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Tree Species Composition of Barro Colorado Island in a Wider Context

The Canal Area and the Nation of Panama

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ABSTRACT. Barro Colorado Island is a center for tropical ecology because of its undisturbed old-growth forest. I arrived in Panama with a focus on the 50-ha plot but soon learned that nearby forests have many tree species not known at Barro Colorado, leading me to design a network of forest inventories across the isthmus with the goal of quantifying forest variation. I discovered turnover in species in every direction from Barro Colorado, even within 10 km of the island. Much of this variation is due to rainfall and geology, and the 50-ha plot has a relatively dry, phosphorus-rich tree community. At a wider scale, I assembled a checklist of Panama's entire tree flora and discovered that tree species of the 50-ha plot are mostly wide-ranging—far more so than average species of the complete flora. Long-term survey plots provide strong results on the demography of common and widespread species, but they are not effective at capturing narrow endemics.

INTRODUCTION

Many scientists visiting Barro Colorado Island (BCI) focus their studies on the remarkable stretch of old-growth forest and its abundant and diverse fauna, but they see little of the forests surrounding the island. Yet wider perspectives beckon. The Barro Colorado Nature Monument includes four times as much forest as the island, and the Gigante Peninsula has become a major research focus (Wright et al., 2011). Across the Canal is a large stretch of forest at Pipeline Road that extends nearly unbroken toward Panama City (Wright et al., 2000). Indeed, land flanking the Panama Canal retains forest across the isthmus (Condit et al., 2001, Ibáñez et al., 2002). Nowhere farther north in Central America does a continuous forest cross the isthmus.

The sizeable protected forest surrounding Barro Colorado offers ample opportunity for comparing the BCI species composition to other sites nearby. When I arrived in Panama in 1991, Robin Foster had been studying local botanical variation for years, and I was fortunate to take many forest walks with Robin, visiting the 50-ha plot often as well as Pipeline Road, Santa Rita, and elsewhere. He was an endless source of details on the tree flora of the region, and he and I discussed several hypotheses about the causes of variation in forest composition. Soon after finishing the 1990 BCI census, I decided to test these hypotheses, and this meant turning Robin's observations into quantitative community analysis. I began a network of tree plots at Cocoli, Fort Sherman, Pipeline Road, Sendero El Charco, Santa Rita, and Parque Metropolitano, all of which are lowland forests within 40 km of BCI (Fig. 1).

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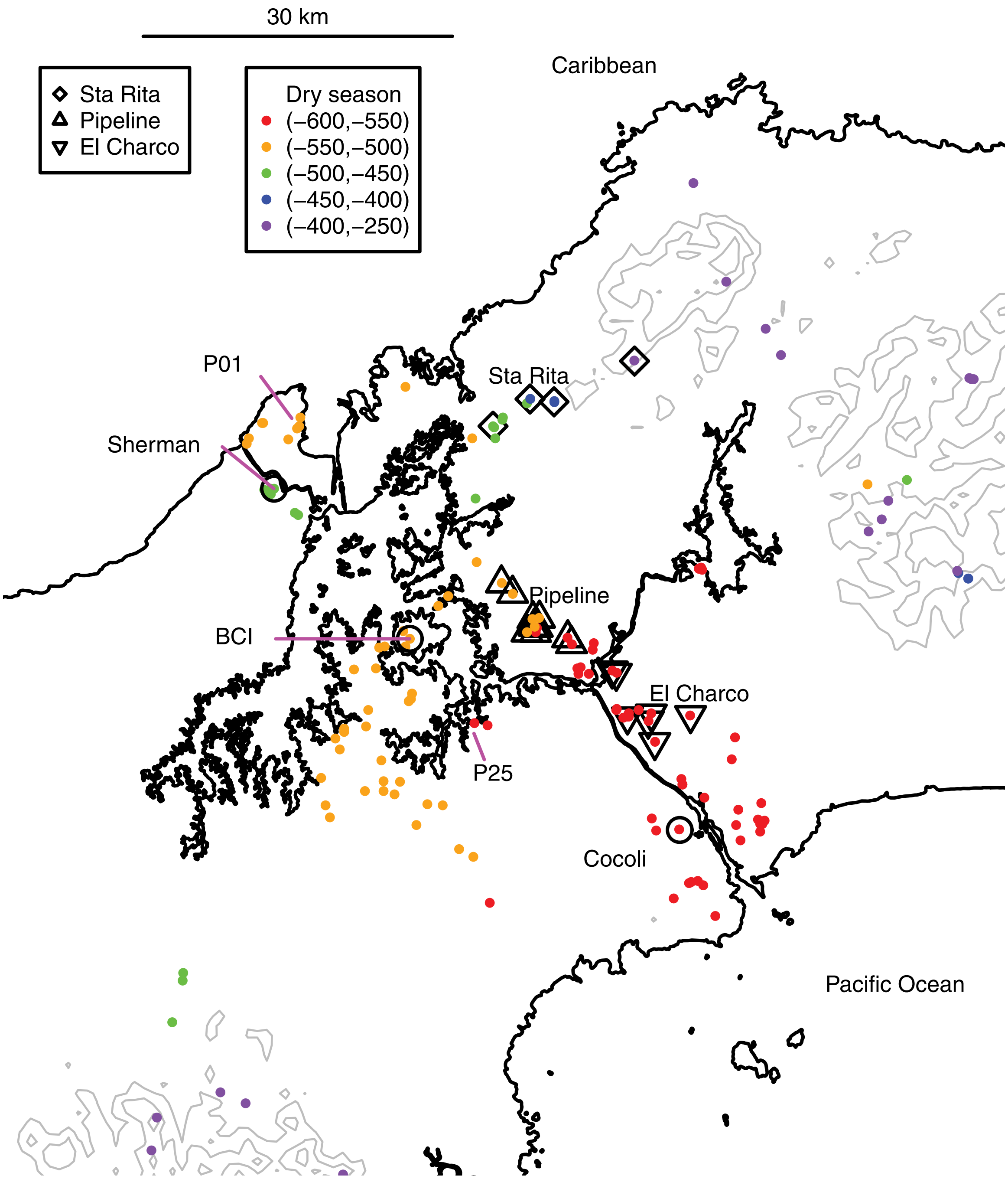

FIGURE 1. Forest regions and the Condit plots around BCI and the Panama Canal. Dots show locations of all plots and inventories, color coded by dry season intensity to show the rainfall pattern: purple are the wettest, with a dry season moisture deficit of less than 400 mm (or > −400 mm), and red are the driest, with a deficit exceeding 550 mm (or < −550 mm). The three larger plots are marked with large black circles and named as follows: the 6-ha Sherman plot, 4-ha Cocoli plot, and 50-ha BCI plot. The 1-ha plots used to define forest regions (Table 1) are marked separately: Santa Rita cluster, including plots Plot31, Plot32, P33, and Fincaroubik (diamonds); Pipeline Road cluster, including plots P05, P06, P07, P08, P09, P15, P16, P17, P19, P20 (upward triangles); and the El Charco cluster, including plots P23, P24, P27, P28; and Carita, Soberania, and Elcharco (downward triangles). Plots P01 and P25, both mentioned in the text, are labeled. Plot names and locations, with the full tree censuses at each, can be found in Condit et al. (2019b). Gray contour lines are at elevations 400, 600, and 800 m above sea level.

Questions about tree community variation were originating themes of the science of ecology, including a lively debate contrasting plant associations with the individualistic hypothesis of ecological communities (Whittaker, 1967). Indeed, in his paper on individualistic plant communities, Gleason (1926) mentions tropical forests as a challenge to the notion of plant associations, given that high diversity makes it difficult to define associations by dominant species. Later, Holdridge (1967) accepted the difficulty of defining species associations and based his description of Central American plant communities on climate, defining forest types based on rainfall and elevation. Although Holdridge's system became widely used, by omitting species it misses a feature that attracts everyone to the tropics—that is, species diversity. Despite the difficulties of working in diverse forests, Robin Foster kept his focus on species, and I intended from the outset to follow his lead, measuring continuous, quantitative variation among the hundreds of tree species that comprise the forests (Borcard, 1992; Tuomisto et al., 1995, 2003; Condit et al., 2002, 2004, 2005, 2013).

In addition to the 50-ha plot that I inherited from Hubbell and Foster (1983), Steve and Robin had other projects in the works that I took over and extended. One was a proposal for several 4-ha plots across the isthmian rainfall gradient. The proposal was not funded by the National Science Foundation (NSF), but in the early 1990s, George Angehr and I managed a Department of Defense Legacy grant to initiate two such plots on former military land, one at Cocoli near the Pacific and across the Canal from Panama City, and the other near the U.S. Army Fort Sherman near the Caribbean (Condit et al., 2004). Later, funded mostly by U.S. Agency for International Development, I set up a larger network of plots, and by switching to the more manageable size of 1 ha, I was able to include far more sites. The network now has 65 plots (Pyke et al., 2001; Condit et al., 2013, 2019b; Turner et al., 2018; Aoyagi et al., 2023).

Another project I inherited from Robin Foster in the early 1990s was a complete checklist of the tree species of Panama, originating from an electronic version of D'Arcy (1987). With help from the botanical expertise of Rolando Pérez and Salomón Aguilar, who had studied under Robin for several years, I updated Robin's version, and I used this species tally in early papers (Condit et al., 1998). More recently, as online botanical databases expanded, I thoroughly vetted the checklist by looking for specimens of every species (Condit et al., 2020).

Drawing from the extensive network of plots that quantify tree communities of the Panama Canal area, I published several papers documenting variation in tree species composition and how it relates to climate and geology. Subsequently, with the updated checklist of Panama trees, I examined global range sizes of all Panama's species, including those found in the Canal Area plots. Here, I review those results with a focus on how the Barro Colorado tree community compares with surrounding forests.

I make the BCI comparison in three ways. First, I identify the dominant species of the 50-ha plot and compare them to dominant species of other nearby forests. This checks whether associations of dominant species can be made across many of the forests, which might hold if species turnover is due mostly to rare species. I addressed this topic briefly but incompletely in Condit et al. (2005). Second, I examine the climatic and soil associations of the Barro Colorado tree species compared with the rest of the tree community. Canal Area climate and soils are highly variable, and where BCI falls helps to explain why its forest community differs. Third, I examine geographic ranges of the BCI plot species to determine where else they occur across the Neotropics. What proportion of the entire tree flora of Panama is represented in the 50-ha plot? Which of the plot species have the widest global ranges?

BETA-DIVERSITY: CHANGES IN FOREST COMPOSITION ACROSS THE CANAL AREA

The hypotheses Robin Foster and I discussed about variation in forest composition included climate and geology. Holdridge (1967) highlighted the importance of annual rainfall in forest variation, but Robin as well as Joe Wright and Egbert Leigh had already concluded that dry season duration was the key to the vegetation, not total rainfall (Wright and Cornejo, 1990; Wright, 1992; Leigh, 1999). Robin also considered geological influences, and he taught me two patterns about how soil and geology influenced the forest. One was the tendency for limestone to harbor conspicuous clusters of deciduous species, easily visible at several locations during the dry season, especially, for example, next to the Madden Dam (Gentry, 1982, Condit et al., 2005). Another was a subtle effect that Robin picked out along Pipeline Road, where flora of the flatter terrain near the Frijoles and Frijolito streams contrasts with that on steep ridges past Limbo Hunt Club. He attributed the contrast to geology. My network of 1-ha plots was designed to test both geological hypotheses.

The importance of limestone was readily quantified. One plot near Fort Sherman, P01 in the network, was deliberately placed on Toro limestone, and its tree flora is, as expected, most similar to drier Pacific sites 55 km away at Cocoli (Pyke et al., 2001; Condit et al., 2005) but unlike nearby non-limestone sites. Two other plots, P25 and P26 at a site called Laguna, were a test of the subtler geological influence that Robin Foster observed. They were placed on an outcrop of andesite south of Barro Colorado that matches the geological formation forming ridges at Pipeline Road. The Laguna plots dramatically confirmed the pattern Robin saw: they harbor many species from Pipeline Road that are absent at Barro Colorado, such as the conspicuous palm *Welgia georgii* (Pyke et al., 2001; Condit et al., 2005). Laguna even has Caribbean wet forest species otherwise known only at Sherman or Santa Rita, such as the giant chicle, *Manilkara bidentata*. A total of 32 species at Laguna are absent from BCI but known at wetter sites. In Condit et al. (2005), we speculated that soils at Laguna have an unusual moisture-holding capacity, converting it to a wet forest despite getting less rain than BCI.

Another metric of forest similarity—that is, the correlation between abundance of all species between two plots—demonstrates high variation in species composition. The correlation between abundances in the 6-ha plot at Sherman and the 50-ha plot at BCI is nearly zero, but there is a weak positive correlation between BCI and the Cocoli 4-ha plot (Condit et al., 2004).

I extended the study of forest plots and forest variation to Amazonia. First, in the mid-1990s, Robin Foster and I started the Yasuni 25-ha plot in Ecuador, where he also had years of experience. At the same time, Nigel Pitman and John Terborgh were asking questions about variation in forest composition in Ecuador and Peru (Pitman et al., 1999), and Pitman and I designed a precise comparison of beta-diversity between Panama and Amazonia. This study clearly demonstrated high beta-diversity of forests near the Panama Canal relative to forests in Ecuador and Peru (Condit et al., 2002). For example, two plots near opposite ends of the Panama Canal rainfall gradient, 55 km apart, share <10% of their species, whereas sites 60–200 km apart in Ecuador share >30%.

The reasons behind this abrupt variation in forest composition near the Panama Canal are easily understood given the rainfall gradient and highly varied geology, both arising from Panama's position on a narrow isthmus between continental plates. Tropical storms move westward, delivering more rain on the Caribbean slope, and the Santa Rita ridge is much wetter than Cocoli (3,230 mm annual rainfall compared with 1,940 mm; Fig. 1). Moreover, the geological formations are abruptly variable (Stewart and Stewart, 1980), caused by collision of the plates, and the geological changes lead to strikingly variable soil chemistry over short distances. In addition to the examples Robin Foster taught me, I discovered more cases where shifts in vegetation conspicuously match geological transitions. A wide vista illustrating one transition can be studied from the top of the canopy tower on Cerro Pelado above the Gamboa Resort, looking northward at two adjacent hills. During the dry season, the hill to the northeast is covered in deciduous trees, mostly *Cavanillesia platanifolia* (Malvaceae) and *Bursera simarouba* (Burseraceae), plus the conspicuous white flowers of *Calycophyllum candidissimum* (Rubiaceae), whereas the next hill west, as well as Cerro Pelado itself, are entirely evergreen. That vegetation boundary is created by a geological fault defining a change in rock formation (Stewart and Stewart, 1980). To the west (evergreen) is the andesite of Pipeline Road; to the east (deciduous) is Gatuncillo sandstone and limestone.

In Condit et al. (2005), I set up a rigorous measure of the impact of geology on forest composition. This showed that plot pairs within 2 km of one another but on contrasting geological formations were slightly less similar than plot pairs on the same geology. The shortcoming, however, was that I had no understanding of how geology affected the soil, so I considered every different rock formation as distinct. Fortunately, the lack of geological expertise changed when Benjamin Turner came to Smithsonian Tropical Research Institute (STRI) and began detailed evaluation of soil chemistry at my tree plots (Turner et al., 2013, 2018).

Armed with direct measures of soil chemistry, I could replace the crude forest divisions based on geology with quantitative variation in nutrients that trees require, and I combined these with a rigorous measure of dry season duration at every plot using detailed rainfall records from the Panama Canal Authority. Based on the Condit et al. (2005) analysis, I expected to find weak associations of tree distributions with soil nutrients, but I did anticipate the strong effects of climate. I was surprised, then, when I found that tree species distributions are limited by soil phosphorus, and conspicuously so, almost as much as they are limited by dry season intensity (Condit et al., 2013). Although many species are associated with the wet or dry zones and do not respond to soil, other species that I understood to be associated with dry climate, such as *Cavanillesia platanifolia*, are in fact more strongly associated with high phosphorus. Even more fascinating is a large group of species that appear only at soils with very low phosphorus, regardless of rainfall. This is the group that dominates the Laguna plots, which have low phosphorus on the drier half of the isthmus. Those species are not wet-forest species, but are rather phosphorus-avoiding species.

CONSISTENCY IN DOMINANT SPECIES: TROPICAL TREE ASSOCIATIONS?

The published analyses on beta-diversity and climate-soil associations were based on the entire communities, from common to rare. But scientists visiting BCI naturally focus on the dominant tree species, because they produce the most biomass and the most food for the island's important herbivores. Visiting naturalists will want to learn these dominants, starting with the most abundant species in the 50-ha plot. The notion of a "species association" is also defined by the abundant species (Whittaker, 1967). How well do the dominant species at BCI represent nearby forests?

Judging from the 10 most abundant species, BCI is not like nearby forests. Seven of the 10 dominants at BCI are not dominant in five nearby forest regions, and only *Faramea occidentalis* is dominant in two other regions (Fig. 1, Table 1). No dominant species at BCI is also dominant in the wet Caribbean forests of Santa Rita. Two species drive home the variation in dominant species: In the 50-ha plot, *Pombalia prunifolia* is the numerically dominant species of the forest understory (Table 1). Its average density is 557 trees per ha, and few places in the plot do not have a *Pombalia* within a few meters. At Pipeline Road, 11 km away, the corresponding understory dominant is *Oxandra longipetala* (Annonaceae), with 409 trees per ha. Yet *Oxandra* is absent from the BCI plot and has never been recorded on the island. Conversely, *Pombalia* is in only 3 of the 10 Pipeline Road plots and has a mean density of only 26 per ha there, less than 5% of its BCI density.

The distinction between BCI and other forests in terms of dominant species is expected given the high species turnover from site to site, and the two other large plots confirm this phenomenon. Only 3 of the 10 dominant species in the Sherman plot are dominant at another site, including *Protium panamense*, which is also dominant at BCI. Cocoli shares 4 of its 10 dominant species with at least one other forest, including *Faramea occidentalis*, which also is dominant at BCI. As a result of the low overlap among the abundant species, Table 1 includes a total of 28 species, out of 30 possible species if none were shared at all. These observations confirm Gleason's (1926) assertion that plant associations are difficult to define in the tropics and illustrate why I avoided species grouping in my analyses of beta-diversity and habitat association, using instead the Gleasonian notion of individualistic plant communities.

CLIMATE AND SOIL PREFERENCES OF BCI TREES

BCI soils are above the median phosphorus concentration of the area (Condit et al., 2013), and this is revealed by how the BCI tree species respond to soil phosphorus (Fig. 2). The median phosphorus response for those species not found in the plot is −0.83, the negative indicating that those species are more often present where phosphorus availability is low. In contrast, the median for species of the 50-ha plot is close to 0. This is evident in Figure 2, which shows that most species strongly favoring high phosphorus (phosphorus response >1) are in the BCI plot, whereas few of those with a highly negative phosphorus response (<−1) are.

In terms of response to moisture, BCI species are slightly below the median (Fig. 2), that is, they favor a drier climate more than non-BCI species. The dominant species of the plot, however, are opposite, falling above zero (8 of the 10 dominant species favor wetter climates; Fig. 2).

Considering moisture and phosphorus together, the most conspicuous distinction of the 50-ha plot community is the group of species that jointly favors low phosphorus and wet climate (see the lower right of Figure 2). That diverse group of species is almost absent at BCI, with the abundant *Protium panamense* being a conspicuous exception. This is the tree community of the true wet forests at Santa Rita Ridge (Fig. 1). BCI shares few species with those diverse, wet, low-phosphorus forests (Pérez et al., 2005).

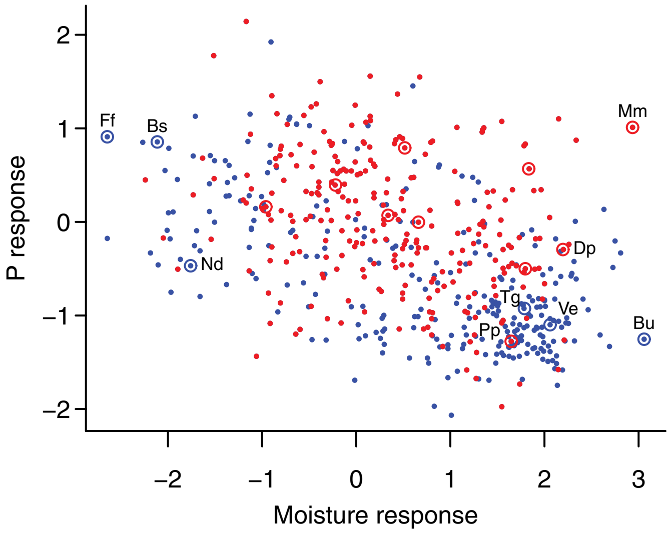

FIGURE 2. Phosphorus-moisture preference of 550 Canal area species. Colors represent species found in the BCI 50-ha plot (red) or not (blue). The phosphorus response (y-axis) is the amount by which the probability (logit-transformed) of finding a species at a site increases with every increase of log(soil phosphorus) by 1 standard deviation; the moisture response is the same for every increase of 1 SD in dry season moisture. Positive responses describe species that are found more often in high phosphrous and wet climate, and responses > 1 or < −1 were often statistically significant. The same scatterplot is Figure 3 in Condit et al. (2013). The 10 dominant species of the plot (Table 1) have larger red circles added, including *Desmopsis panamensis* (Dp), *Mouriri myrtilloides* (Mm), and *Protium panamense* (Pp). Several common non-BCI species are also named (larger blue circles: Ff = *Fissicalyx fendleri* [Fabaceae], Bs = *Bursera simarouba* [Burseraceae], Nd = *Neea delicatula* [Nyctaginaceae], Tg = *Tapirira guianensis* [Anacardiaceae], Ve = *Virola elongata* [Myristicaceae], *Bu* = *Brosimum utile* [Moraceae]).

GLOBAL RANGES OF BARRO COLORADO TREES

My update of Robin Foster's complete tree flora of Panama identified many tree species with extremely narrow ranges: 16.2% of the 3043 tree species known in Panama have global ranges <20,000 km^2 (Condit et al., 2020). But few of these narrow endemics appear in any of my surveys: of 550 species across 72 plots and inventories analyzed in Condit et al. (2013), only 17 have such narrow ranges (3.1%). Among the 321 species known in the 50-ha plot, only 6 (1.9%) have ranges <20,000 km^2; indeed, only 16 have ranges <200,000 km^2 (Table 2; Condit et al., 2017, 2020). The narrow endemics are conspicuous among the wet forest group identified in the lower right of Figure 2, which includes those with joint

TABLE 1. The 10 numerically dominant species in the three larger plots, including (a) the BCI 50-ha plot as well as (b) a 4-ha Cocoli plot and (c) a 6-ha Sherman plot, compared with the 10 dominant species at other sites. The other sites include the three large plots plus three other groupings of 1-ha plots: Santa Rita, Pipeline Road, and El Charco (Fig. 1). The density per ha of all trees larger than 1 cm diameter at breast height (dbh) in the respective plots is given, as well as the global geographic range (in millions of km^2) from Condit et al. (2020). For each species, all other locations where the species was also one of the 10 dominants are listed. *Pombalia prunifolia* has long been known as *Hybanthus prunifolius* at BCI, *Protium stevensonii* as *Tetragastris panamensis*, *Garcinia recondita* as *G. intermedia*, and *Tachigali panamensis* as *T. versicolor* (for all synonyms, see Condit et al., 2019a).

Top ranking species	Density in plot	Other sites where dominant	Range size
	(a) At BCI		
Pombalia prunifolia (Violaceae)	556.9	None	1.39
Faramea occidentalis (Rubiaceae)	499.7	El Charco (2nd rank) Cocoli (3rd rank)	13.5
Desmopsis panamensis (Annonaceae)	220.7	Pipeline (7th rank)	0.23
Trichilia tuberculata (Meliaceae)	216.8	None	4.48
Alseis blackiana (Rubiaceae)	158.6	None	1.65
Mouriri myrtilloides (Melastomataceae)	136.1	None	8.42
Garcinia recondita (Clusiaceae)	96.4	None	0.67
Protium stevensonii (Burseraceae)	92.4	None	8.57
Hirtella triandra (Chrysobalanaceae)	88.1	None	13.08
Protium panamense (Burseraceae)	60.4	Sherman (top rank) Pipeline (4th rank)	0.25
	(b) At Cocoli		
Eugenia principium (Myrtaceae)	195.5	None	0.47
Protium tenuifolium (Burseraceae)	173.5	El Charco (top rank)	10.90
Faramea occidentalis (Rubiaceae)	158.5	El Charco (2nd rank) BCI (2nd rank)	13.5
Coussarea curvigemmia (Rubiaceae)	154.0	None	0.07
Sorocea affinis (Moraceae)	140.5	Pipeline (9th rank)	0.64
Brosimum alicastrum (Moraceae)	133.2	El Charco (9th rank)	11.85
Heisteria concinna (Olacaceae)	75.5	None	1.94
Trichilia pleeana (Meliaceae)	74.2	None	12.12
Astronium graveolens (Anacardiaceae)	65.0	None	14.87
Alibertia edulis (Rubiaceae)	56.0	None	13.30
	(c) At Sherman		
Protium panamense (Burseraceae)	224.8	BCI (10th rank) Pipeline (4th rank)	0.25
Tovomita longifolia (Clusiaceae)	209.4	Santa Rita (6th rank)	9.46
Tovomita stylosa (Clusiaceae)	162.1	None	1.77
Perebea xanthochyma (Moraceae)	154.2	Pipeline (6th rank)	5.65
Tapirira guianensis (Anacardiaceae)	122.5	None	13.24
Socratea exorrhiza (Arecaceae)	108.1	None	8.01
Geonoma congesta (Arecaceae)	105.5	None	0.55
Unonopsis panamensis (Annonaceae)	104.2	None	0.07
Marila laxiflora (Calophyllaceae)	95.8	None	6.16
Tachigali panamensis (Fabaceae)	88.4	None	0.02

TABLE 2. Species of the BCI 50-ha plot having global geographic ranges <200,000 km^2, sorted by range size (given in km^2, not millions of km^2 as in Table 1). Density per ha in the plot in 2010 is included. Only six species are narrow endemics, with ranges <20,000 km^2. *Virola fosteri* was named in honor of our mentor, after being split off from *V. multiflora* (Santamaría-Aguilar et al., 2019), the name used in earlier papers (Condit et al., 2004). *T. panamensis* has been known as *T. versicolor* at BCI, but it is now segregated as a Panama endemic (van der Werff and Zamora, 2010). Five species of *Piper* might be added to the list, but Callejas's (2020) massive revision of the genus rearranged most taxa, and ranges are currently not reliable.

Species (family)	BCI density	Range size
Mosannona garwoodii (Annonaceae)	10.1	610
Eugenia nesiotica (Myrtaceae)	10.1	8,050
Virola fosteri (Myristicaceae)	0.8	11,010
Coccoloba manzinellensis (Polygonaceae)	7.0	15,730
Tachigali panamensis (Fabaceae)	41.7	19,310
Virola nobilis (Myristicaceae)	3.5	19,920
Spachea membranacea (Malpighiaceae)	0.2	25,830
Anaxagorea panamensis (Annonaceae)	17.7	42,460
Guatteria lucens (Annonaceae)	17.5	64,970
Coussarea curvigemmia (Rubiaceae)	40.3	69,670
Cordia lasiocalyx (Cordiaceae)	22.9	101,000
Annona spraguei (Annonaceae)	3.0	114,000
Eugenia coloradoensis (Myrtaceae)	12.2	145,000
Cecropia longipes (Urticaceae)	0.3	156,000
Conostegia bracteata (Melastomataceae)	0.1	166,000
Protium costaricense (Burseraceae)	14.0	189,000

preferences for low phosphorus and wet climate. Most species shown in Figure 3 with ranges <20,000 km^2 fall in this group, having a moisture-response >1 (Fig. 3b) and a phosphorus response <−1 (Fig. 3a).

Although unusual, there are impressive examples of narrow endemics from the 50-ha plot. *Mosannona garwoodii* has a tiny range at 610 km^2, encompassing a few Condit plots near the Canal, and two other prominent and well-studied BCI species, *Tachigali panamensis* and *Virola nobilis* (Foster, 1977; Howe, 1990), are also narrow endemics. Overall, however, plots do not provide much information about narrow endemics. The flip side is that the plots offer numerous examples of species with wide ranges. The median global range of species in the 50-ha plot is 6.1 million km^2, which is nearly 10 times higher than the median of all Panama species (693,000 km^2), and 83% of the plot species occur beyond Colombia in South America, compared with 53% of the entire tree flora of Panama. Hubbell (2013) defined species as locally rare if they had <1 per ha in the 50-ha plot, but with the median range of plot species, that density would lead to a global population >100 million individuals. Even the exceedingly scarce *Spachea membranacea*, with 10 trees in the 2010 census of 50 ha (Table 2), would have a population of 100,000 trees even if 80% of its known range is clear-cut.

Thus, species with only a few individuals in the 50-ha plot might have enormous global populations. This is especially so because plot abundance is not at all correlated with global range size (Fig. 4). Some of the dominant species of the plot have ranges <250,000 km^2, far below the plot median, whereas species with a handful of individuals are among the widest ranging. Indeed, the widest range of all, 1.69×10^7 km^2, is *Ficus citrifolia*, and it has only two trees in 50 ha.

CONCLUSIONS

Researchers at BCI should understand that most dominant species there are not abundant anywhere nearby. Although density within the 50-ha plot BCI may affect pest pressure, abundance is certainly not a consistent species trait: range sizes cover thousands of kilometers, while local density varies sharply over tens of kilometers. Moreover, even the species that are relatively

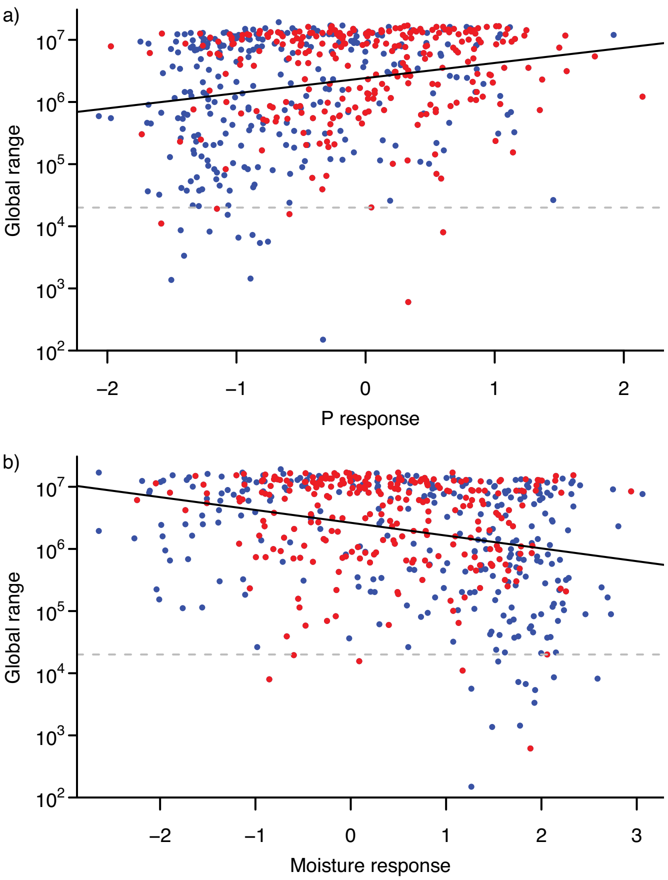

FIGURE 3. Global range size and local habitat preferences in Panama tree species. (**a**) Phosphorus preference on the x-axis, measured as change in occurrence probability in response to increasing phosphorus concentration (Fig. 2). (**b**) Moisture preference on the x-axis, measured as change in occurrence probability in response to increasing dry season moisture (Fig. 2). Range size (log scale) is on the y-axis in both panels (from Condit et al., 2019, 2020). All 550 species analyzed in Condit et al. (2013) are included; species from the BCI 50-ha plot are red points, and the rest are blue. Points are concentrated at the top, with a range just below 2 × 10^7 km^2, because the entire Neotropics is about 1.5 × 10^7 km^2, that is, the widest-ranging species reach a limit at the Tropics of Cancer and Capricorn (a few exceptions extend outside the tropics). The lines are regressions, using log (range size), and both are highly significant.

rare in the BCI plot are not rare globally. This is not something odd about the BCI forest—it is a fact about the high environmental variability within Panama. Dominant species at the other two large-size plots are likewise not abundant elsewhere.

Where do BCI tree species lie relative to the habitat preferences of other species of the Canal Area? They are clearly a high-phosphorus group, while climatically, BCI species are closer to

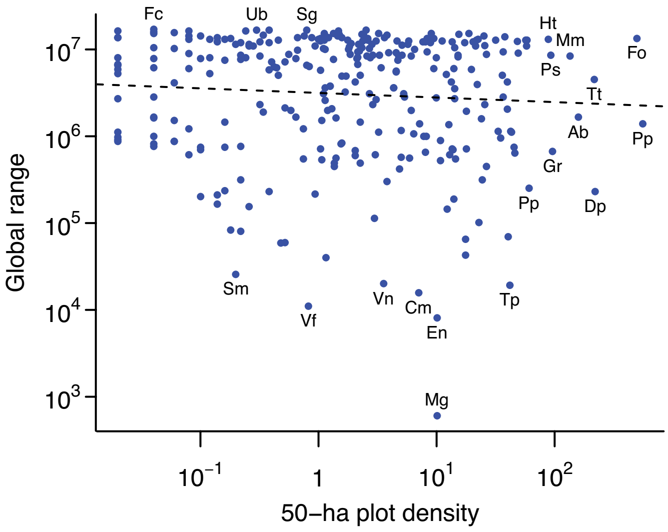

FIGURE 4. Global geographic range and abundance in the 50-ha plot. Both axes are logarithmic. The line is a regression, and it is not statistically significant. Several species are labeled, using initial letters of genus and species. Names of the 10 most abundant can be read out of Table 1a, and those of the seven smallest ranges out of Table 2. The other labels are the three widest-ranging species in the plot, *Ficus citrifolia* (Moraceae), *Urera baccifera* (Urticaceae), and *Sapium glandulosum* (Euphorbiaceae), all having ranges of 1.7 × 10^7 km^2.

the dry side of the isthmus. The greatest forest division in the area separates forests of the dry half of the isthmus, from wet, low-phosphorus Caribbean forests (Fig. 1). BCI is a high-nutrient site on the dry half.

The Barro Colorado forest is very much like other Neotropical forests in important features, such as tree diversity, canopy height, tree density, basal area, and biomass. The taxonomic families of the tree species of BCI are typical as well. In many ways, then, Barro Colorado is a good representative of a moist, mature tropical forest. Species associations do not repeat in central Panama, however, and the forest composition of BCI does not reappear in other forests. Moreover, the plot misses the many tropical tree species with tiny ranges. From a wider perspective, nearly all the species encountered in census plots are wide-ranging and are not rare. Understanding the biology of Panama's narrow endemics will require approaches much different from arbitrarily located plots.

REFERENCES

Aoyagi, R., R. Condit, and B. L. Turner. 2023. Breakdown of the growth–mortality trade-off along a soil phosphorus gradient in a diverse tropical forest. *Proceedings of the Royal Society. B* 290: 20231348.

Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the Spatial Component of Ecological Variation. *Ecology,* 73: 1045–1055.

Condit, R., S. Aguilar, A. Hernandez, R. Pérez, S. Lao, G. Angehr, S. P. Hubbell, and R. B. Foster. 2004. Tropical Forest Dynamics Across a Rainfall Gradient and the Impact of an El Niño Dry Season. *Journal of Tropical Ecology*, 20: 51–72.

Condit, R., S. Aguilar, A. Hernandez, R. Pérez, S. Lao, and C. R. Pyke. 2005. Spatial Changes in Tree Composition of High-Diversity Forests: How Much Is Predictable? In *Tropical Rainforests: Past, Present and Future*, ed. C. Dick and C. Moritz, pp. 271–294. Chicago: University of Chicago Press.

Condit, R., S. Aguilar, and R. Pérez. 2020. Trees of Panama: A Complete Checklist with Every Geographic Range. *Forest Ecosystems*, 7: 42.

Condit, R., B. M. J. Engelbrecht, D. Pino, R. Pérez, and B. L. Turner. 2013. Species Distributions in Response to Individual Soil Nutrients and Seasonal Drought Across a Community of Tropical Trees. *Proceedings of the National Academy of Sciences*, 110: 5064–5068.

Condit, R., R. B. Foster, S. P. Hubbell, R. Sukumar, E. G. Leigh, N. Manokaran, S. Lao, J. V. LaFrankie, and P. S. Ashton. 1998. Assessing Forest Diversity on Small Plots: Calibration Using Species-Individual Curves from 50-ha Plots. In *Forest Biodiversity Research, Monitoring and Modeling,* ed. F. Dallmeier and J. A. Comiskey, pp. 247–268. New York: Parthenon.

Condit, R., R. Pérez, and S. Aguilar. 2019a. Complete Tree Species of Panama, DataONE, Dataset, Version: July 7, 2020. https://doi.org/10.15146/R3M97W

Condit, R., R. Pérez, S. Aguilar, and S. Lao. 2019b. Census Data from 65 Tree Plots in Panama, 1994–2015. https://doi.org/10.15146/mdpr-pm59

Condit, R., R. Pérez, S. Aguilar, S. Lao, and S. P. Hubbell. (2017). Demographic Trends and Climate Over 35 years in the Barro Colorado 50 ha Plot. *Forest Ecosystems*, 4: 1–13.

Condit, R., N. Pitman, E. G. Leigh, J. Chave, J. Terborgh, R. B. Foster, P. Núñez, S. Aguilar, R. Valencia, G. Villa, H. C. Muller-Landau, E. Losos, and S. P. Hubbell. 2002. Beta-Diversity in Tropical Forest Trees. *Science*, 295: 666–669.

Condit, R., W. D. Robinson, R. Ibáñez, S. Aguilar, O. Sanjur, R. Martinez, R. F. Stallard, T. Garcia, G. R. Angehr, L. Petit, J. Wright, T. R. Robinson, and S. Heckadon-Moreno. 2001. The Status of the Panama Canal Watershed and Its Biodiversity at the Beginning of the 21st Century. *BioScience*, 51: 389–398.

D'Arcy, W. G. 1987. Flora of Panama. Checklist and Index. Part 1: The Introduction and Checklist. Monographs in Systematic Botany from the Missouri Botanical Garden, 17.

de Paula-Souza, J., and H. E. Ballard, Jr. 2014. Re-establishment of the Name *Pombalia*, and New Combinations from the Polyphyletic *Hybanthus* (Violaceae). *Phytotaxa*, 183: 1–15.

Foster, R. B. 1977. *Tachigalia versicolor* Is a Suicidal Neotropical Tree. *Nature*, 268: 624–626.

Gentry, A. H. 1982. Patterns of Neotropical Plant Species Diversity. *Evolutionary Biology*, 15: 1–84.

Gleason, H. A. 1926. The Individualistic Concept of the Plant Association. *Bulletin of the Torrey Club*, 53: 7–26.

Holdridge, L. R. 1967. *Life Zone Ecology*. San Jose, Costa Rica: Tropical Science Center.

Howe, H. F. 1990. Survival and Growth of Juvenile *Virola surinamensis* in Panama: Effects of Herbivory and Canopy Closure. *Journal of Tropical Ecology,* 6: 259–280.

Hubbell, S. P. 2013. Tropical Rain Forest Conservation and the Twin Challenges of Diversity and Rarity. *Ecology and Evolution*, 10: 3263–3274.

Hubbell, S. P., and R. B. Foster. 1983. Diversity of Canopy Trees in a Neotropical Forest and Implications for Conservation. *Tropical Rain Forest: Ecology and Management*, ed. T. Whitmore, A. Chadwick, and A. Sutton, pp. 25–41. Oxford: British Ecological Society.

Ibáñez, R., R. Condit, G. Angehr, S. Aguilar, T. García, R. Martínez, A. Sanjur, R. Stallard, S. J. Wright, A. S. Rand, and S. Heckadon. 2002. An Ecosystem Report on the Panama Canal: Monitoring the Status of the Forest Communities and the Watershed. *Enviromental Monitoring and Assessment*, 80: 65–95.

Leigh, E. G. 1999. *Tropical Forest Ecology: A View from Barro Colorado Island*. New York: Oxford University Press.

Pitman, N., J. Terborgh, M. R. Silman, and V. P. Nuñez. 1999. Tree Species Distributions in an Upper Amazonian Forest. *Ecology*, 80: 2651–2661.

Pyke, C. R., R. Condit, S. Aguilar, and S. Lao. 2001. Floristic Composition Across a Climatic Gradient in a Neotropical Lowland Forest. *Journal of Vegetation Science*, 12: 553–566.

Santamaría-Aguilar, D. A., R. Aguilar-Fernández, and L. P. Lagomarsino. 2019. A Taxonomic Synopsis of *Virola* (Myristicaceae) in Mesoamerica, Including Six New Species. *PhytoKeys*, 134: 1–82.

Stewart, R. H., and J. L. Stewart. 1980. *Geologic Map of the Panama Canal and Vicinity, Republic of Panama*. United States Geological Survey, Map No. I-1232.

Tuomisto, H., K. Ruokolainen, M. Aguilar, and A. Sarmiento. 2003. Floristic Patterns Along a 43-km Long Transect in an Amazonian Rain Forest. *Journal of Ecology*, 91: 743–756.

Tuomisto, H., K. Ruokolainen, R. Kalliola, A. Linna, W. Danjoy, and Z. Rodríguez. 1995. Dissecting Amazonian Biodiversity. *Science*, 269: 63–66.

Turner, B. L., T. Brenes-Arguedas, and R. Condit. 2018. Pervasive Phosphorus Limitation of Tree Species But Not Communities in Tropical Forests. *Nature*, 555: 367–370.

Turner, B. L., J. B. Yavitt, K. E. Harms, M. N. Garcia, T. E. Romero, and S. J. Wright. 2013. Seasonal Changes and Treatment Effects on Soil Inorganic Nutrients Following a Decade of Fertilizer Addition in a Lowland Tropical Forest. *Soil Science Society of America Journal*, 77: 1357–1369.

van der Werff, H., and N. A. Zamora V. 2010. Note on *Tachigali* (Leguminosae) in Central America with the Description of a New Species. *Harvard Papers in Botany*, 15: 149–153.

Whittaker, R. H. 1967. Gradient Analysis of Vegetation. *Biological Reviews*, 42: 207–264.

Wright, S. J., and F. H. Cornejo. 1990. Seasonal Drought and Leaf Fall in a Tropical Forest. *Ecology*, 71: 1156–1175.

Wright, S. J. 1992. Seasonal Drought, Soil Fertility and the Species Density of Tropical Forest Plant Communities. *Trends in Ecology and Evolution*, 7: 260–263.

Wright, S. J., J. B. Yavitt, N. Wurzburger, B. L. Turner, E. V. J. Tanner, E. J. Sayer, L. S. Santiago, M. Kaspari, L. O. Hedin, K. E. Harms, M. N. Garcia, and M. D. Corre. 2011. Potassium, Phosphorus, or Nitrogen Limit Root Allocation, Tree Growth, or Litter Production in a Lowland Tropical Forest. *Ecology*, 92: 1616–1625.

Wright, S. J., H. Zeballos, I. Dominguez, M. M. Gallardo, M. C. Moreno, and R. Ibañez. 2000. Poachers Alter Mammal Abundance, Seed Dispersal, and Seed Predation in a Neotropical Forest. *Conservation Biology*, 14: 227–239.