque Nacional Soberania. BCI has accommodations for thirty-five visitors, air-conditioned office and laboratory space, an insectary, a screened growing house with a plant physiology laboratory, a herbarium, a small reference library, and equipment for general use, such as freeze driers, autoclaves, drying ovens, a muffle furnace, analytical balances, microcomputers, and small boats for access to mainland sites. These facilities will be augmented when a new, fully equipped laboratory is completed in 1992. Launch service to BCI is provided twice a day from the roadhead at Gamboa (where STRI also maintains a small dormitory), allowing mainlanders to visit BCI for the day and researchers on BCI to

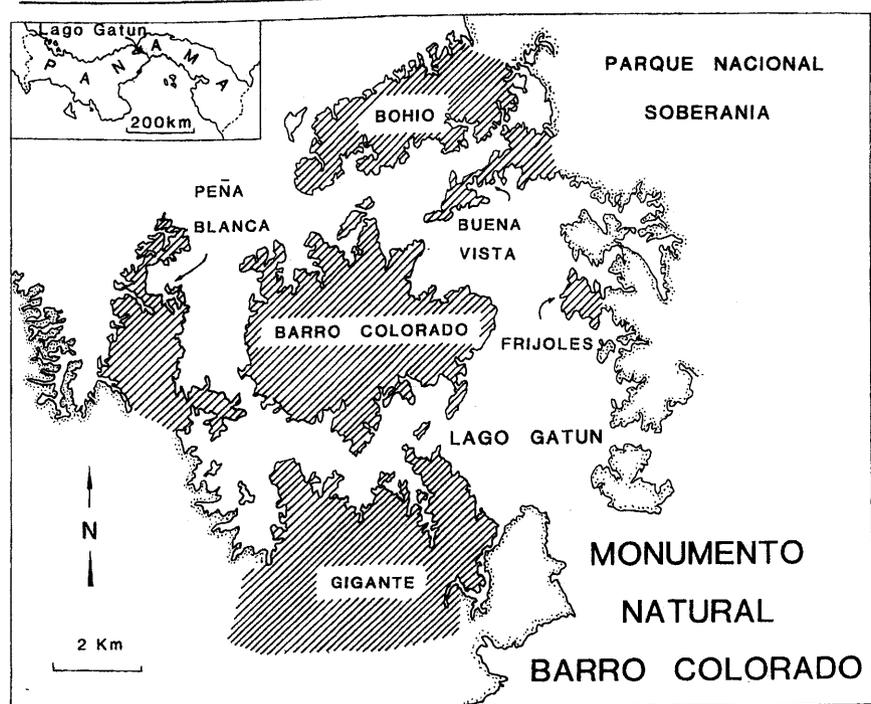


FIGURE 2.1. Map of Barro Colorado Nature Monument. This reserve includes Barro Colorado Island and five mainland peninsulas. Inset: position of the nature monument within the Republic of Panama.

consult STRI's extensive library in Panama City. Further information on facilities, availability of space, and charges for their use may be obtained from the Visitors Desk, Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Republic of Panama. Information on predoctoral and postdoctoral fellowships may be obtained from the education coordinator at the same address.

To set the work on BCI in perspective, we provide some background on climate, vegetation, and soil. We then show how the diversity of projects on BCI has provided a community-level understanding of the forest. We consider two main themes: the seasonal rhythms of the forest and their roles in limiting animal populations, and why there are so many kinds of plants and animals in the tropics.

Barro Colorado Island and its environs are covered by tropical moist forest whose canopy can attain a height of 35–40 m. Judging by the amount of litter fall and the amount of light reaching the forest floor, the

TABLE 2.1. Litter fall and light interception in different tropical forests

| | Litter Fall: g (dry weight)/m ² per year | | Total LAI ¹ | Light ² penetration (%) | Height of sensor (cm) | Understory light in sunflecks (%) |
|--------------------------|---|-------|------------------------|------------------------------------|-----------------------|-----------------------------------|
| | Leaves | Fruit | | | | |
| BCI, Panama | 789 | 127 | 1,366 | 0.3 | 61 | 0.43 |
| La Selva, Costa Rica | | | 915 | 0.9-1.5 | 70 | 0.44 |
| Central Amazonia, Brazil | 441 | | 742 | | | |
| Makokou, Gabon | 650 | 36.0 | 1,390 | 3.0 ³ | 130 | |
| Pasoh, Malaysia | 703 | 5.0 | 1,082 | 0.3 | 0 | |

Sources: BCI: litter fall is from Wright and Cornejo (1990b), leaf area index from Leigh and Windsor (1982), and light data from A. P. Smith and P. F. Becker (p.c.). La Selva: litter fall from D. W. Cole, quoted by Leigh and Windsor (1982); light data from Chazdon and Fetcher (1984: table 1) and Chazdon (1986: table 3). Brazil: litter fall from Luizao and Schubart (1987). Gabon: litter fall from Hladik (1978), light data from Hladik and Blanc (1987). Malaysia: all data from Kira (1978). Percent liana leaves in Pasoh litter is assumed equal to percent of liana leaves among the leaves weighed from a harvested plot.

1. LAI is Leaf Area Index, the number of m² of leaf per m² of ground.
2. Percent light penetration is measured as photosynthetically active radiation, except for Gabon, where radiation between 400 and 1,100 nm wavelength was measured instead. At La Selva, Makokou, and Pasoh, % light penetration is an average for shady areas; on BCI, it is the median of the rainy season averages for 400 sites, spaced 2.5 m apart along a line in mature forest, passing through light gaps and shady places.
3. Judging by Johnson and Atwood (1970: table 4), penetration of photosynthetically active radiation to 130 cm above ground level in Gabon would probably lie between 1.5% and 2%. Some far-red, but little photosynthetic, radiation passes through leaves.

forest on BCI is as productive, and suffers as intense competition for light, as tropical forests elsewhere (table 2.1; see also Leigh and Windsor 1982; Alexandre 1982).

On the southwest half of BCI, the forest has been little disturbed since the Spanish conquest. Some stands have not been cleared for two thousand years (Piperno 1989). The remainder of BCI was much disturbed during the French attempt to build a canal: its forest is clearly secondary (Kenoyer 1929; Foster and Brokaw 1982).

The island receives an average of 2,600 mm of rain a year. A sharp dry season usually begins in December and ends in April: median rainfall during the first thirteen weeks of the year is only 88 mm (compiled from Windsor et al. 1989:app.). In most years, nearly all BCI's streams cease flowing by the end of the dry season, when exposed soil is dry and deeply cracked and soil water potentials are as low as -1.6 MPa, or -16 bars (Wright and Cornejo 1990a; Becker et al. 1988). In the open, the average annual temperature is 27°C , and the average diurnal temperature range is 8°C (Dietrich et al. 1982).

The soils of BCI vary with the underlying geologic formations (Woodring 1958; M. Keller, p.c.). An andesite (R. F. Stallard, p.c.) flow underlies a central plateau of some 3 km^2 , whose highest point is 165 m above sea level. The soils of the plateau are well-weathered oxisols, as poor in nitrogen and phosphorus as the oxisols near Manaus, Brazil, and probably much poorer in potassium (M. Keller and R. F. Stallard, p.c.). Occasional "weathering spheroids" of andesite occur in the soils of this plateau, always a meter or more below the surface: these spheroids are surrounded by roots, as if competition for nutrients is fairly intense (R. F. Stallard, p.c.). Sedimentary formations of terrestrial, marine, and volcanic origins underlie the remainder of BCI (Woodring 1958). Relatively rich alfisols have developed on the terrestrial and marine sediments surrounding the central plateau. A second well-weathered oxisol, derived from sedimentary rock of volcanic origin, covers the eastern lobe of the island (M. Keller, p.c.). Conrad Stream, draining the deeply weathered soils of BCI's plateau, is hardly richer in cations than streams of western Amazonia, and hardly richer in nitrogen and phosphorus than streams of the nutrient-poor regions of central and eastern Amazonia. Lutz stream, on the other hand, which drains relatively fertile slopes near the laboratory clearing on BCI, is richer in cations than is the Amazon at Iquitos, which drains the rapidly eroding eastern slopes of the Andes (R. F. Stallard, p.c.: see table 2.2).

Curiously, the litter that falls on the "infertile" plateau is unusually

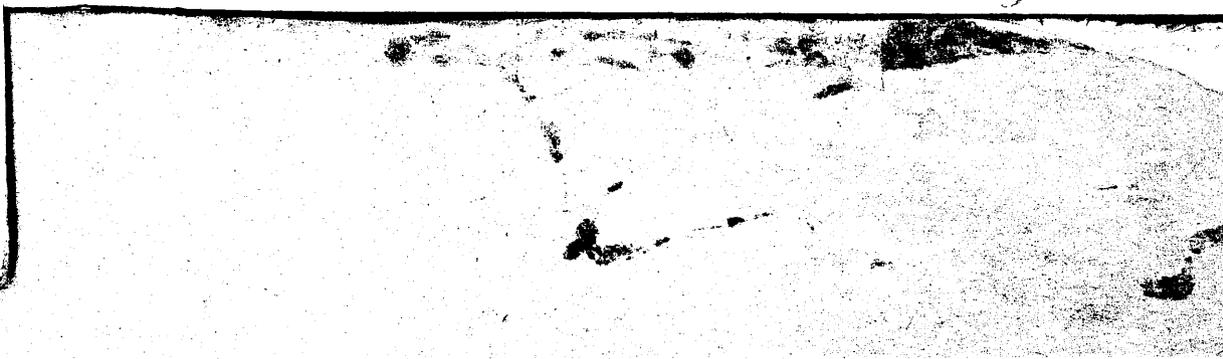


TABLE 2.2 Comparison of nutrient levels in streams and rivers of Amazonia and BCI

| | Ca ²⁺ (mg/L) | Mg ²⁺ (mg/L) | K ⁺ (mg/L) | inorganic N (mg/L) | inorganic P (mg/L) |
|---|----------------------------|----------------------------|--------------------------|-----------------------|-----------------------|
| <i>Amazonia</i> | | | | | |
| Lower Amazon River (Obidos) | 5.0 | 0.9 | 0.9 | 0.10 | 0.009 |
| Eastern Amazon Tributaries ¹ (Xingu, Tapajos, Trombetas) | 1.6 | 0.5 | 0.8 | 0.04 | 0.0012 |
| Central Amazonia (Rio Negro at Manaus) | 0.35 | 0.14 | 0.4 | 0.06 | 0.0022 |
| Western Amazonia Tributaries ¹ (Purus, Juruá, Javari) | 4.0 | 0.8 | 0.9 | 0.08 | 0.007 |
| Andean Amazon (Iquitos) | 20.0 | 2.2 | 1.2 | 0.16 | 0.022 |
| Amazon rain: showers over river ² | 0.03 | 0.012 | 0.03 | 0.04 | — |
| Amazon rain: rainfall over Manaus ³ | 0.14 | 0.12 | — | 0.28 | 0.003 |
| <i>Barro Colorado Island</i> | | | | | |
| Conrad stream | 2.6 | 1.0 | 0.5 | 0.07 | 0.002 |
| Lutz stream (at weir) | 50.0 | 4.0 | 2.2 | 0.08 | 0.010 |
| BCI rain, early wet season ² | 0.10 | 0.08 | 0.09 | 0.20 | 0.0026 |

Source: Data from R. F. Stallard

Notes: Most Amazon water samples were taken during the period of high discharge. All BCI stream samples were taken during times of free flow during the rainy season. Inorganic nitrogen includes nitrate, nitrite, and ammonia.

1. Lakes at mouths of the eastern and western Amazon tributaries may explain the low N and P values

2. These figures are based on a limited number of samples

3. These data are from an anonymous author in Amazoniana (1972), 3: 186-98

rich in nitrogen, phosphorus, and calcium (Leigh and Windsor 1982), and the flora of BCI is considered representative of tropical forest on fertile soil (Foster and Brokaw 1982). We have no explanation for this remarkable contradiction.

Tree diversity is lower on BCI than in Amazonia (Gentry, this volume). On BCI, an average hectare of old forest contains 55 species among 158 trees twenty centimeters diameter at breast height and over, whereas in Manaus 214 such trees include 126 species (Foster and Hubbell 1989:table 5). Most canopy trees and lianas on BCI have ranges extending to Amazonia, whereas most shrubs and epiphytes on BCI belong to more rapidly speciating groups with centers of diversity in the northern Andes (Gentry 1982a).

The Rhythms of the Forest

Seasons of scarcity and abundance alternate for frugivores and herbivores on BCI (Smythe 1970; Foster 1982a; Leigh and Windsor 1982). This seasonal rhythm is governed by the times when plants produce fruit and new leaves. For the forest as a whole, fruit and new leaves are both most abundant at or near the beginning of the rains. A second peak in fruit and leaf production occurs in the middle of the rainy season; a third peak in leaf production, restricted primarily to evergreen trees and understory shrubs, occurs at the beginning of the dry season (Foster 1982a; Leigh and Windsor 1982; T. M. Aide 1988).

Smythe (1970) suggested that seasonal shortages of fruit and new leaves play a fundamental role in limiting animal populations on BCI. In the season of fruit shortage, for example, the fruit supply is demonstrably too low to maintain populations of manakins and terrestrial frugivores. Manakins stop breeding in the season of shortage, spend more time foraging, and eat more insects (Worthington 1989). In the season of shortage, agoutis abandon their young at an earlier age, spend more time foraging, consume more stored food, grow more slowly, and are more likely to die (Smythe et al. 1982). The abundance of squirrels on BCI fluctuates from year to year as if governed by the effect of food supply on reproductive success (Giacalone et al. 1989). Evidence of one or more of these types suggests that on BCI most mammal populations are limited by seasonal shortage of food (Leigh et al. 1982).

Food limitation does not necessarily imply death by starvation. It can, instead, render animals more vulnerable to parasites, as in howler



monkeys (Milton 1982), or to predators, as in agoutis (Smythe et al. 1982).

To be sure, food limitation does not explain everything. The densities of territorial adults of some species of antwrens are nearly constant, fixed by the number of suitable territories (Greenberg and Gradwohl 1986); here, regulation is social. Dry weather depresses insect numbers (Levings and Windsor 1984), and birds appear to play a crucial role in protecting plants from insect herbivores (Leigh and Windsor 1982). The rhythms of some frog populations are governed by the seasonal availability of predator-free bodies of water for their tadpoles (Rand and Myers, this volume). Nevertheless, the seasonal shortage of fruit and new leaves is decisive for many mammals, as well as for many insects (Wolda 1978a).

To assess the reliability of food supplies for animals, we must decipher the cues for flowering, fruiting, and leaf flush in plants. For example, no mid-rainy-season peak of fruit production occurred in 1970, and many frugivorous mammals died. The dry season of 1970 was unusually wet, and Foster (1982b) believed that either flowering or pollination was inhibited as a result. He also found that previous famine years tended to follow wet dry seasons. Other evidence also suggested that moisture availability is an important cue for plant phenology on BCI. Leaf fall increases in apparent response to the onset of the dry season (Haines and Foster 1977; Leigh and Smythe 1978; Wright and Cornejo 1990a), and many species flower and flush leaves in apparent response to the onset of the rainy season (Croat 1978; Leigh and Windsor 1982; Coley 1982).

"Rain flowers" provide another example for which moisture availability seems to govern phenology. These species typically flower synchronously after a dry season rain. On BCI, the shrub *Hybanthus prunifolius* flowers synchronously several days after a heavy rain in February, March, or April. Augspurger (1982) induced flowering in February and March by watering the roots of the shrubs concerned just once. Individuals watered every third day through most of the dry season did not flower, however, as if bud break in *Hybanthus* requires a dry period followed by release from water stress. Unfortunately, Augspurger's experiment stopped before a rain that could have triggered flowering occurred.

One of us, SJW, has undertaken a large-scale manipulation of soil moisture availability to determine how soil moisture affects the seasonal rhythms of the forest on BCI. Two 2.25-ha plots of mature forest are being irrigated throughout the dry season, starting in 1985–86 and ending in 1989–90. Irrigation keeps the soil in the root zone saturated (over

-0.04 MPa) throughout the year, while in nearby control plots soil moisture potential falls to -1.6 MPa late in the dry season. The effect on plant water status is equally dramatic. Late in the dry season, midday water potentials of plants in the irrigated plots are similar to rainy season values recorded for some of the same species by Rundel and Becker (1987) and are significantly greater than values recorded during the dry season for these species in the control plots (Wright and Cornejo 1990b).

Preliminary results from this experiment indicate that increasing soil moisture content has little effect on the phenology of most trees, treelets, and lianas. Fruit production has not failed in the irrigated plots. For most species of trees and lianas, the timing of flowering is indistinguishable in irrigated and control plots, although irrigation did delay leaf fall in *Dipteryx panamensis*, greatly delayed flowering in *Tabebuia guayacan*, and disrupted the synchrony of flowering within and between *Tabebuia* individuals (Wright and Cornejo 1990a). Irrigation had no effect on the seasonal rhythm of leaf fall in the forest as a whole (Wright and Cornejo 1990b). Moreover, patterns of leaf fall in many species of trees and lianas were scarcely affected (Wright and Cornejo 1990a).

Yet some shrubs have responded to irrigation. Irrigation has advanced leaf and flower production by two to four weeks in several species of *Psychotria*. After three years of irrigation, synchrony of their leaf production is steadily declining, suggesting the breakdown of an endogenous circannual rhythm normally reset and synchronized by seasonal changes in humidity or soil moisture (SJW, unpubl. data). Other shrubs, however, have not responded. Irrigation inhibited gregarious flowering in *Hybanthus* less than 2 m tall, but taller *Hybanthus* flowered simultaneously in control and irrigated plots (SJW, unpubl. data), in remarkable contrast with the predictions of Augspurger (1982).

We do not yet understand what aspects of the seasonal rhythm in climate control plant phenology. In singling out rainfall, early students of BCI may have repeated the error of the early students of dipterocarps in Malaysia. There, the drop in nocturnal air temperature following the end of prolonged, unusually high insolation appears to trigger gregarious flowering (Ashton et al. 1988): the end of a prolonged drought had previously been thought to be the cue.

The timing or intensity of flowering may depend not only on the climate of the moment but also on the intensity of flowering in the previous year. On BCI, *Faramaea occidentalis* treelets that put out unusually many flowers one year tend to put out unusually few the next, and vice versa (E. W. Schupp, p.c.). The same appears true for fruit production



in the canopy tree *Dipteryx panamensis* (Smithsonian Environmental Sciences Program, unpubl. data). Once again, the clearest example is provided by Malaysian dipterocarps: the stimulus required for gregarious flowering is weaker, the longer the time elapsed since the previous episode of gregarious fruiting (Van Schaik 1986). Obviously, we need to learn far more about the physiological mechanisms governing the timing of flowering, fruiting, and leaf flush.

What role do these rhythms play in the life of the forest? Some believe that natural selection on seasonal rhythms of fruit and leaf production "assembles" a community-wide rhythm that protects the forest from its herbivores and helps seed dispersal (Sabatier 1985; Leigh and Windsor 1982; Charles-Dominique et al. 1981; Foster 1982a). Chan (1980) and Janzen (1974) have argued that the community-wide synchrony of fruiting in Malaysian dipterocarp forests reflects adaptive design. There, trees of many species fruit synchronously in apparent response to a common signal (Ashton et al. 1988), but flowering, though necessarily a response to the same signal, is much less synchronous, perhaps allowing more efficient use of pollinators (Chan and Appanah 1980). Fruits produced at times other than a synchronized mass fruiting are usually damaged (Chan 1980). By contrast, Gautier-Hion et al. (1985) see no sign of adaptive design in the phenological rhythms of rain forest in Gabon.

On BCI, natural selection imposed by herbivores reinforces the seasonal rhythms of many plants. Understory shrubs on BCI concentrate their leaf production near the beginning of the dry season and again during the peak of canopy leaf flush at the beginning of the rains (Aide 1988). By synchronizing leaf production in this way, plants create a temporary surfeit of new leaves, many of which survive because there are too few herbivores to eat them (Coley 1982). Shrubs that produce new leaves out of turn are more likely to lose them to herbivores (Aide 1988). Natural selection within populations for herbivore avoidance thus strengthens the community-wide rhythm.

On BCI, the best evidence for adaptive design in the flowering and fruiting times of species comes from Augspurger's (1981, 1982) studies of *Hybanthus prunifolius*. Individuals that flower out of synchrony attract fewer pollinators, more seed predators, and mature one-tenth as many seeds as individuals flowering in synchrony with many conspecifics. Seasonal rhythms may originally have evolved in response to seasonal drought, but they persist in its absence and play a fundamental role in limiting animal populations, even in ever wet forests (Fogden 1972; Terborgh 1986).

The Diversity of Tropical Communities

Our discussion of the rhythms of the forest drew on results from fields as diverse as ethology, plant physiology, and community ecology. Understanding why there are so many kinds of plants and animals in the tropics depends on a similar variety of approaches.

Trade-Offs and Specialization

The understanding of biotic diversity begins with an understanding of the trade-offs that lead to specialization. On BCI, "pioneer" trees are specialized for treefall gaps of differing sizes (Brokaw 1987). *Trema micrantha* survives only in large gaps, but they are the tallest plants in these gaps, growing up to 7 m per year. *Cecropia insignis* survive only in large and mid-sized gaps but are the tallest plants in mid-sized gaps, growing up to 5 m per year. *Miconia argentea* survives in small gaps but grows no more than 2.5 m per year. This specialization appears to be enforced by a trade-off between growing quickly in large gaps and surviving in smaller ones (see also Oberbauer and Strain 1984). This trade-off implies that the "jack of all trades is master of none": no one species can dominate, or even persist, in gaps of all sizes. Each species does best in a particular type of gap, governed in part by its adjustment of the trade-off between rapid growth in well-lit large gaps and survival in poorly lit small gaps.

Hogan (1986) has analyzed the mechanisms which, in two midstory palms, enforce the trade-off between surviving economically in the shade and using sunlight fully when in the open. *Scheelea* leaves photosynthesize more effectively (fix more carbon per unit leaf area) than *Socratea*'s, *Scheelea*'s leaves overlap more, and they are less horizontal. Thus *Scheelea* needs more light to grow at all but uses abundant light more effectively. Yet *Socratea* leaves photosynthesize more effectively in the shade than *Scheelea*'s, and *Socratea*'s leaf arrangement is more suited to using dim light effectively. Mulkey (1986) has analyzed the trade-off between adaptability to different light levels and economical survival in the shade among three species of understory bamboo. The one species flexible enough to grow leaves with increased photosynthetic capacity when in the sun has leaves needing more light to "break even" when grown in the shade.

Predatory robberflies (Asilidae) face an analogous trade-off between foraging in light gaps and foraging in the shade (Shelly 1984). Basking in light gaps increases body temperature, allowing quicker take-off and

speedier, more maneuverable flight, but the physiology that makes an insect more effective in light gaps makes it more torpid, and less effective, in the shade.

The antbirds that follow swarms of army ants over the forest floor, consuming the insects flushed by these ants, also face a trade-off. The antbirds most capable of dominating their competitors at antswarms feed at the head of large swarms, where the most insects are flushed, but they cannot feed away from antswarms and are absent from the smallest swarms, which flush the fewest insects. Less dominant species, which feed at smaller swarms and at the less productive margins of large swarms, can feed more effectively away from antswarms (Willis and Oniki 1978).

Specialization, Population Fluctuations, and Extinction

If, as in the examples above, the jack of all trades is master of none, selection leads to specialization. The more specialized a species, however, the more sensitive its members will be to environmental variation, and the more its population will fluctuate in response to this variation. This suggests that species specialize as much as the variability, or predictability, of the environment allows: the more stable the environment, the more species can coexist therein (Levins 1968).

Although rainfall is unpredictable at any latitude, tropical environments are more stable than their temperate-zone counterparts because seasonal variation in temperature is much lower in the tropics (Allee 1926). Does greater stability of tropical environments reduce population fluctuations or enhance species diversity? To answer this question, the Smithsonian's Environmental Sciences Program monitors fluctuations in aspects of the physical environment, and appropriate biotic responses, on BCI, at a reef flat on the Caribbean coast of Panama, and at aquatic and terrestrial sites near Edgewater, Maryland (Windsor 1975; Correll 1975).

The amplitudes of population fluctuation vary enormously on BCI. The normally abundant understory lizard *Anolis limifrons* fluctuates greatly in numbers, more than any lizard yet reported from the temperate zone (Andrews and Rand 1982, 1989), whereas the densities of territorial adults in some antwren populations are nearly constant (Greenberg and Gradwohl 1986). In general, insect populations fluctuate as much on BCI as they do in the temperate zone (Wolda 1978). The evidence from BCI does not suggest that tropical populations vary less than their temperate-zone counterparts.

There does appear, however, to be a connection between the ampli-

tude and rapidity of a population's fluctuations and its prospects of extinction. Since Barro Colorado is an island, the relation between population fluctuations and susceptibility to extinction is of great interest (Leigh 1982). The understory bird species that have disappeared from Barro Colorado since it became an island are those whose mainland populations vary most or whose individuals are shortest-lived. Curiously, rarity has little to do with it (Karr 1982, this volume). More generally, homeotherms have disappeared more rapidly from BCI than poikilotherms (Wright 1981).

Although specialization is a volatile concept, difficult to define operationally, Willis (1974) feels that on BCI those ant-following antbirds that are more specialized are the ones whose populations fluctuate more, and the ones that were most specialized to (most dependent on) feeding at antswarms are the ones that have now disappeared from BCI.

Environmental Stability and Plant Diversity

Trade-offs between quick growth in large gaps and survival in small ones, between efficient use of bright sunlight and economical existence in the shade, or between effective use of water on wet soils and minimizing water loss on dry ones, allow trees to specialize to different sizes of light gaps, different strata of the forest, or different soil types. Nevertheless, many of the most common tree species on BCI are distributed without regard to availability of soil moisture or the time elapsed since the last major treefall (Hubbell and Foster 1986).

Trade-offs can enhance tree diversity by a different means, however. Trade-offs between detoxifying different compounds cause specialization on a grand scale among those insects that eat seeds or seedlings (Janzen 1975; Gilbert 1979). Plants can escape their enemies by inventing novel defenses.

Such pests as seed and seedling predators may also enhance species diversity by creating space for trees of other species to grow between a tree and its offspring (Gillett 1962). A tree can reduce the damage to its seeds and seedlings by dispersing its seeds effectively. The advantages of seed dispersal have been shown for several species on BCI and elsewhere (Howe et al. 1985; Augspurger 1984; Wright 1983; Clark and Clark 1985). Dispersal is not always advantageous. Schupp (1987) found that where there are 100–200 adult *Faramea occidentalis* treelets per ha, seeds dispersed 5 m from parent crowns were two to six times more likely to survive and germinate than seeds under the parent, but that in tracts with



300 adults per ha, dispersal reduced a seed's survival prospects by 30%. Because 11 of the 50 ha in the plot of old forest on BCI mapped by Hubbell and Foster (1986) each contain over 275 adult *Faramia*, dispersal must often be disadvantageous for this species. Seed dispersal nevertheless appears advantageous for most kinds of plants on BCI. In their 50-ha plot, where every stem 1 cm or more in diameter has been mapped, Hubbell and Foster (this volume) find that saplings whose nearest neighboring canopy tree is a conspecific grow more slowly, and die more quickly, than those whose nearest canopy neighbor is of another species.

If pest pressure is to allow so many more kinds of trees in the tropics, then pest pressure must be higher there. Is this true? One might expect so, since tropical pest populations suffer less from "harsh" seasons than their temperate-zone counterparts. In the Neotropics, moreover, tree diversity is highest in those lowland rainforests where rainfall is least seasonal (Gentry 1982b) and where pest populations presumably suffer least from harsh seasons. Nevertheless, Coley (1982) noted that insect damage to leaves is no higher on BCI than in various temperate-zone forests. This observation is not necessarily inconsistent with the idea that pest pressure contributes to latitudinal gradients in plant diversity. Pest pressure may be more influential in the tropics, but damage may be reduced by the diversity of tropical plants or by increased investment in defense. Neither proposition will be easy to demonstrate.

Interdependence and Diversity

Another feature enhancing tropical tree diversity is the complex web of mutualisms that plants have evolved with pollinators, dispersers, and the like. These mutualisms can be quite subtle. The understory shrub *Hybanthus* must flower in synchrony to create a blaze of bloom sufficient to attract its pollinators from the canopy: in turn, synchronized flowering enhances survival of the seeds (Augsburger 1982). Two vegetatively different species of the understory herb *Costus* have evolved similar flowers, cooperating, as it were, to provide sufficient flowers to command the attention of their shared pollinator (Schemske 1981). By the way its fruit are designed, packaged, and displayed, *Virola* attracts toucans to disperse its fruits while repelling other frugivores (Howe 1982). Toucans carry these seeds far enough away that the seeds' chances of survival, germination, and establishment are forty-four times higher than those of seeds under the crown of the parent (Howe et al. 1985).

Mutualisms among plants and the dispersers of their seeds or the

defenders of their leaves can be strict. Seeds of the palm *Astrocaryum* cannot survive to germinate unless agoutis peel the flesh from them and bury them (Smythe 1989). These mutualisms can also be perverted in strange ways. The pioneer tree *Croton billbergianus* uses extrafloral nectaries to attract ants to patrol its leaves and defend them from herbivores. Caterpillars of the riodinid butterfly *Thisbe irenea* consume the fluid from these nectaries and transform it into a fluid that the ants prefer. The ants accordingly defend the caterpillars rather than the leaves that the caterpillars eat (P. DeVries and I. Baker, 1989).

Populations of dispersers, seed-eaters, and seedling-browsers vary asynchronously. The incredible variety of seed and seedling defenses, modes of pollination, and dispersal strategies, many possible only in the tropics, may cause different trees to achieve maximum reproductive success in different years. Theory suggests that such "temporal sorting" of reproduction enhances tree diversity (Chesson and Warner 1981). This idea warrants further study.

How general are the conclusions one might draw from BCI? Barro Colorado has been an island since 1914. Large predators (pumas, jaguars, and harpy eagles) are essentially absent from the island. The island does not include the diversity of habitats available to mobile animals in some mainland areas. Moreover, BCI represents part of a narrow isthmus, which never had the diversity of plants and animals characteristic of core areas in Amazonia. What difference do these limitations make?

The obvious point of comparison is Manu National Park, Peru (Terborgh, this volume). The floristics of the two sites are similar (Foster, this volume), as are their annual rates of fruit fall and their total biomass of frugivores (Terborgh 1986). Both places are noteworthy for their abundance of mammals, and in both, fruit shortage plays a dominant role in limiting frugivore populations (Terborgh 1986). Manu, however, has jaguars, pumas, and harpy eagles, although the abundance of ocelots is the same ($0.8/\text{km}^2$) in both places (Emmons 1987; Glanz, this volume), and both sites harbor several large eagles and hawk-eagles. In Manu, pumas eat many agoutis and pacas, the two mammal species that are unusually abundant on BCI, but the abundances of most other mammals on BCI accord reasonably well with those of other Neotropical sites where jaguars do live (Glanz, this volume). Absence of big cats seems an insufficient basis for denying the conclusions BCI suggests concerning the significance of seasonal rhythms of fruit and leaf production or the causes of tropical species diversity.

The restricted habitat diversity of BCI seems, at first sight, a more valid reason to limit the generality of conclusions drawn from the island. Barro Colorado has nothing comparable to the amazing diversity of successional habitats, with a diversity of inhabitants to match, created by the wanderings of the Rio Manu. So stunning a diversity of habitats, however, is not to be found in upland sites such as Lovejoy and Bierregaard (this volume) describe. Nor was there such diversity of habitats near BCI before 1800. The valley of the Chagres, which was relatively narrow near Barro Colorado, gave its river far less room to wander than Manu now has.

Studies on BCI have played an important role in the development of tropical biology. Today, the legacy of sixty-five years of research is available to build on, providing a perspective essential to interpreting the significance of current research and an unparalleled foundation for attacking new questions. More than thirteen hundred publications on the biota of BCI are available for consultation on that island: these are indexed to species.

Until recently, the successes of BCI were based largely on skillful fieldwork. Recent additions to the BCNM and projected improvements in laboratory facilities will allow new problems to be tackled and will enable a more detailed analysis of processes and mechanisms. The mainland peninsulas include areas of early successional forest and offer opportunities for large-scale field experiments. The new facilities will place modern laboratories at the edge of the Neotropical forest.

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