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Spatial Changes in Tree Composition of High-Diversity Forests: How Much Is Predictable?

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ABSTRACT

Beta diversity refers to the change in species composition with distance. It is an important feature in theories of conservation biology, since it determines where protected areas must be located to include most species in a region. Yet it is poorly studied in tropical forests, where species' ranges are seldom known in much detail. In this chapter we report a study of the variation in species composition in tropical forest of central Panama, along a rainfall gradient and on a highly variable geologic background. Trees were censused in a total of thirty-six different plots, mostly 1 ha in size, but including three larger plots (4, 5, and 50 ha). The similarity in tree species composition between plot pairs declined with distance, both within the 50 ha plot, where distances were less than 1.2 km, and across the whole 55 km region. Plots more than 3 km apart nearly always had similarity scores less than 50%, and usually much lower. Thus, the only case in which two plots were similar in species composition was when they were close together. This decay with distance happened even when plots matched in geologic substrate, forest age, and total rainfall. Thus, geology, climate, and forest age all played some role in forest composition, but distance between plots was the strongest predictor of similarity. This finding suggests that forest composition is highly variable in central Panama, and is only partly predicted by substrate and climate. Abiotic features would be a poor surrogate on which to base conservation decisions in this area.

INTRODUCTION

Tropical forests are renowned for their alpha diversity. Very high numbers of species can coexist in small regions. Single hectares of forest can have three hundred tree species (Phillips et al. 1994; Valencia, Balslev, and Paz y Miño 1994), and 50 ha plots with over a thousand tree species have been censused (Romoleroux et al. 1997; Lee et al. 2002). Beta diversity is a much less studied aspect of tropical forests. How much does species composition change spatially? There is no necessary association between alpha diversity and beta diversity: there could be high numbers of species at any one site, but different sites could have the same complement of species. This is the pattern that Terborgh, Foster, and Nuñez (1996) described in tropical forest in Peru. Conversely, single sites could have few species, but adjacent sites completely different species. Forests of western North America are like this, with sites at different elevations having very different species, yet no one site having more than a handful of species.

Beta diversity is harder to document than alpha diversity because it requires many species inventories across a fairly large region. But from the perspective of conservation, beta diversity may be even more important than alpha diversity, because it speaks directly to which and how many natural areas should be protected. Moreover, beta diversity has much to say about the forces that organize community composition. Terborgh, Foster, and Nuñez (1996) used similarity in tree composition across sites to indicate that predictable, deterministic forces control species composition. Tuomisto and Ruokolainen (1994), Tuomisto et al. (1995), and Ruokolainen, Tuomisto, and Kalliola (chap. 13 in this volume) interpreted changes in species composition that were predicted by environmental features to support the notion that tree community composition is the result of predictable, niche-based forces. According to these views, within a given habitat, the same tree community will become established repeatedly and predictably, but in a different habitat, a different set of species will dominate. To the extent that habitat can be used as a predictor of species composition, conservation biologists can focus on preserving samples of each habitat to ensure maximum species protection.

Other views of tropical tree communities predict a different structure to beta diversity. If tree species are competitively similar, then their relative abundances will be determined entirely by dispersal limitation and by chance. Indeed, a quantitative community drift model predicts that all sites will differ in species composition, and that if dispersal is limiting, the difference will increase monotonically with the distance between sites (Hubbell 2001; Condit et al. 2002). If species composition changes independently of habitat change, then habitat preservation is a poor approach to conservation.

Condit et al. (2002) tested the dispersal model for beta diversity. Although dispersal alone predicted the qualitative form of the decay of similarity with distance in both Panama and in South America (Pitman et al. 1999, 2001; Condit et al. 2002), it was not adequate to predict differences among sites. In that analysis, and in that of Pyke et al. (2001), we inferred that climate or geology (and thus soil) must be at least partly responsible for the high species turnover in Panama relative to that in Amazonia. Here we examine explicitly how important geology, climate, and forest history are in predicting beta diversity. We compare species turnover across sites identical in habitat (geology, climate, forest age) to species turnover where habitat varies. In principle, with this kind of analysis, it should be possible to make quantitative statements about the relative contribution of deterministic and random forces in structuring the community. This, in turn, would let us judge how well a habitat preservation plan for conservation would protect the full complement of tree diversity in a region.

We carried out this study in central Panama, using three large plots (4, 5, and 50 ha) and thirty-one small (1 ha) plots. The 50 ha plot allowed detailed examination at a local scale of how forest composition changes with distance. The small plots were deliberately placed across geologic and climatic gradients (as in Gillison and Brewer 1985) in order to separate the effects of distance, geology, and climate on forest composition. Pyke et al. (2001) and Condit et al. (2002) analyzed the same data set.

STUDY SITE

The area of the Panama Canal is covered in substantial areas of natural vegetation: about half of the 300,000 ha of the canal's watershed is forested. Most of the remainder is grassland or cropland, including abandoned farms and active pastures mixed with sporadic tree cover. A strip of land on either side of the canal is forested, largely due to the presence of the U.S. military. On the east side of the canal, this strip forms two national parks, Camino de las Cruces and Soberania. There is also a large block of forest in Chagres National Park, a largely uninhabited and remote area east of the canal and east of Lake Alajuela (see Condit et al. 2001 and Ibáñez et al. 2002 for details on forest cover and park status).

Much of this forest, however, has been cleared and regrown over the past two centuries. Only a small area of forest near the canal is old growth, apparently standing in a relatively undisturbed state for more than 250 years. These patches of old growth are on Barro Colorado Island, where palynological evidence suggests there has been no human impact on the western half of the island for 600 years (Piperno 1990), and at Pipeline Road in Soberania National Park (between plots m20 and m16 in fig. 14.1). Chagres National Park is also mostly old growth, but most of the remaining forest near the canal is probably less than 150 years old, and some is much younger (Condit et al. 2000 and Ibáñez et al. 2002).

Annual rainfall even in the driest sites near the Panama Canal greatly exceeds evapotranspiration and is ample to sustain tall, moist, high-biomass forest.

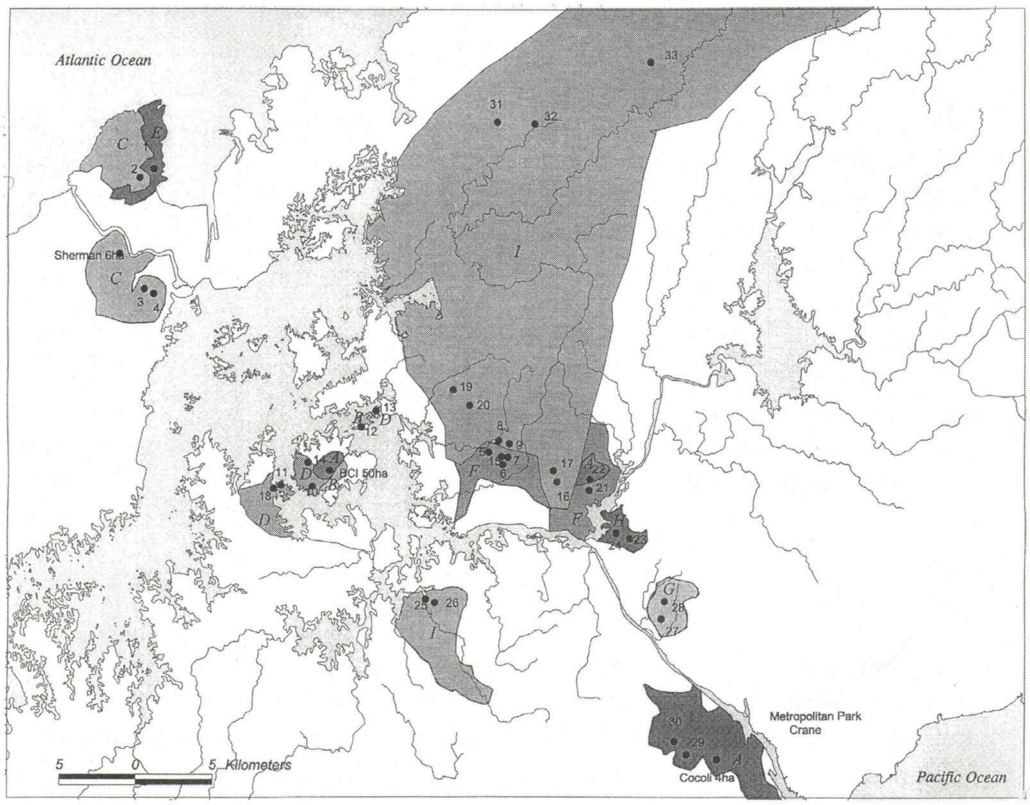


Figure 14.1 Map of plots and geology. The plot at Fort Sherman is 5 ha, and the separate hectares there are referred to as s0–s4 in the text and other figures. The plot at Cocoli is 4 ha, and these hectares are referred to as c1–c4. The six individual hectares from the 50 ha plot at Barro Colorado Island used in the landscape-scale analyses are designated b1–b6. The remaining plots are isolated hectares, and are designated L1–L4 and m5–m31; on this map, just the numbers 1–31 are used. Only geologic regions underlying plots are designated on this map: A = Miocene basalt; B = conglomerate of basalt and sandstone (Bohio Formation); C = Chagres sandstone; D = tuffaceous siltstone, sandstone, and limestone (Caimito Formation); E = Toro limestone; F = mudstone, siltstone, sandstone, limestone (Gatuncillo Formation); G = mudstone, siltstone, sandstone, tuff, limestone (La Boca Formation); H = agglomerate and fine-grained tuff (Las Cascadas Formation); I = pre-Tertiary basaltic and andesitic lavas and tuff (see Stewart, Stewart, and Woodring 1980 for further details). Lake Alajuela is the large lake east of the canal.

There is a long dry season, however, during which many trees lose all their leaves. Near the Pacific end of the canal, near Panama City, total annual rainfall is 2,000 mm, the dry season lasts 129 days, and more than 40% of the canopy is deciduous, but near the Atlantic, rainfall is 3,000 mm, the dry season is 102 days, and only 12% of the canopy is deciduous (Condit 1998a). A ridge 15–30 km east of the canal (around plot m31 in fig. 14.1) is far wetter, having a dry season of only 67 days and rainfall of 3,300 mm. The entire region is underlain by a complex geology, with a variety of rock formations in close proximity (fig. 14.1).

The forests of the canal area are well known floristically. According to the checklist for the flora of Panama (D'Arcy 1987, now computerized and updated), there are 863 tree species documented in the Panama Canal Zone, which covers about 125,900 hectares. A well-documented flora is a great advantage in studies of beta diversity, and we have been able to identify large numbers of trees over a wide area in a timely fashion.

METHODS

Forest inventories were done in thirty-one 100 × 100 m plots and two 80 × 40 m plots, censusing all trees 10 cm or greater in diameter at breast height (DBH). (Methods are described in detail in Condit 1998b.) If trees could not be named immediately, leaves were collected and compared with specimens in herbaria at the Smithsonian Tropical Research Institute and the University of Panama. In addition, we used data from a 50 ha plot on Barro Colorado Island (BCI) that was set up in 1981 (Hubbell and Foster 1983; Condit, Hubbell, and Foster 1995, 1996a, 1996b), a 5 ha plot near the Atlantic coast at Fort Sherman, and a 4 ha plot near the Pacific coast, on the Cocoli River (Condit et al., forthcoming). All stems of 1 cm DBH or greater were censused throughout these larger plots. In all plots, for all stems sizes, 286,829 individuals of 686 species were censused; 40,021 individuals of 517 species were 10 cm DBH or greater.

We report one set of analyses on forest composition within the 50 ha plot using all stems counted in the 1990 census (244,070 individuals of 1 cm DBH or greater). In the remaining analyses, we compare the composition of trees 10 cm DBH or greater across all 1 ha plots, plus six hectares of the BCI plot and individual hectares from Sherman and Cocoli (for a total of forty-six individual hectares). These forty-six hectares had 21,554 individuals and 493 species 10 cm DBH or greater.

Plots were located with the express purpose of examining how forest composition varies with distance, geology, climate, and human disturbance. To do so required estimates of forest age, a precipitation map, and a geologic map (Stewart, Stewart, and Woodring 1980). We categorized forest age as young secondary (largest trees < 50 cm DBH but with a canopy taller than 20 m), mature secondary (largest trees < 100 cm DBH), or old-growth (trees ≥ 100 cm DBH). We generated the precipitation map from data collected by the Panama Canal Commission at twenty-six meteorological stations, then estimated total annual rainfall at each plot by interpolating between the two nearest stations. Annual precipitation is highly correlated with the length of the dry season, which is probably the key limiting factor for tree distributions (Condit 1998a; Condit et al. 2000).

Plots were placed in local clusters, each of which served as one "experiment." Some clusters were placed so that all plots were in forest of approximately the same age, in close proximity so that rainfall did not vary, but on different geologic substrates. Other clusters were on a single rock formation at various distances from one another, or had different disturbance histories. This approach is similar to the "gradsect" design advocated by Gillison and Brewer (1985), since we positioned plots across gradients of precipitation, forest age, and geology.

Within the 50 ha plot, we also considered a finer habitat classification based on substrate. Each 20 × 20 m quadrat was classified as one of the following: swamp, a 1.2 ha region that is flooded with standing water most of the year; streamsides, regions within 20 m of small streams (1.9 ha); slopes, quadrats inclined by 7° or more (11.4 ha); and plateau, which is flat, nonflooded terrain. The plateau was subdivided into three sections: a 6.8 ha block in the eastern part of the plot that is at least 150 m above sea level, a 2.1 ha section of young forest, and a 24.8 ha western block that is less than 150 m in elevation. The remaining 1.8 ha of the 50 ha plot consisted of quadrats with a mixture of habitats, and these quadrats were not used in analyses. The habitats differ in soil moisture because of a perched water table that meets the surface along the slopes; the high plateau is farthest from the water table and thus driest (Condit, Hubbell, and Foster 1996a, 1996b; Harms et al. 2001). They also parallel geologic substrates: the plateau is a basalt cap at the summit of the island, which gives way to softer sedimentary rocks on the slopes.

One important shortcoming of the study is that the three independent variables—geology, climate, and forest age—often covary. Human agriculture is associated with drier climates and tends to avoid steep areas and rock formations that hold little water. Thus, forests on flatter areas closer to the Pacific side of the Isthmus of Panama are mostly young forests, with less than 100 years since major disturbances. Old growth occurs mainly on steep ridges and in wet sites. Also, the geology of the area is so complex that it is difficult to study sites at any great distance from one another that are on the same rock formation. Nevertheless, by deliberately placing plots near transitions in geology or forest age, we could test hypotheses about the effects of disturbance and geology on forest composition, and some clear results emerged.

Communities were compared using the Sørensen index of similarity calculated between pairs of square plots—either entire 1 ha plots, 1 ha quadrats within larger plots, or 20 × 20 m quadrats within the 50 ha plot. The Sørensen index is calculated as follows (Barbour, Burk, and Pitts 1987): Let x_i be the number of individuals of species i in plot 1, and y_i the number of individuals of the same species in plot 2. Call $\min_i$ the smaller of the two. Then the index is

$$\frac{\sum_i \min_i}{\sum_i (x_i + y_i)}$$

It is simply the proportion of individuals in each plot that can be matched (by species) with individuals in the other plot. All results presented here are very similar whether this similarity index or a version of the Sørensen index based only on presence-absence of species (Condit et al. 2002) is used.

RESULTS

Habitat and Distance Effects in the BCI Plot

Similarity between hectares in the 50 ha plot on BCI decayed with distance (fig. 14.2). Although there was scatter, the data are fit well by a logarithmic decay curve. Similarity between 20 × 20 m quadrats also declined logarithmically, and habitat differences were clear, although mostly very slight. Figure 14.3 shows similarity as a function of distance for quadrat pairs within the slope habitat as well as for pairs in which one quadrat was on the slope and one in a different habitat. (A graph based on plateau habitats was almost identical.) The swamp habitat stood out as very distinct from the slope, with similarities of less than 50% and with no distance effect. Differences between the slope and the other habitats were evident, but much less pronounced.

We can use figure 14.3 to make a quantitative assessment of the effects of habitat and distance on similarity, using the slope habitat as an example. When habitat was held constant—that is, when two quadrats on the slope were compared—mean similarity declined from 57% to 42% with distance. When distance was held constant, at 200–300 m, similarity between two slope quadrats was about 48%, while cross-habitat similarities were about 45%, except for the swamp, which had just 28% similarity to the slope. Thus, the distance effect on forest

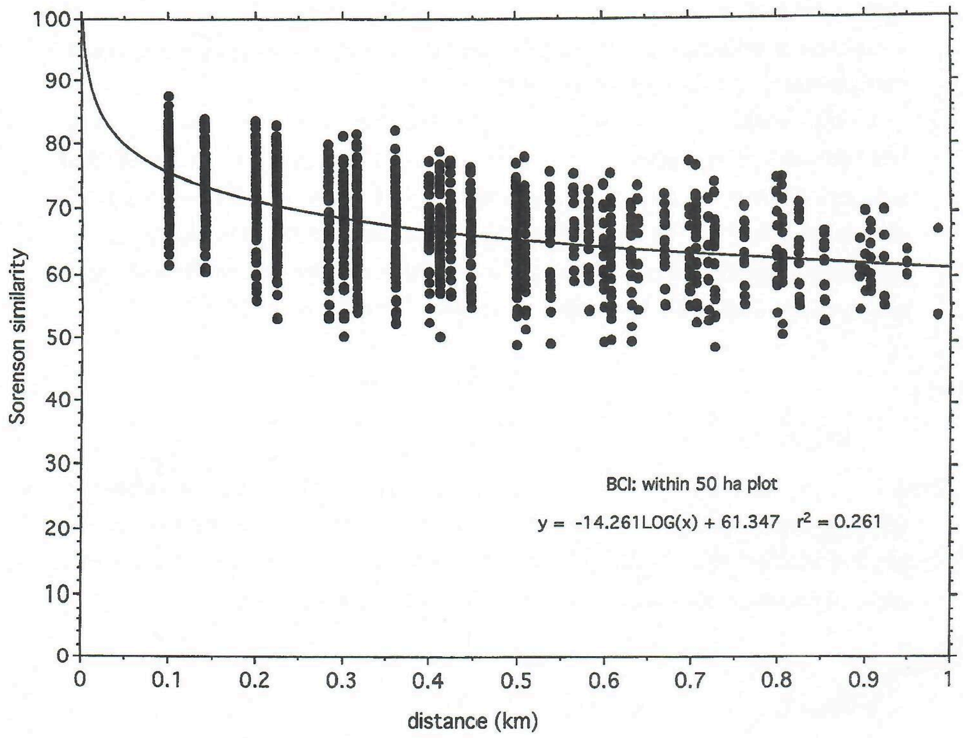


Figure 14.2 Similarity versus distance for all pairs of square hectares within the 50 ha plot at Barro Colorado Island, with only trees 10 cm DBH or greater included. There are 50 × 49/2 = 1,225 comparisons and thus 1,225 points on the graph. The curve through the points is the regression between similarity and the logarithm (base 10) of distance.

composition can be given as 15 similarity points—the change in similarity due to distance for a given habitat—while the habitat effect—the change in similarity with habitat at a given distance—was 20 points for the swamp, but only 3 points for the other habitats. Notice that most of the distance effect dissipated in less than 200 m, and that habitat effects were not evident beyond 500 m (except for the swamp).

Results comparing the plateau and streamsides to other habitats were quite similar to those shown for the slopes in figure 14.3; however, the swamp was qualitatively different. It had low similarity to other habitats, and to itself, and showed only very weak distance effects. We conclude that distance had a five times greater effect on tree species composition than habitat, at least for the slope and plateau habitats, which cover most of the plot. The swamp habitat was more distinct, however.

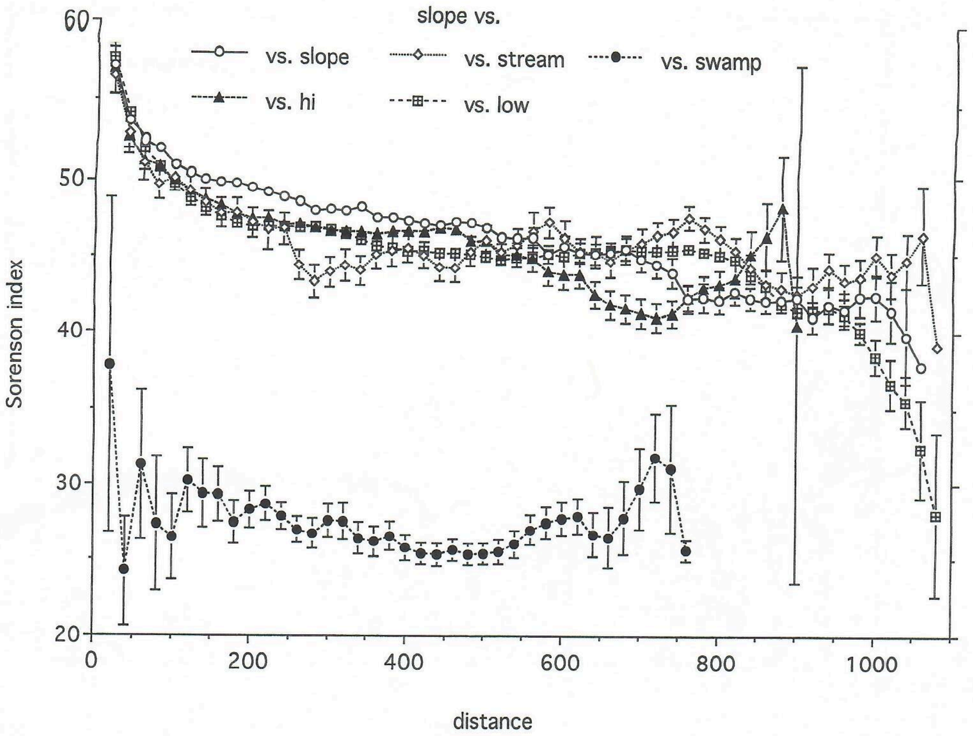


Figure 14.3 Similarity versus distance (m) for pairs of 20 × 20 m quadrats within the 50 ha plot, with all trees 1 cm DBH or greater included. Each point represents the mean similarity for a given habitat comparison, over a discrete distance range, starting with 20–39.9 m and continuing in 20 m brackets; confidence limits around each mean (calculated from a *t*-test) are given also. There are five curves on the graph, each for a different habitat comparison. The highest curve (open circles) is for comparisons of slope quadrats with other slope quadrats. The lowest curve (solid circles) is for comparisons of slope quadrats with swamp quadrats. Other curves are for slope quadrats versus streamside (stream), high plateau (hi), and low plateau (low) habitats.

Similarity and Sample Size

The mean similarity of adjacent 20 × 20 m quadrats, with all stems 1 cm DBH or greater included, was 57%. The mean similarity of adjacent 1 ha quadrats, with all stems 10 cm DBH or greater included, was 75%. Thus, similarity increased with the number of individuals sampled. We calculated the mean similarity for pairs of quadrats a fixed distance apart (500 m), but with varying quadrat size and DBH cutoff. Similarity increased with the logarithm of the number of individuals sampled. Thus, much larger samples yielded only slight increases in similarity; for example, while adjacent hectares were 75% similar, the two halves of the

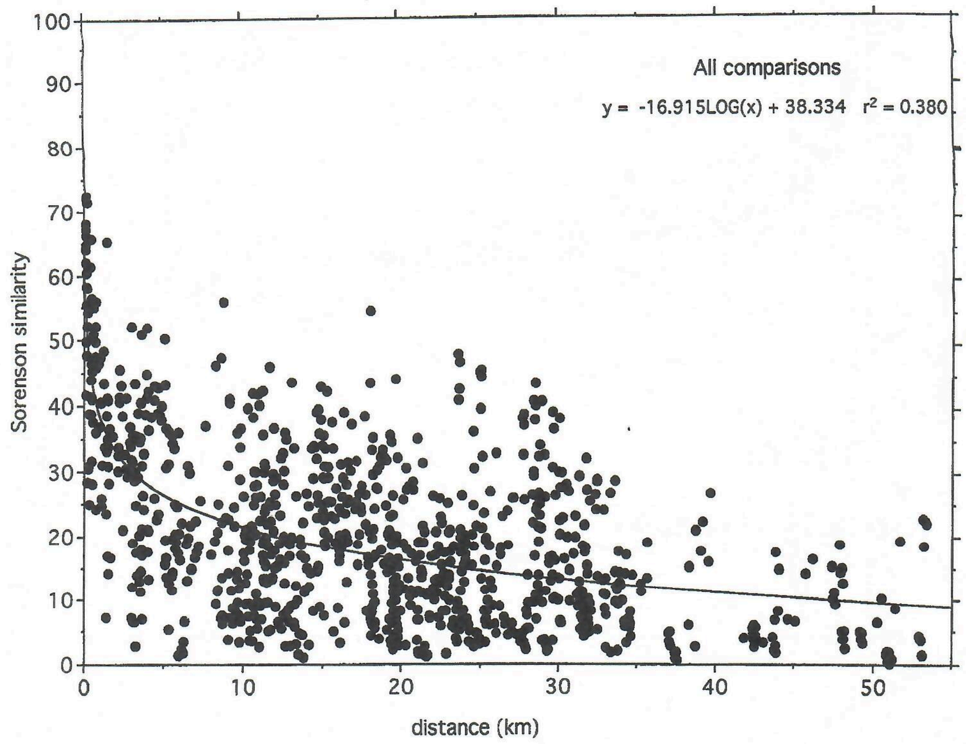


Figure 14.4 Similarity versus distance for pairs of square hectares, including thirty-one isolated hectares, four hectares at Cocoli, five hectares at Fort Sherman, and six of the fifty hectares at Barro Colorado Island, with only trees 10 cm DBH or greater included. There are 46 × 45/2 = 1,035 comparisons and thus 1,035 points on the graph. The curve through the points is the regression for similarity versus the logarithm (base 10) of distance.

50 ha plot had a similarity of 82%. Similarity was nearly independent of the DBH category used in the calculation when the number of individuals and distance were matched. For example, 20 × 20 m quadrats of stems 1 cm DBH or greater, 100 × 100 m quadrats of stems 10 cm or greater, and 250 × 250 m quadrats of stems 40 cm DBH or greater were roughly matched for stem number (195, 425, and 295 individuals, respectively). When separated by 500 m, the similarity indexes from pairs of each quadrat size were 45%, 53%, and 55%, respectively.

Similarity at a Landscape Scale

Similarity among 1 ha plots also decayed logarithmically with distance at much wider scales (fig. 14.4). Plots within 1 km of each other usually had simi-

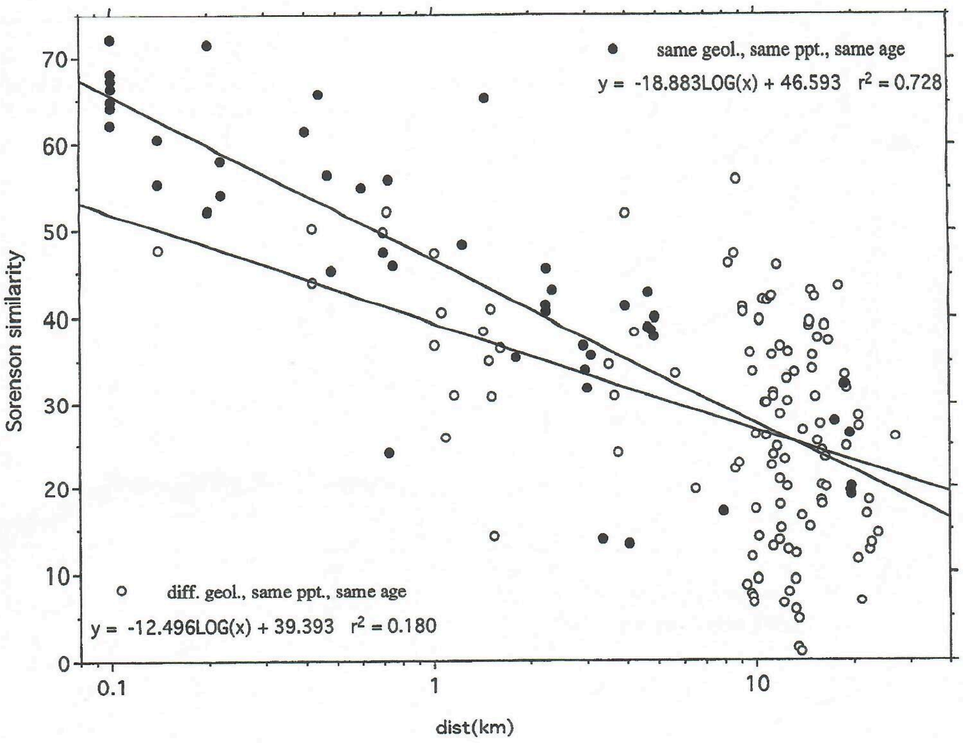


Figure 14.5 Similarity versus distance for some of the pairs from figure 14.4. Comparisons involving two plots, both of which are on identical geologic substrates, under the same climate (within 300 mm annual rainfall), and in the same forest age category, are shown with solid circles and fit by the upper regression line. Comparisons involving pairs of plots differing in geology but matching in climate and forest age are shown with open circles. The intercepts of the two regression lines do not differ significantly.

larities above 50%, but similarity declined quickly and was seldom above 50% in plots more than 2 km apart. Mean similarity fell below 30% at all distances beyond about 3 km.

How much of the decay with distance was due to habitat (geologic or climatic) differences? Figure 14.5 summarizes a test for geology. All pairwise comparisons involving two plots on the same geologic substrate, with the same precipitation (annual total within 300 mm of each other), and with the same forest age category are shown. Overlain are all pairwise comparisons of plots that differ in geology but match in precipitation and forest age. The regression for the first set is higher than for the second set, but the difference is not significant at the 5% level. The same test for forest age, however, did give a significant result (fig. 14.6),

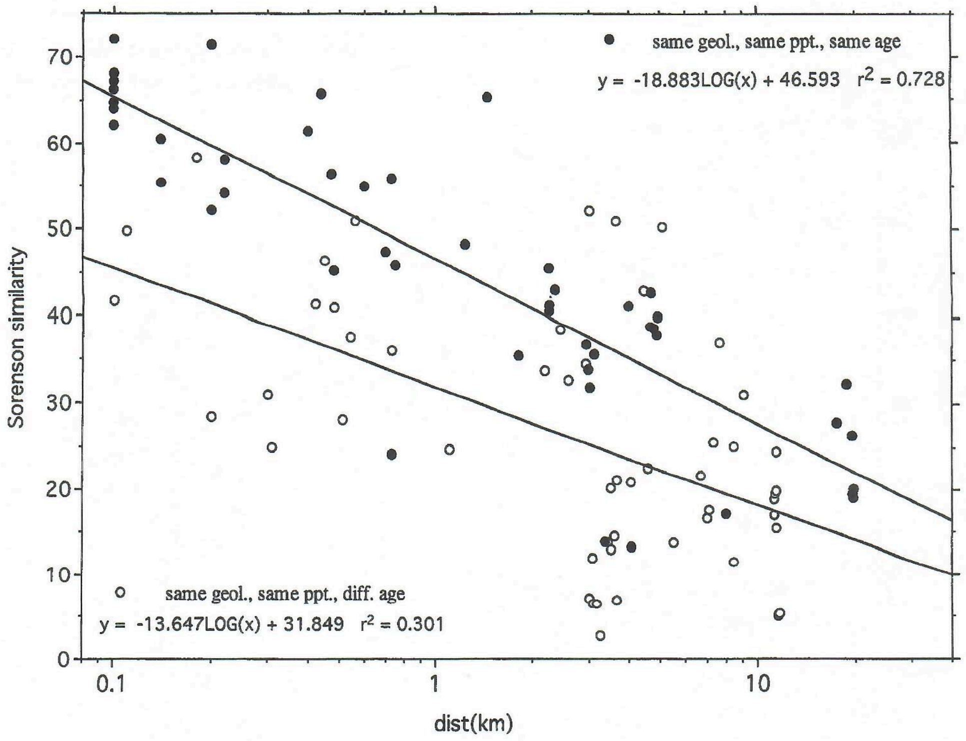


Figure 14.6 As in figure 14.5, but comparing pairs of plots in the same geology, climate, and forest age categories (solid circles) with pairs of plots that differ in forest age only (open circles). The intercepts for the two regression lines are significantly different ($p < .05$), with comparisons differing in forest age having a lower intercept. The four very low values within 1 km of distance are comparisons of plot s4 (young forest) with plots s0–s3 (old growth).

principally because young secondary forest was quite different in composition from mature forest.

A similar graph based on precipitation (not shown) showed that plots differing in rainfall (annual total differing > 300 mm) were more different than plots with similar rainfall at distances of 10–20 km. It was impossible to assess a rainfall effect for plots less than 10 or more than 20 km apart, because in the former case, annual rainfall never differed by more than 300 mm, whereas in the latter case, other factors always differed. Regression lines for this test did not differ significantly, however.

Even if we accept the effects of geology, climate, or forest age as real, they are small effects. Plots separated by less than 3 km in matching habitat categories had similarity scores of 40%–70%. Plots separated by the same distance but differing in one of the three habitat characteristics had similarities of 30%–50%.

Plots differing in more than one habitat characteristic had similarities of 15%–40%. Moreover, even plots on identical habitat showed a decay of similarity with distance, and plots more than 7 km apart had similarity scores of less than 30% even when matching in all three habitat characteristics.

Local Plot Clusters

Examining all plot comparisons together mixes many different kinds of geology. Comparisons of local plot clusters offer a more powerful way to assess the importance of habitat characteristics because they were deliberately designed with that end in mind. Understanding the following examples requires close scrutiny of the geologic map and the plot locations (see fig. 14.1).

PLOTS M25 AND M26

Plots m25 and m26 were deliberately placed on a southern outcrop of pre-Tertiary lava, a rock formation that extends well to the north. The Pipeline Road plots (m8, m9, m16, m17, m19, m20) and plot m31 are on the same formation, but get much more rain, whereas plots m21–m24 get amounts of rainfall similar to m25 and m26, but are on a different geologic substrate. Plots on or near BCI (m10–m14 and m18, plus b1–b6 within the 50 ha plot on BCI) get more rain than m25 and m26 and are on different substrates.

Plots m25 and m26 were indeed more similar to the other plots on the same rock formation than to plots on different formations, even when distances were matched (fig. 14.7). Both plots were more similar to m8, m9, m16, m19, and m20 than they were to m21–m24, m13, m23, and b1–b6. There were some peculiarities that are not so easy to explain, however. Plots m25 and m26 were also quite similar to m6, m7, m15, and m16, even though the latter are on a different rock formation. And they were quite different from m17, even though m17 is on the same substrate as (and very close to) plots m16, m8, and m9.

Also striking in figure 14.7 is the similarity of plots m25 and m26 to the plots at Fort Sherman (s0–s3 and L2). In fact, except for their similarity to each other, m25 and m26 were more similar to s1–s3 than to any other plots, even though the Sherman sites are 30 km away. This finding suggests some sort of similarity in soils, but the Sherman sites are on a different substrate.

However, plots m25 and m26 were not particularly similar to any other plots. Their similarity to the Pipeline Road sites and the Sherman sites was less than 30%. Also, in this case, forest age and precipitation played no role in the similarities, or at least a minor role relative to geology. Plots m25 and m26 are on young secondary forest, yet were much more similar to older and wetter forest

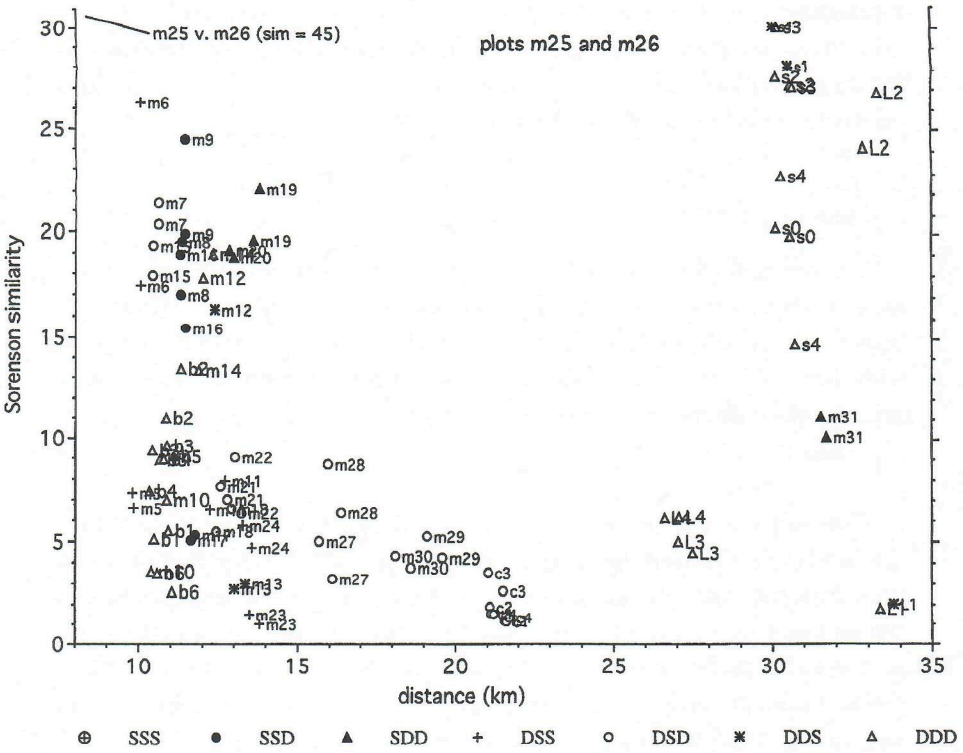


Figure 14.7 Similarity of plots m25 and m26 to all other 1 ha plots (including six from within the 50 ha plot on Barro Colorado Island). The different symbols indicate a habitat comparison for each plot, with the first of the three letters indicating whether geology is the same (S) or different (D), the second letter whether climate is the same or different, and the third letter whether forest age is the same or different: SSS = same geology, same climate (within 300 mm annual rainfall), same forest age category; SSD = same geology, same climate, different forest age; and so forth. Plots m25 and m26 are on pre-Tertiary lavas, which extend well north and also underlie plots m8, m9, m16, m17, m19, m20, and m31 (see fig. 14.1). They get 2,210 mm of rain annually and are in young secondary forest.

at Fort Sherman than they were to young forest on plots m21–m24, where rainfall is similar.

PLOTS M8 AND M9

Two plots at Pipeline Road, m8 and m9, are on the same rock formation as plots m25 and m26. But comparing them to other plots leaves a more equivocal picture (fig. 14.8). They were more similar to each other and to plots m19 and m20, on the same rock formation, than to any other plots (even though m19 and m20 are in mature secondary forest, whereas m8 and m9 are in old-growth forest). They were

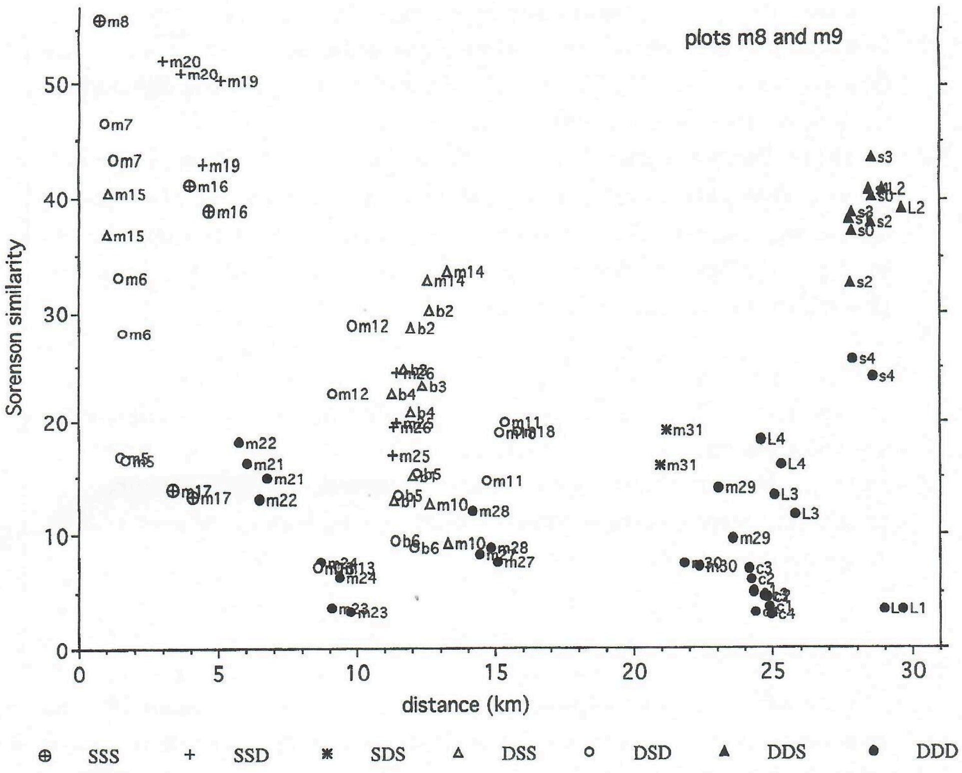


Figure 14.8 Similarity of plots m8 and m9 to other 1 ha plots. Abbreviations are as in figure 14.7. These two plots are on the same pre-Tertiary lavas as plots m25 and m26. They get 2,500 mm of rain annually and are in old-growth forest.

also similar to plot m16, on the same rock formation, but completely different from plot m17, m16's replicate. Plots m8 and m9 were quite similar to plots m7 and m15, even though they are on different rock formations. Beyond 10 km, plots m8 and m9 were more like plots on or near BCI, which have a similar climate but differ in geology, than plots m23, m24, m27, and m28, which get less rainfall. Plots m8 and m9 were remarkably similar to the plots at Fort Sherman, 30 km away—almost as similar as they were to sites within a couple of kilometers.

PLOT L1

Plot L1 was deliberately placed on a limestone formation near Fort Sherman because it is obvious that this formation carries a much different flora than anything around it. Large slabs of Toro limestone lie just at the surface, with virtually no soil. This site and several others like it in the canal area (but on different rock formations) are conspicuously deciduous in the dry season. Other plots at Fort Sherman have almost no deciduous species (Condit et al. 2000). Gentry (1982) commented on the limestone flora near the Panama Canal, although he worked on a rock formation near Lake Alajuela.

The similarity analysis bears out the distinctness of the forest on plot L1. Plot L2 is less than 2 km from L1, but the pair had a similarity of only 7%. Remarkably, L1 was more like the Cocoli forest, over 50 km away, than it was like any other plot. However, the latter comparison involved a similarity of only 23%, so L1 was also not much like anything else.

PLOTS M10 AND M14

Plots m10 and m14 are in old-growth forest on BCI, less than 2 km west of the 50 ha plot, but on a different rock formation. They were just as similar to the BCI plots on a different substrate, or in younger forest, as they were to each other (fig. 14.9). In this region, geologic substrate and forest age had no measurable effect on species composition.

Abundant Species

Variation in species composition can also be illustrated by examining the dominant species in the area, which were extremely variable from site to site. For example, *Faramea occidentalis* was the most abundant tree of 10 cm DBH or greater in the 50 ha plot on BCI (it ranked first in eighteen of the fifty hectares), but it was not top-ranking in any other plot and occurred in the top ten in just six out of thirty-eight hectares off BCI. *Quararibea asterolepis* ranked first in basal area in the 50 ha plot at BCI, and ranked in the top five in stems 10 cm DBH or greater in twenty-one of the fifty hectares, yet it did not reach the top ten ranks in any other plot. The top-ranking species in the 4 ha plot at Cocoli, *Calycophyllum candissimum,* was top-ranking at only one plot away from Cocoli (L1) and ranked in the top ten in just two others. No species ranked first in abundance in more than six of the forty-six hectares (only the palm *Socratea exorrhiza* ranked first in six plots), and no species appeared in the top ten ranks more than ten times (only *Socratea* made ten appearances).

Table 14.1 lists the top-ranking species in selected plots. For this comparison, we deliberately chose several plots that were most likely to be similar to one another: groups of plots that match in geology, climate, and forest age. In addition, plots m19, m20, s0, and s1 are compared because they had high similarity scores even though they are 30 km apart. It is clear that even at very nearby sites with

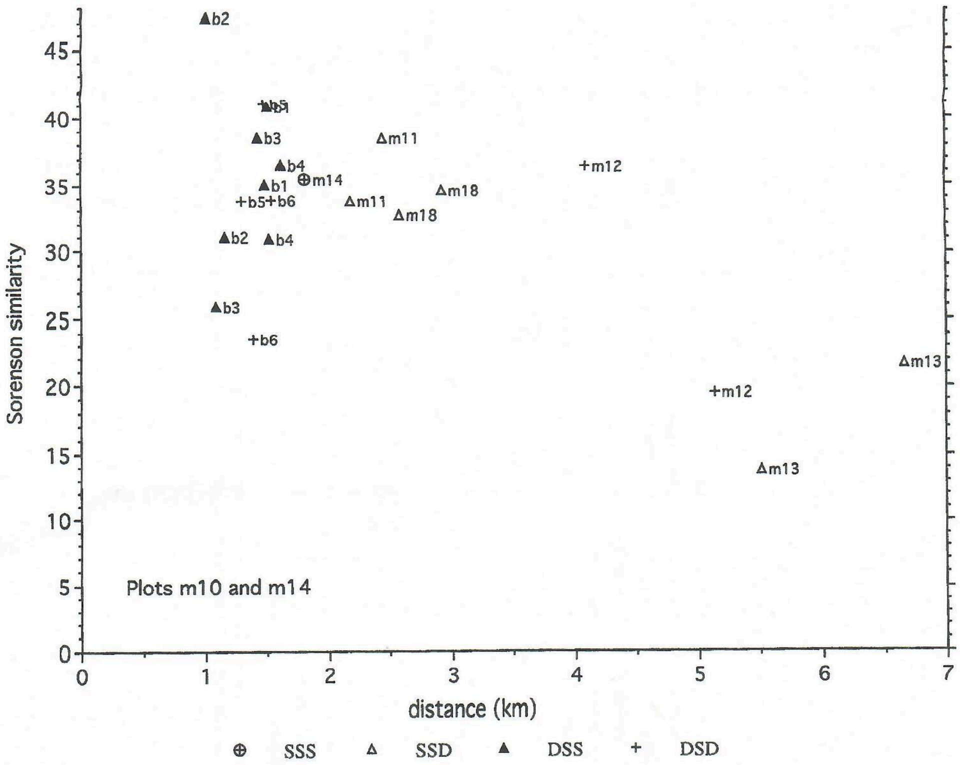


Figure 14.9 Similarity of plots m10 and m14 to other plots. Abbreviations are as in figure 14.7. Plots m10 and m14 are on Barro Colorado Island, west of the 50 ha plot, on the Caimito Formation. They get 2,580 mm of rain annually and are in old-growth forest.

the same geologic substrates and forest ages, the dominant species were not consistent in ranking. Indeed, only one pair of plots in table 14.1 shared more than half of their top ten species (s0 and s1 shared seven of ten). More typical are m29 and c3, only 2.3 km apart and on the same rock formation, but sharing just four of their top ten species. Plot m31 was included as the greatest contrast—the wettest site. The most abundant species there, the palm *Iriartea deltoidea*, did not occur in any other plot (though it is also the most abundant species of 10 cm DBH or greater in a large plot in Amazonian Ecuador: Romoleroux et al. 1997).

Range maps can summarize some key results, and figure 14.10 gives examples. *Tapirira guianensis* clearly shows the link among Fort Sherman and plots m19, m20, m8, m9, m25, and m26. *Bursera simaruba*, a familiar dry-forest species, appeared only in areas of less rain and on the limestone of plot L1.

Table 14.1 Top ten species (ranked by number of individuals ≥10 cm DBH) in selected plots

Plot	m22	m29	c3	m16	m19	m20	s0	s1	L2	m31
Precipitation	2,200 mm	2,030 mm	2,030 mm	2,330 mm	2,600 mm	2,600 mm	3,050 mm	3,050 mm	3,060 mm	3,350 mm
Forest age	Mature secondary	Mature secondary	Mature secondary	Old growth	Mature secondary	Mature secondary	Old growth	Old growth	Old growth	Old growth
Geologic substrate	Miocene basalt	Miocene basalt	Miocene basalt	Pre-Tertiary lavas	Pre-Tertiary lavas	Pre-Tertiary lavas	Chagres sandstone	Chagres sandstone	Chagres sandstone	Pre-Tertiary lavas
1.	*Swartzia*	*Heisteria*	*Anacardium*	*Poulsenia*	*Socratea*	*Perebea*	*Socratea*	*Socratea*	*Protium p.*	*Iriartea*
2.	*Astrocaryum*	*Anacardium*	*Calycophyllum*	*Gustavia*	*Perebea*	*Socratea*	*Brosimum u.*	*Marila*	*Mortoniodendron*	*Socratea*
3.	*Faramea*	*Scheelia*	*Swartzia*	*Socratea*	*Malouetia*	*Dendropanax*	*Marila*	*Tovomita*	*Virola s.*	*Welfia*
4.	*Scheelia*	*Antirhea*	*Trichilia p.*	*Heisteria*	*Marila*	*Malouetia*	*Perebea*	*Perebea*	*Tetragastris*	*Pithecellobium*
5.	*Oenocarpus*	*Luehea*	*Protium t.*	*Oenocarpus*	*Virola s.*	*Tapirira*	*Theobroma*	*Brosimum u.*	*Perebea*	*Cassipourea*
6.	*Cryosophila*	*Calycophyllum*	*Brosimum a.*	*Perebea*	*Maranthes*	*Oxandra*	*Tapirira*	*Tapirira*	*Socratea*	*Eschweilera*
7.	*Protium t.*	*Guarea gl.*	*Posoqueria*	*Brosimum l.*	*Brosimum g.*	*Oenocarpus*	*Dendropanax*	*Aspidospermum*	*Heisteria*	*Tovomita*
8.	*Alseis*	*Oenocarpus*	*Scheelia*	*Trichilia t.*	*Tapirira*	*Poulsenia*	*Cespedezia*	*Vochysia*	*Brosimum g.*	*Cespedezia*
9.	*Cavanilesia*	*Coussarea*	*Antirrhea*	*Virola s.*	*Aspidospermum*	*Pourouma*	*Guatteria*	*Dendropanax*	*Hirtella*	*Pouteria*
10.	*Brosimum a.*	*Tetrathylacium*	*Faramea*	*Alseis*	*Brosimum l.*	*Marila*	*Tovomita*	*Manikara*	*Manikara*	*Virola k.*

Note: Plot locations are shown in figure 14.1. Only generic names are given except for *Brosimum*, *Guarea*, *Protium*, *Trichilia*, and *Virola*, which have multiple species in the table; their species' initials are included.

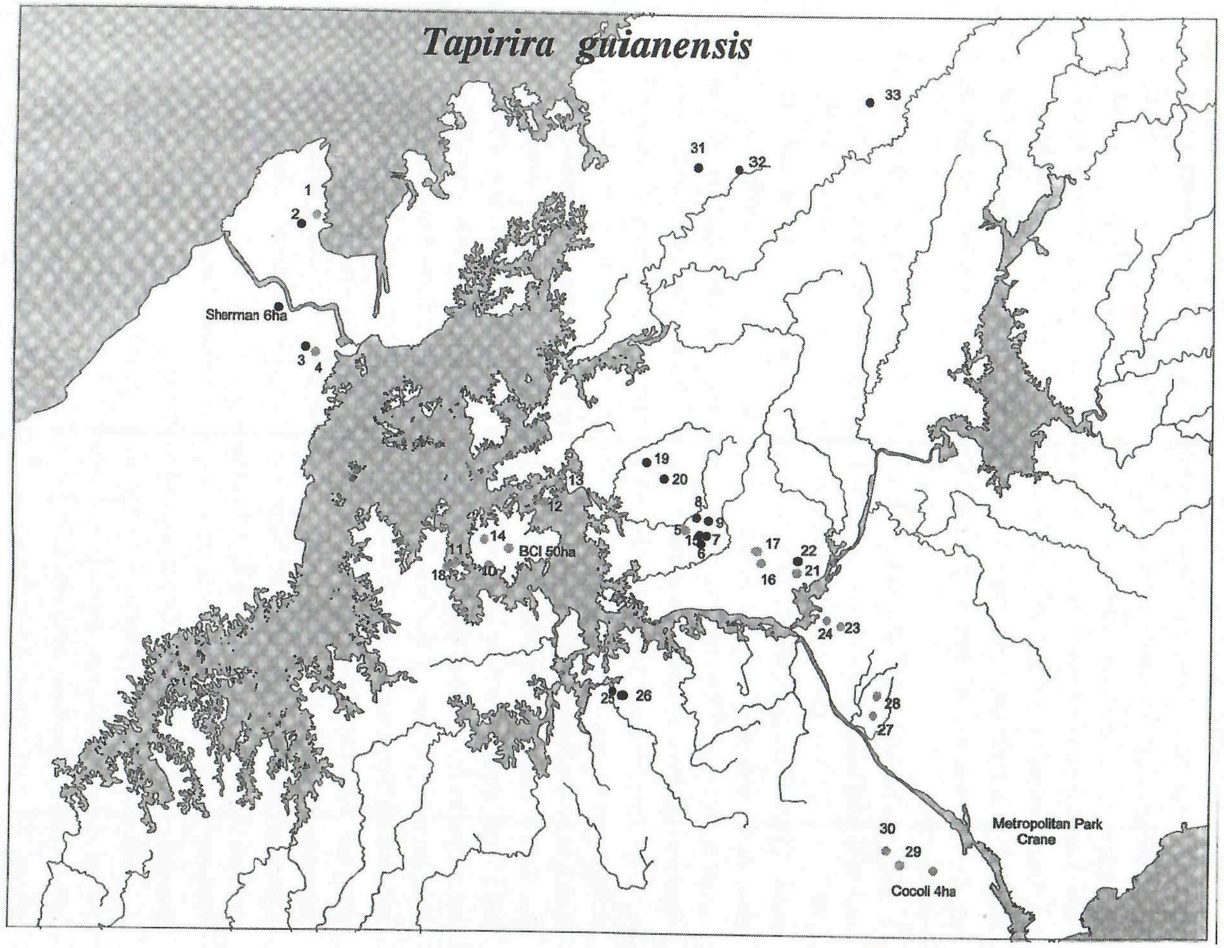
DISCUSSION

Beta diversity in Panama forest is high. Condit, Hubbell, and Foster (1996c) noticed that 50 ha of forest in Malaysia has three times as many tree species as 50 ha in Panama, but that the entire nation of Panama has about the same number of tree species as the Malay Peninsula (in about the same land area). Condit et al. (2002) documented elevated beta diversity in Panama relative to South America. Our current results give some insight into this beta diversity. A highly varied geology and climate in Panama certainly plays a role in species turnover, but we also see evidence of unexplained, apparently random, turnover in species composition.

The clearest indication of a habitat effect is the similarity between plots m25 and m26 and other plots on the same rock formation, but at some distance. Other examples of unusually high similarity at considerable distance are the plots at Fort Sherman (s0–s3) compared with those at Pipeline Road (m8, m9, m19, m20) and the limestone plot L1 compared with sites at Cocoli (c1–c4) across the isthmus. These two examples do not involve matched geology, but the similarity of these distant plots suggests that substrate is playing a role in community composition. Further knowledge about soils ought to support the substrate connections, and our vegetation data provide working hypotheses on which to base soil tests. We have two favored hypotheses: One is that soils on the pre-Tertiary basalt at Pipeline Road and at plots m25 and m26 are deeper, or hold water more effectively, than other soils in the area, and thus carry a number of species from wetter regions, even though they get no more rain than BCI. The second hypothesis is that the pre-Tertiary basalt produces a nutrient-poor soil, and the flora associated with it is not specialized for moisture, but rather for poor soil. A recent evaluation of the water-releasing capacities of soils (T. Kursar and B. Engelbrecht, personal communication) favors the former hypothesis: soils near plots m25 and m26 have more water available to trees at a given water volume than soils on BCI. Fort Sherman has a flora similar to that on the pre-Tertiary basalt; its water-releasing capacity and its nutrient status will also be important in distinguishing between the two hypotheses.

Aside from the Toro limestone supporting a deciduous forest and the pre-Tertiary basalt supporting a moisture-dependent flora, there is little indication of an effect of geology on forest composition. Different geologic formations around BCI and various formations south of plots m21 and m22 did not have any obvious effect on species composition. This is presumably why the overall test of the effect of geology gave an insignificant result.

Forest age showed a significant effect on species composition. Our impression



Tapirira guianensis
1
2
Sherman 6ha
3
4
31
32
33
19
20
13
12
14
BCI 50ha
11
18
10
8
9
5
15
7
6
17
22
21
16
24
23
25
26
28
27
30
29
Cocoli 4ha
Metropolitan Park Crane

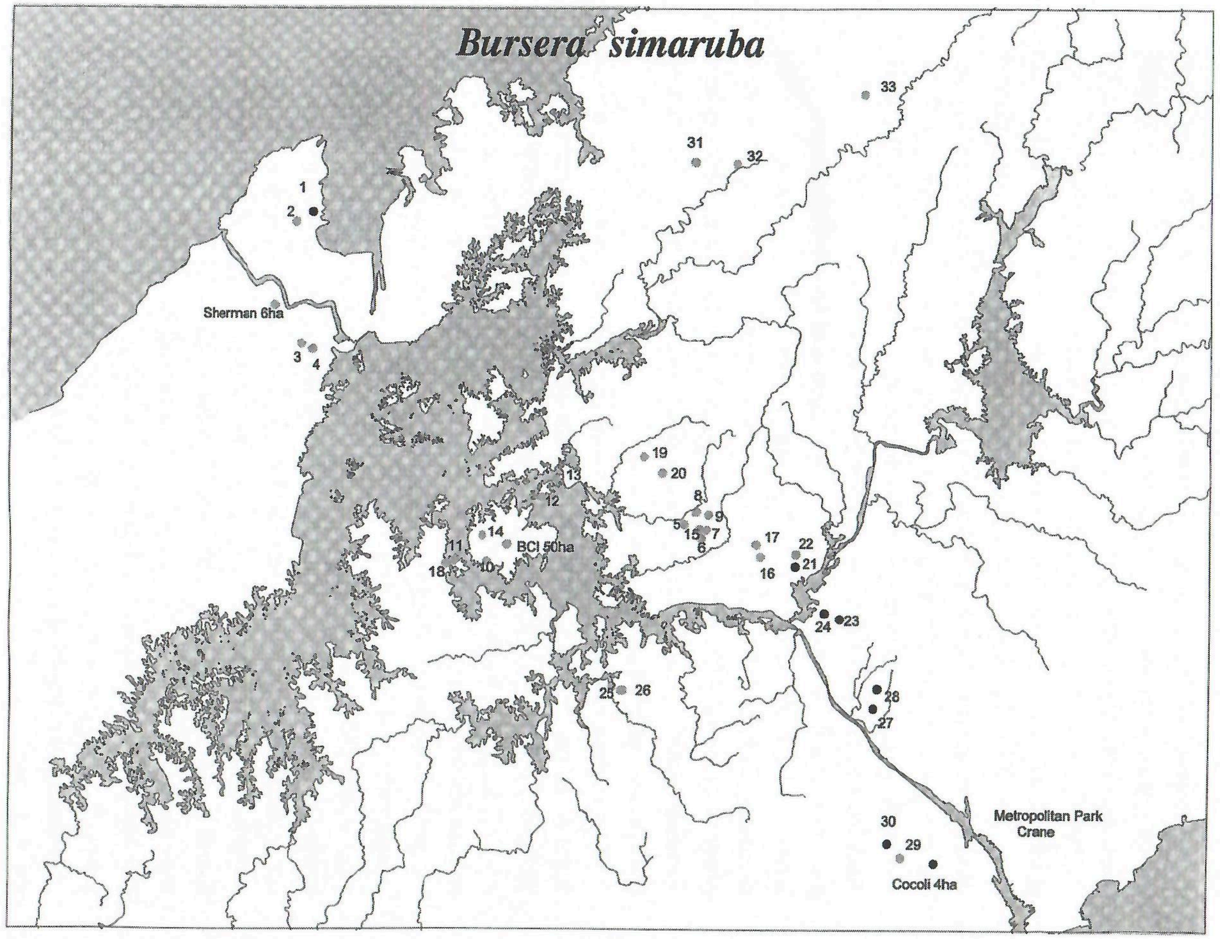


Figure 14.10 Range maps of selected species. Plots where a species was found are indicated by solid circles, and where it was not found by shaded circles.

is that this effect is mostly due to young forest having a distinct composition, especially in plots s4, m12, and m13. In comparisons involving mature secondary and old-growth forest (e.g., m10 and m14 versus nearby plots), forest age had no effect. Despite its distinctiveness, we doubt that young forest contributes much to beta diversity because it mostly harbors a consistent set of widespread invasive trees; however, we have not tested this hypothesis with the data.

The effect of climate was not clearly discernable in our data, probably because nearly all sites that differ in climate also differ in geology. In some conspicuous cases, the effect of geology overrode any effect of forest age or precipitation on species composition. But we certainly do not reject any role for climate. Indeed, one of our hypotheses is that the main effect of geology, and thus soils, on forest composition acts through moisture-holding capacity or soil depth, which obviously interacts with climate. Sollins (1998) reviewed eighteen studies on the importance of soils to tropical forest composition and found that edaphic factors—drainage and topography—had the greatest effects, as opposed to soil chemistry. In Pyke et al.'s (2001) ordination analysis of our data set, climate does prove to be an important factor predicting species composition. Ruokolainen, Tuomisto, Chave et al. (2002) offer more discussion of the effect of climate on tree species composition in this data set.

Despite these habitat effects on forest composition, we must emphasize that distance alone accounts for fairly high species turnover, and that the predictability of forest composition is low (but see Ruokolainen, Tuomisto, Chave et al. 2002). In fact, there is only one way to make a firm prediction about which species will be found at a new site: do an inventory next to the site. Nearby sites usually had forests of 60%–70% similarity. No sites more than a couple of kilometers apart had scores this high, and most had much lower similarity. Even plots with matching substrates, matching forest ages, and similar precipitation levels had low similarity when more than a few kilometers apart. Table 14.1 shows that dominant species were seldom the same, and is meant as a contrast to Terborgh, Foster, and Nuñez's (1996) table of abundant species for Peru. They found that plots 30 km apart in floodplain forest always shared six to eight of their ten most abundant tree species. Here in central Panama, even nearby sites seldom shared more than five of their top ten species. Forest composition in this part of Panama is evidently more variable than in Peru, even when fairly similar substrates and climates are deliberately selected (Pitman et al. 1999, 2001; Condit et al. 2002).

We recognize, though, that our analysis of substrate and other habitat variables is preliminary. We assumed that forests growing on the same rock formation experience similar soil conditions, and there are reasons to be cautious about this assumption. First, some of the formations are mixtures of rocks, and different sites within a formation may thus expose different rocks. Second, we have ignored topographic position and how it affects soil (Johnsson and Stallard 1989; Silver et al. 1994). We have topographic data for each plot, and a digital elevation map for the entire region is now done (R. Stallard, personal communication); T. Kursar and B. Engelbrecht (personal communication) have begun soil analyses. We intend to assemble this information, along with precipitation data, into a more complete model of tree species distributions. A similar approach has been used successfully for modeling forest structural types in the tropics (Mackey 1993; Mackey and Su, chap. 11 in this volume) and for modeling species distributions in other systems (Miller 1994; Cherrill et al. 1995; Sanderson et al. 1995).

At any rate, we feel that our results demand a pluralistic view about the forces that structure tree species composition in the tropics. Earlier studies seem to have emphasized what is predictable from simple habitat considerations, but have ignored what is not predictable (Hall and Swaine 1981; Baillie et al. 1987; ter Steege et al. 1993; Tuomisto and Ruokolainen 1994; Tuomisto et al. 1995; Terborgh, Foster, and Nuñez 1996). We believe that random forces and dispersal limitation are also important components of tree species composition in the tropics, along with niche differences among species and habitat differences.

Recently Ando et al. (1998), Pimm and Lawton (1998), and Van Jaarsveld et al. (1998) discussed the importance of species ranges and beta diversity in conservation. In the tropics, data on species ranges are scarce and usually have poor resolution. In central Panama, however, we now have sufficient information to examine how efficiently different arrangements of national parks would protect tree species. We know, for example, that plots L1, m25, m26, and m31 have unusual flora for the area, with species assemblages not seen elsewhere near the canal. Plots L1 and m31 were most unusual—their maximum Sørensen scores when compared with other plots were each 23%. In terms of localized species, however, plot m31 was by far the champion: it added 83 species to the data set (that is, the data set without m31, including all fifty hectares from the large plot on BCI, had 434 species, while with m31 added there were 517 species). Plot L1 added just three species, and plots m25 and m26 added five and seven species respectively. Since new parks may still be created in the canal area, we have an opportunity to influence conservation policy with good scientific information. Plot m31 is not currently in a protected area, and this part of the Santa Rita Ridge clearly merits some consideration in terms of plant species protection. Plots L1, m25, and m26 are also unprotected.

Perhaps more importantly, we would like to contribute to broader theories about beta diversity in species-rich forests in order to develop general policies for species preservation throughout the tropics. Results from the canal area of Panama suggest that the tree species composition of tropical forests can be predicted by abiotic features to only a limited extent, while much is unpredictable. This conclusion has important implications, for it suggests that conservation plans cannot simply be based on habitat designations. Because there is substantial species turnover within habitats, one cannot protect one section of a given habitat and hope to conserve most of the species found across that habitat. This conclusion is analogous to the growing concern about the use of "indicator" groups to designate conservation areas, since many studies to date show poor correlations between the distributions of species in one group, such as birds, and those in another group, such as plants (Wilcox et al. 1986; Kremen 1992; Balmford and Long 1995; Oliver, Beattie, and York 1998). Our parallel conclusion is that species distributions among tropical trees correlate poorly with abiotic habitat designations. If indicator groups or habitats do not work, conservation planning must be based on more empirical data on the ranges of individual species.

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