

ECOLOGICAL IMPLICATIONS OF CHANGES IN DROUGHT PATTERNS: SHIFTS IN FOREST COMPOSITION IN PANAMA

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Abstract. CO₂ concentration is increasing, temperature is likely to rise, and precipitation patterns might change. Of these potential climatic shifts, it is precipitation that will have the most impact on tropical forests, and seasonal patterns of rainfall and drought will probably be more important than the total quantity of precipitation. Many tree species are limited in distribution by their inability to survive drought. In a 50 ha forest plot at Barro Colorado Island in Panama (BCI), nearly all tree and shrub species associated with moist microhabitats are declining in abundance due to a decline in rainfall and lengthening dry seasons. This information forms the basis for a simple, general prediction: drying trends can rapidly remove drought-sensitive species from a forest. If the drying trend continues at BCI, the invasion of drought-tolerant species would be anticipated, but computer models predict that it could take 500 or more years for tree species to invade and become established.

Predicting climate-induced changes in tropical forest also requires geographic information on tree distribution relative to precipitation patterns. In central Panama, species with the most restricted ranges are those from areas with a short dry season (10–14 weeks): 26–39% of the tree species in these wet regions do not occur where it is drier. In comparison, just 11–19% of species from the drier side of Panama (18 week dry season) are restricted to the dry region. From this information, I predict that a four-week extension of the dry season could eliminate 25% of the species locally; a nine-week extension in very wet regions could cause 40% extinction. Since drier forests are more deciduous than wetter forests, satellite images that monitor deciduousness might provide a way to assess long-term forest changes caused by changes in drought patterns.

I predict that increasing rainfall and shorter dry seasons would not cause major extinction in tropical forest, but that drying trends are a much greater concern. Longer dry seasons may cause considerable local extinction of tree species and rapid forest change, and they will also tend to exacerbate direct human damage, which tends to favor drought-adapted and invasive tree species in favor of moisture-demanding ones.

1. Introduction

Dry season duration is probably the single most important environmental factor affecting the distribution of tropical trees and forests. Forest structure and composition correlate with total precipitation (Holdridge et al., 1971; Gentry, 1988), but in most cases this results from a correlation with dry season length, which in turn correlates with total rainfall. Other factors, such as soil nutrients, temperature, biotic interactions, and history, have secondary effects. Clearly, in regions where rainfall patterns are constant over wide areas, such as Sarawak in Borneo, the Congo basin, or western Amazonia, factors other than rainfall seasonality must take the primary role in determining forest composition (Ashton, 1977; Hart et al., 1989; Tuomisto et al., 1995), but in areas with sharp gradients in rainfall, such as Central America or southern India, the most conspicuous spatial variation in forest composition is

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caused by differences in drought patterns. This is why Hartshorn (1992) predicted that shifts in rainfall patterns will be the key climatic change in tropical forests. Year-to-year variation in dry season length will also be important, since occasional extreme droughts can have a disproportionately large impact (Woods, 1989; Leigh et al., 1990).

Predicting the impact of changes in drought patterns on tropical forests requires information on the distribution and performance of species relative to climate. Forest models can then be run under different climate scenarios to predict long-term impacts. There is a successful history of this approach in the temperate zone (Delcourt and Delcourt, 1987; Overpeck et al., 1990; Shugart and Smith, 1992; Urban et al., 1993), but the data needed for tropical forest models are not available. Few records of quaternary forest distributions exist (Bush et al., 1990; Hamilton and Taylor, 1991; Sukumar, et al., 1993), and climatic effects on the demography and distribution of individual species are seldom known. The Center for Tropical Forest Science is attempting to remedy this data shortage with its network of large, permanent plots distributed throughout the major tropical forest blocks of the world (Manokaran et al., 1992; Sukumar et al., 1992; Condit, 1995). Each plot provides demographic data on tens or hundreds of species, most never before studied in detail. Currently, there are eight large plots completed and four more underway, and eventually close to 5000 species will be studied. But other kinds of data will be needed to predict the impact of climatic change; in particular, geographically extensive information on species distribution relative to climate must complement demographic data from single sites.

Here I examine how forests respond to changes in the dry season with a case study: the forests in and around the large plot on Barro Colorado Island in Panama. The data available allow two complementary approaches. First, I directly assess forest response to climatic change by reviewing published studies on how supra-annual shifts in the length of the dry season have affected the forest (Leigh et al., 1982; Condit et al., 1992, 1995, 1996a,b). Second, I use data from forests around Barro Colorado to examine how forest composition correlates with spatial variation in the duration of the dry season; this offers an indirect means of predicting how the forest might respond to climatic change. Based on these two approaches, I will make a series of predictions on how future changes in drought patterns might affect tropical forests.

2. Background

2.1. THE FOREST

A corridor of forest 15–20 km wide and 65 km long stretches from the Pacific coast to the Atlantic coast along the banks of the Panama Canal. Much of this forest has been disturbed in the last two centuries, particularly on the Pacific side, but there are



Figure 1. Map of central Panama, showing sites of the 50 ha plot on BCI, the 4 ha plots at Cocolí and Fort Sherman, and 13 other forest inventory sites. The Santa Rita and Metropolitano sites had one 20 × 20 m plot each, Fort Sherman had two (apart from the 4 ha plot), El Charco three, and Gamboa seven; six sites at Pipeline Road had a total of 13 small plots. The Cuatro Calles site and the most northwestern site at Pipeline Road had no plots, but only presence-absence inventories of 1 km².

patches of old-growth forest on the Atlantic side, including Barro Colorado Island (BCI). BCI holds 1500 ha of diverse, moist, lowland tropical forest and is the home of a Smithsonian Tropical Research Institute reserve. It has been completely protected from human disturbance (other than research) for 70 years, and most of the island (including 48 ha of the 50 ha forest-dynamics plot) has seen no human disturbance for over 500 years (Foster and Brokaw, 1990; Piperno, 1990).

2.2. THE CLIMATE

Total annual rainfall increases from the Pacific coast toward the Atlantic in Panama, from 1600 mm per year in Panama City to about 4000 mm at some sites along the Atlantic (Windsor et al., 1990, Figure 1). Rainfall is highly seasonal, mostly falling from April through December (Windsor et al., 1990), but because total precipitation is higher on the Atlantic side, the duration of the dry season is shorter there (defining the dry season as the period when rainfall is less than evapotranspiration, which I estimate as 100 mm per month). Thus, the mean dry season is 129 days near Panama City, 107 days at BCI, and 102 days near the Atlantic side (Figure 2). The wettest site in the region is on the Santa Rita ridge at about 400 m elevation (Figure 1), where the dry season is only 67 days and the driest months are only slightly below evapotranspiration (Figure 2).

Of special interest from the perspective of climatic change is the abrupt 14% decline in rainfall that began at BCI around 1966 (Windsor et al., 1990; Condit et al., 1992). This decline has been observed only in the center of the isthmus, not near either coast (Windsor et al., 1990), but it has been registered at many other sites in the northern tropics (Diaz et al., 1989).

2.3. THE CENSUSES

All free-standing woody stems ≥ 10 mm in dbh (diameter at breast height) in the 50 ha plot on BCI were censused and measured in 1981–1983, 1985, 1990, and 1995 (Hubbell and Foster, 1983, 1986, 1990; Condit et al., 1992). In 1994, the same methodology was used to census 4 ha of forest on the Pacific side of the isthmus, about 5 km from Panama City, near the Rio Cocolí (Figure 1). The latter plot is in the most mature forest that could be found near the Pacific coast – about 100 years old – and is thus much younger than the BCI forest. In 1996, another 4 ha plot was censused at Fort Sherman near the Atlantic coast (Figure 1); this site has mature forest, but appears to have suffered some logging or clearing in the last 150 years.

In addition, I report inventories from 27 smaller plots (20 m \times 20 m) across the isthmus. These data are preliminary, as sampling effort to date is uneven, but they allow broad conclusions about species' ranges relative to climate. All trees and shrubs ≥ 10 mm dbh were mapped and identified in each plot. The 27 plots are grouped into 11 sites, with one to seven small plots within 1 km² at each site (Figure 1). Additional inventories were carried out at two of the sites (Metropolitano, Gamboa) by walking two times across the surrounding square kilometer (taking 5–8 hours) and recording every species seen; these walks were also done at two more sites where no plots were established (Figure 1). The sites at Pipeline Road, BCI, and Santa Rita are in old growth forest, while the small plots at Fort Sherman and everywhere from Cuatro Calles toward Panama City are in secondary forest, probably 60–150 years old (Figure 1).

A total of 674 native tree and shrub species were recorded in all the inventories and plots. One-hundred-and-twenty-six of these were ‘morphospecies’, recognized consistently but not named to species (most were named to genus). For assessing species ranges, inventories were pooled into three groups: 0–20 km from the Pacific Coast (Cocolí, Metropolitano, El Charco), 0–20 km from the Atlantic Coast (Sherman, Santa Rita), and in between (BCI, Pipeline Road, Cuatro Calles, Gamboa), and only presence-absence data were used.

3. Drought at BCI

3.1. PHENOLOGY AND THE DRY SEASON

The annual dry season is without question the main controlling agent of the BCI forest. Few aspects of the island’s biology do not hinge on the annual drought, indeed, seasonality has been a main focus of research there (Leigh et al., 1982). I will not review the many examples of drought-controlled seasonality presented in Leigh et al. (1982), covering most animal and plant groups. Instead, I will focus on key points relevant to predictions on the impact of future climatic change.

Most tree species flower and fruit seasonally at BCI. Different species show different patterns relative to the rains, but a common pattern is to flower during the dry season and to fruit during the first half of the wet season (Croat, 1978; Foster, 1982a). Interestingly, during and after unusually wet dry seasons, many species fail to flower and fruit (Foster, 1982b). Foster (1982b) documented failures in 1931 and in 1970, and J. Wright and O. Calderón (Smithsonian Environmental Sciences Program, unpub. data) have an even more complete description for a 1993 failure. Their data include nine years of quantitative information on fruit and flower production for over 400 tree species within the 50 ha plot, and clearly show the annual cyclicity and the 1993 failure (Figure 3). J. Wright (pers. comm.) hypothesizes that the 1993 failure was caused by a wet dry season in 1993 that followed the year of high fruit production in 1992 (Figure 3). Animals clearly suffered during these fruit failures: mammals died at unusually high rates (Foster, 1982b), and several large birds disappeared from BCI during the 1993 wet season (J. Wright, pers. comm.). Short-term climatic fluctuations can thus have a dramatic impact on both animal and plant populations at BCI. Climatic effects on plant phenology are also well-documented in Asian forests (Corlett and LaFrankie, 1998).

3.2. LONG-TERM CHANGES IN PRECIPITATION AND THE BCI FOREST’S RESPONSE

Before 1966, one year in six at BCI had <100 mm of rain during the dry season (mid-December to mid-April), but since 1966, one in three has (Condit et al., 1996b). This drying trend was punctuated by an extreme drought in 1983, associated

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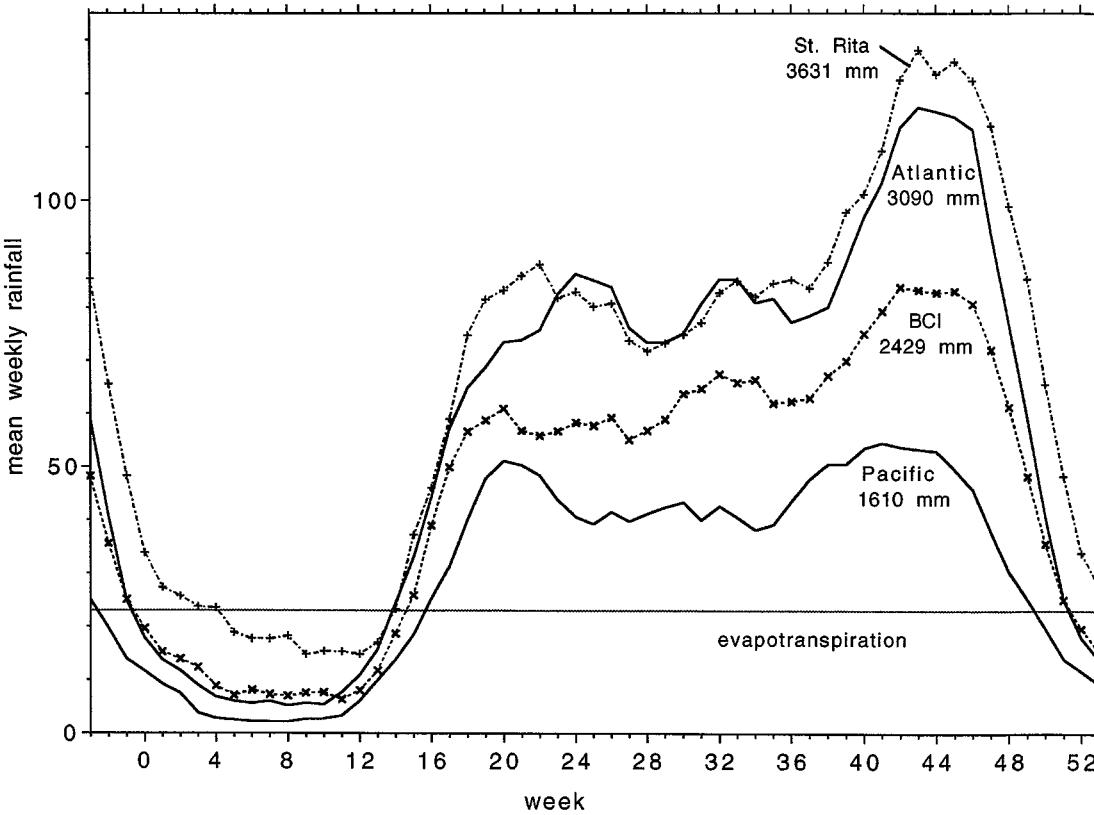


Figure 2. Weekly rainfall at four sites in central Panama, from 27 years of Panama Canal Commission data (Windsor et al., 1990; S. Paton, unpub. data from the Smithsonian Environmental Sciences Program). The mean for each week was calculated from all 27 years then smoothed by a 5-point running average. The horizontal line is at 23 mm per week, equivalent to 100 mm per month. The total mean annual rainfall is also given for each site. The Pacific site is near Panama City, the Atlantic near Colón; BCI and Santa Rita are indicated on Figure 1.

with a strong El Niño event. During early 1983, just 3 mm of rain fell over a 12-week period and temperatures were 2 °C above normal (Leigh et al., 1990).

The 50 ha plot has allowed precise documentation of the impact of the drying trend. The 1983 drought killed 4.3% of all trees ≥ 200 mm dbh, above and beyond the background mortality (2% per year; Condit et al., 1995). Smaller trees were less affected. Of 205 tree species examined, 70% had higher mortality during the drought interval than during 1985–1990 (Condit et al., 1995). But the forest responded very quickly to the excess mortality: tree growth was elevated during the drought, and increased recruitment into the canopy layer made up for the excess mortality. By 1985 the total density of trees in the canopy layer was similar to the 1982 density (Condit et al., 1992).

Other structural aspects of the forest showed no sign of change between 1982 and 1990. None of the following groups changed in abundance: canopy trees, treelets, shrubs, deciduous species, nor pioneer species (Condit et al., 1996a). If the long-term drying trend is having an effect on these structural features of the forest, it has not shown up yet.

At the level of species composition, though, the long-term drying trend has had an impact. One subset of species is declining markedly in abundance: those defined as moisture-demanding by an independent criterion (their abundance in the moist regions of the 50 ha plot; see Condit et al., 1996a; Condit, 1997; Harms, 1997). There were 37 species which were defined as moisture-demanding in at least one of the four censuses by this criterion, and 33 of these declined in abundance between 1982 and 1995 (Condit, 1997; note that these figures have been updated since Condit et al., 1996a, b). One of these moisture-specialists, *Poulsenia armata* (Moraceae), is a large, prominent canopy species that has undergone a striking crash, from 3426 stems in 1982 to 1777 stems in 1995. But it was small-stature moisture-specialists (shrubs and treelets) that were most affected: 17 of 18 declined in abundance, one went extinct (the tree-fern *Cnemidaria petiolata*), and their total abundance fell by 35% over 13 years (Condit, 1997). These moisture-demanding species presumably have shallow root systems and require moist soils throughout the year (Condit et al., 1996b). They were able to invade the plot during the wetter period prior to 1966, but can no longer persist.

The 37 moisture-specialists represent 12% of the 314 species recorded in the plot. If drying trends continue, it seems likely that most of these 37 will be lost within 25 years. The entire genus *Piper* – a well-known wet forest group – may be lost, as all eight species have suffered population declines, several precipitous (Condit et al., 1996b). But so far, the decline of moisture-demanding species has been mirrored by an increase in the number of individuals of drought-tolerant trees and shrubs, and the overall structure of the forest has not changed (Condit et al., 1996a).

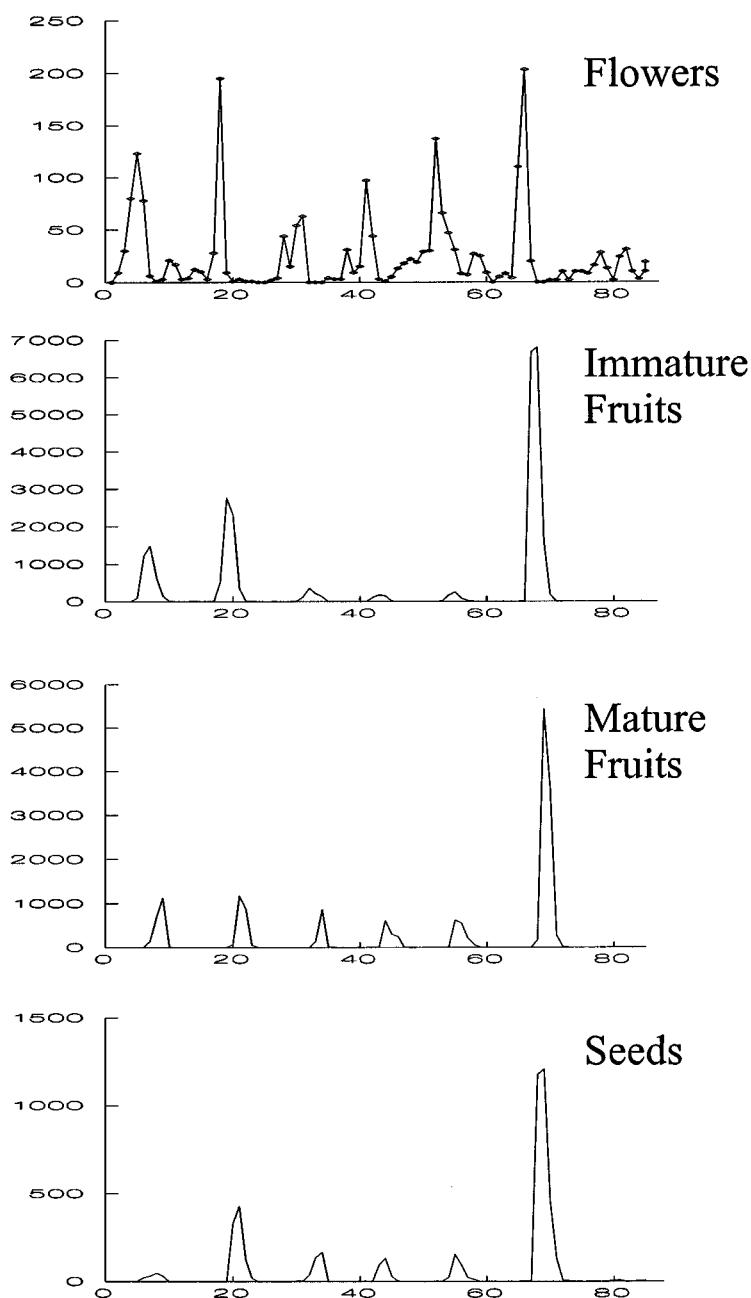


Figure 3. Phenology of flower, fruit, and seed production in *Trichilia tuberculata* (Meliaceae), as estimated by total counts of reproductive parts in 200 permanent traps in the 50 ha plot on BCI. Traps are 0.7 m × 0.7 m, supported 1 m above the ground. Time is given on the horizontal axis in months since January, 1987 (data courtesy of J. Wright and O. Calderón, Smithsonian Environmental Sciences Program). Note the low number of seeds and lack of mature fruits around month 80 (September, 1993), during the usual season of fruit fall.

4. Variation in Dry Season Length at Wider Scales

4.1. SPECIES DISTRIBUTIONS

The pattern observed at BCI, where certain tree species are limited to moist regions, is a microcosm for the Central American isthmus. At this wider scale, species' distributions are certainly limited by drought intensity, and quantifying the number of species so limited and their precise ranges is critical for making predictions about how a changing climate will affect the forests.

The forest inventories across the isthmus give preliminary indications of what fraction of the tree and shrub species are restricted by the climatic gradient. Most species of the drier Pacific coast have distributions reaching across to the Atlantic side of the isthmus, while <20% are restricted to the Pacific coast (Figure 4). Species from the two Atlantic sites are more restricted, with <50% having ranges that extend the 65 km to the Pacific side and >25% restricted to the Atlantic coast (Figure 4). The very wet site on the Santa Rita ridge has the highest fraction of restricted species, 39% (Figure 4).

These data suggest that a four week increase in the length of the dry season – the difference between Fort Sherman and Cocolí – would be sufficient to eliminate 25% of the species. A nine-week increase (Santa Rita to Cocolí) could cause 40% extinction. A decrease in dry season length would have a lesser impact, because fewer species are restricted to the dry sites. These inventories are preliminary, however, and the conclusions should be interpreted with some caution. For one, some of the restricted distributions may not be due to climate (Condit, 1996). Moreover, some species that appear restricted may yet turn up elsewhere, and conversely, more complete inventories might uncover additional species with restricted distributions. I have already begun a more rigorous sampling program, with more plots carefully placed to separate the impact of climate from other factors. Meantime, the comparison of the wettest and the driest sites should be an unbiased result – the wettest site has the higher fraction of restricted distributions and would be more prone to lose species when faced with a changing climate.

4.2. DECIDUOUSNESS

As predicted, deciduousness follows the moisture gradient. At Cocolí, 37% of canopy species are deciduous, at BCI, 25%, and at Fort Sherman, 14% ($n = 38$ species at Cocolí, 143 at BCI, and 64 at Sherman; canopy species are those reaching 300 mm dbh). At the peak of leaf loss in late February to March, 1997, 30.3% of canopy individuals were deciduous at Cocolí, 6.5% at BCI, and 4.8% at Sherman (K. Watts and R. Condit, unpub. data; these figures are lower than the percent of species, or the percent of individuals given in Condit et al., 1996a, because not all individuals are deciduous simultaneously).

Deciduousness should provide an indicator of rainfall seasonality, since it is generally associated with seasonal drought in the tropics. Quantitative estimates of

deciduousness may provide a means for predicting species ranges as well as other forest characteristics. Since deciduousness ought to be fairly easily measured from satellites, it may be a key parameter for studies on the effect of climatic change on tropical forests. Estimates such as the ones from these three plots can be used as ground truth for satellite studies, and need to be made at many more sites in tropical forests.

5. Drought and Reforestation

The most important impact of changing drought patterns in tropical forests in Central America may be on reforestation. There is plenty of abandoned farmland in Panama, ripe for reforestation, but which remains covered in grass. Along the Pacific slope of Panama, the single most important factor preventing natural forest regeneration is fire. In 1993, I began a research project on the growth of native trees in abandoned grassland (*Saccharum spontaneum*) near the Barro Colorado forest, planting 4500 tree seedlings at 90 sites. Fires were excluded by firebreaks, and during the 1994 dry season, fires in the area did not enter the plots. In April, 1995, however, most of the 'protected' plots in tall grassland burned, despite 4-m wide firebreaks. Again in April, 1997, during an exceptionally long dry season, fires jumped into a new set of protected plots where forest regeneration was under study. Even with concerted efforts to prevent fire and to encourage forest growth, young trees burned (not all was lost: some plots, including 4500 trees planted on farmer's land, did not burn).

The fires are anthropogenic and burn during the latter half of the dry season. Changes in drought patterns could certainly have large impacts on the incidence of these fires, and thus the likelihood and rate of reforestation. This topic deserves careful study.

6. Predictions

Predictions are necessarily qualitative at this stage, but even broad predictions might be useful. Following is my preliminary analysis of the potential impact of changes in drought length on tropical forests.

If climates get wetter and dry seasons shorter, changes should not be severe. In natural forest, evergreen species restricted to the wettest areas will advance, but dry forest species will persist for a very long time. In Hubbell et al. (1990), we modeled the invasion of tree species into a forest, starting from a small number of stems and using optimal demographic parameters taken from the BCI plot. It took 500–1500 years for a rare species to increase until it occupied 10–20% of the BCI forest. I thus predict that it would take on the order of several centuries for wet-adapted species to extend their range by substantial distances, and thus for forests to shift in

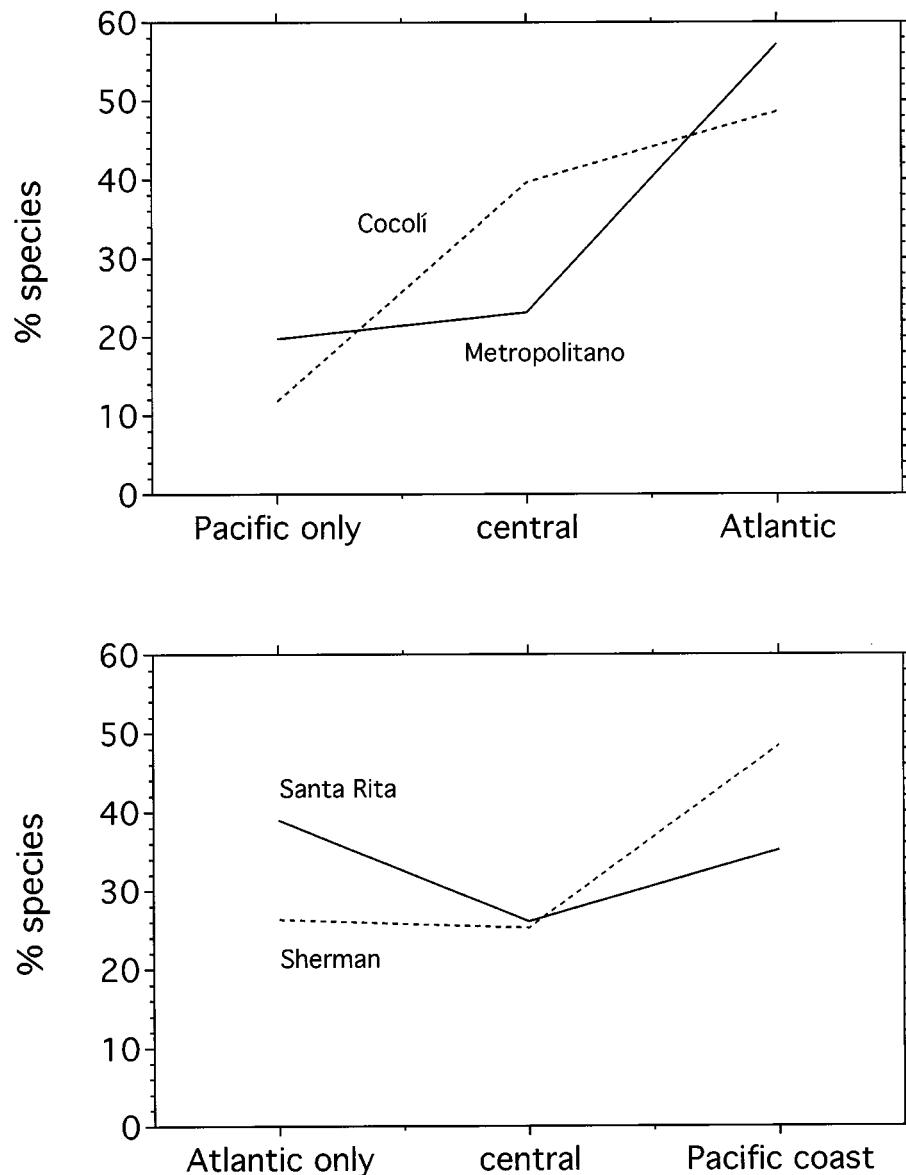


Figure 4. Fraction of species restricted to different sections of the Panama isthmus, based on all plots and inventories mapped in Figure 1. The top frame shows data for trees and shrubs found at Cocolí (173 species) and Metropolitano (144 species), giving the fraction of those species whose ranges extended 0–20, 20–40, and >40 km from the Pacific coast. The lower frame gives parallel information for trees and shrubs found at Fort Sherman (353 species) and Santa Rita (154 species), giving the fraction whose ranges extended 0–20, 20–40, and >40 km from the Atlantic coast.

composition to the wetter mixture. Moreover, many dry forest species will be able to persist in disturbed areas, and since human disturbance is only going to increase, we need not fear loss of these species. Hence, extinction should be minimal. Also, shorter dry seasons should enhance the rate of forest recovery in deforested areas.

Increase in dry season length should cause more concern. First, the pattern seen at BCI is immediate, heavy mortality and rapid loss of moisture-demanding species. Moreover, since wet areas harbor higher fractions of climate-specialists (restricted to the wet climate), extinctions could be severe. Eventually, some species from drier areas would invade, but this will happen much more slowly than extinction. Unfortunately, the predictions of Hulme and Viner (1998) do call for longer dry seasons over much of South America, India, southeast Asia, and parts of Africa (curiously, in Panama, where we are recording a drying trend, the predictions are for wetter weather).

In addition, drying trends will tend to exacerbate human disturbance, and vice versa. In both Thailand and India, for example, when humans open moist evergreen forests for farming, fires become common and dry forest species tend to invade. Even without climatic change, deciduous species can spread (P. Ashton, pers. comm.). Under a drying climate, then, the exceedingly diverse group of evergreen, moisture-demanding species will suffer on two fronts, and severe extinction of tree species and loss of habitat for animals may result.

One important factor in predicting the spread of tree species under climatic change is the existence of small dry pockets in moist regions, and vice versa. For example, in central Panama there are conspicuous pockets of highly deciduous, drought-adapted species close to the Atlantic Ocean, associated with shallow soils on limestone. Conversely, moisture-demanding species occur in wet microhabitats in dry regions, as on BCI. These pockets can play a role in range extension, since they should allow tree species to increase their range more rapidly as climate changes. In Panama, for instance, the dry-forest species could spread off the limestone patches into surrounding moist forest if the climate becomes much drier. Knowing the distribution of such patches would allow more precise predictions about the rate of spread of different tree species.

More precise estimates on the retraction of wet forests and rates of extinction could be generated by forest models. Other than O'Brien et al. (1992), such modeling efforts have not been attempted in the tropics. This is a main goal of our research in large plots, and we have begun to adapt the SORTIE forest simulator (Pacala et al., 1993) to the BCI forest. Meantime, though, the threat of increasing drought stress in the already seasonal tropics should be taken very seriously. Efforts to protect wetter forests must be doubled if drier climates threaten these forests on top of human invasion. Areas where rainfall is predicted to increase cause less concern, although the on-going problem of human invasion remains.

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