Chapter 6

BIOGEOGRAPHIC HISTORY AND THE HIGH β-DIVERSITY OF PANAMANIAN RAINFOREST TREES

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Abstract: In a recent study examining the degree to which tree species composition differs among rainforest sites (*i.e., β*-diversity), Condit *et al.* (2002) found that plots in the Panama Canal watershed separated by 50 km were more highly differentiated than plots in Western Amazonia separated by nearly 1400 km. The high *β*-diversity of trees in Panama was attributed to sharp environmental gradients between the Atlantic and Pacific coasts. However, the pattern may also result from Panama's history as a land bridge over which floras from Central and South America mixed during the Great American Biotic Interchange (GABI) roughly 3 million years ago. Under this scenario, it would be expected that wetter Panamanian forests would contain more trees of South American origin, whereas drier Panamanian forests would have more trees of Mesoamerican origin due to the historical prevalence of dry habitats in Mesoamerica. This was tested by quantifying the geographic distributions of 714 tree species found in three sites in the Panama Canal watershed, which represent a gradient in annual rainfall. Nearly identical proportions of geographic representation of trees among the three sites, with species distributions of *ca.* 15% Mesoamerican, 17% South American, 9% Panama endemic, and 59% widespread. These data do not support the biotic interchange hypothesis. However, this analysis found that 433 of the 714 tree species (61%) have a cross-Andean distribution, which suggests that these tree species may be old enough to have participated in the GABI.

Key words: Panama, rain forest, tree species, biotic interchange, β-diversity, biogeography

1   INTRODUCTION

In species-rich tropical rainforests, most ecological studies are performed within forest inventory plots of ≤50 ha, which have yielded huge numbers of tree species and, thus, high levels of α diversity (Condit *et al.,* 2000). Networks of small inventory plots have also shed light on patterns β diversity (change in species composition between sites) of Neotropical rainforest trees. In a comparison of forest inventory plots from Panama and the western Amazon, Condit *et al.* (2002) observed that β-diversity was higher along a 50 km latitudinal transect in Panama than between the widely scattered Amazonian sites. Rainfall gradients are steeper and soils more variable in Panama, and local adaptations may result in high β-diversity (Ruokolainen *et al.,* 2002). However, Panama is also a contact zone for floras that originated in North and South America, so biogeographic history may also explain landscape patterns of species diversity. In order to understand how these forests communities were assembled, one must consider the geographic origins of their constituent species.

1.1   Tertiary History of North and South American Rain Forests

The rainforests of Amazonia have experienced a relatively stable and moist climate since the mid-Tertiary time, and its flora may be largely autochthonous (Hooghiemstra and van der Hammen, 1998). Mesoamerica, on the other hand, was a refuge for the broadly distributed North American rainforest flora that persisted through the greenhouse climates of the Paleocene (*ca.* 65-55 Ma) and Eocene (*ca.* 54-35 Ma) time (Morley, 2000). Following a period of drying during the Oligocene (ca. 35-24 Ma) North American rainforests receded into Mesoamerica, and the core Mesoamerican forests were dry and seasonal, with wetter forests clinging to narrow strips of coastline (Morley, 2000).

The floras of Central and South America have had two major opportunities for floristic interchange since South America separated from Africa in the mid Cretaceous (*ca.* 96

million years ago). In the late Paleocene (*ca.* 54 Ma), the eastward migrating Proto-Antillean archipelago (see Harmon, this volume) permitted some rainforest plants to island hop between North and South America (Raven and Axelrod, 1974; Gentry, 1982). This may explain some taxonomic affinities between South America and the Eocene flora (*ca.* 54 MA) of the southeast United States (*e.g.,* Herendeen and Dilcher, 1990). South America remained an island continent for roughly 50 million years, until the consolidation and uplift of Panama about 3 million yeas ago (Coates and Obando, 1996) provided the first continuous land bridge between North and South America. The Panama land bridge allowed two independently evolved biotas to mix, producing the so-called "Great American Biotic Interchange" - GABI (Simpson, 1940). Although studies of the interchange usually consider migrations between Central and South America, the islands that formed the Pre-Isthmian archipelago (Harmon, this volume) may have harbored their own endemic floras and faunas, much as the West Indies do today. Excavations of mid-Miocene (*ca.* 18 Ma) fossils from the Gatun Formation in Central Panama provide evidence of rainforest vegetation and large grazing animals, such as horses and rhinoceroses (Whitmore and Stewart ,1965).

1.2   Weedy Amazonian Trees

The exchange of plant taxa between North and South America could have greatly enriched the floristic diversity of both continents. Gentry (1982) has suggested, however, that the exchange was disproportional. North America contributed many of the montane taxa (>2000 m) found in the Andes, a few of which have descended into the lowland forests (<1000 m), whereas the great majority of lowland plant taxa crossed the landbridge from South America. Gentry (1982) suggested that lowland Mesoamerican forests are comprised largely of widespread Amazonian species, with few representatives of the original North American lowland flora. Gentry's conclusion was based on extensive observations and field collections in the northern South America and in the Panama Canal watershed area, but it finds only limited support in a study by Croat and Busey (1975) of the

geographic distributions of the known tree species of Barro Colorado Island (BCI), which were 13% endemic to Panama, 17% widespread endemic between Costa Rica, Panama, and Colombia, 13% South American (extending as far north as Costa Rica), and 45% widespread (Table 6-1).

Table 6-1. Geographic affinities of the Barro Colorado Island, Panama flora (modified from Table 1 of Croat and Busey, 1975). Included are trees, lianas, and epiphytes. N refers to the number of species per life form. PE = Panama endemic; WE = wide endemic and refers to a range that includes Costa Rica and/or Colombia; CA = Central America and refers to a range that extends from Mexico to Colombia; SA = South America and refers to a distribution that extends as far north as Costa Rica; W = Widespread and applies to species that occur in most of the Neotropical countries and extend occasionally to the West Indies.

life form	N	PE	WE	CA	SA	W
Tree	53	15%	17%	9%	13%	45%
Liana	103	11%	11%	16%	16%	46%
Epiphyte	147	12%	8%	15%	7%	55%

The years following Croat and Busey (1975) brought a surge of information on the taxonomy and species distribution of Panamanian trees, due to (i) the intensive forest inventories in Panama initiated in the 1980's (Hubbell and Foster, 1983; Pyke *et al.*, 2001), and (ii) the electronic cataloguing of herbarium collections, from which species ranges may be quickly tabulated. Whereas Croat and Busey (1975) were able to consider 53 tree species on Barro Colorado Island (BCI), we now have information about 983 tree species in the Panama Canal watershed (Condit *et al.,* 2001).

2   OBJECTIVES

This study had two primary objectives. The first was to expand upon the analysis of Croat and Busey (1975) and

address the observation by Gentry (1982) about geographic distributions. Under Gentry's hypothesis, the tree species in Panama should have widespread distributions between Central and South America, with the broadest geographic coverage in South America or the Amazon basin. However, if the flora represents a mixture of floral elements from Central and South America, one would expect to find a comparable number of species with primarily Mesoamerican and primarily South American geographic distributions. This question was addressed through reference to the geographic distributions of Panamanian trees obtained from the TROPICOS-VAST database of the St. Louis Botanical Garden, the Flora Neotropica monograph series, and the checklist of the Flora of Panama (D'Arcy, 1987).

The second objective of the study was to examine the hypothesis that high β-diversity in Panamanian trees derives in part from the mixing of independently derived floras during the Great American Biotic Interchange, first suggested by Dick *et al.* (2003). Under this hypothesis, we expected that the seasonal forests of the Panama Canal watershed would contain more species with Central American distributions, whereas the wetter forests in the Canal watershed should contain species with geographic affinities to South America, since Mesoamerican forests were highly seasonal compared to Amazonian forests prior to the biotic interchange. Our approach assumes that geographic distributions reflect dispersal from areas of origins (Willis, 1922), and that many of the tree species under consideration in fact participated in the biotic interchange.

3   MATERIALS AND METHODS

3.1   Study Species and Sites

Our analysis considered 714 tree species found in the Center for Tropical Forest Sciences (CTFS) inventory plots in the Panama Canal watershed. The species are classified into 327 genera and 40 families, and are all angiosperms, with the exception of the conifer *Podocarpus oleifolius* (Podocarpaceae).

We compared the geographic distributions of species from three tree communities located along a climatic gradient in the Canal watershed (Fig. 6-1; Table 6-2). The information on rainfall and geological substrate is drawn from Pyke *et al.* (2001). The Upper Rio Chagres area (327 species) is the wettest and most northern location. It is situated close to the Atlantic coast in an area where soils have developed over pre-Tertiary basaltic bedrock (see Wörner *et al.*, this volume). The Barro Colorado National Monument (BCNM; 275 species) falls in the center of the north-south climatic gradient and contains several geological substrates, including Oligocene limestone and sandstone and Miocene basalt. The Pacific lowland sites (358 species) contain the most seasonal forests and lie on a bedrock of pre-Tertiary basalts. Because of seasonality and an intense dry season along the Pacific side of Panama, we expected that the Pacific lowland forests would contain the greatest number of Mesoamerican-derived species.

Table 6-2. Three Central Panamanian sites considered in this study, number of tree species (N) and annual rainfall (drawn from Pyke *et al.* (2001).

site	N	annual rainfall
Chagres	337	3500 mm
BCNM	275	2637 mm
Pacific	358	1800 mm

3.2   Geographic Range Data

We evaluated the geographic ranges of the Panamanian trees through reference to the TROPICOS-VAST database of the Missouri Botanical Garden (www.mobot.org). TROPICOS provides collection information on 1,634,040 specimens housed at the Missouri Botanical Garden, with links to the collections database of the New York Botanical Garden. Additional range information was obtained from Flora Neotropica, which provided information for about 10% of the

species in this study. For each species, presence or absence was determined in all of the Neotropical countries that contain rainforest: Mexico, Belize, El Salvador, Guatemala, Honduras, Costa Rica, Panama, Colombia, Ecuador, Peru, Bolivia, Paraguay, Argentina, Brazil, French Guiana, Surinam, Guyana, and Venezuela. We determined if populations were found east and/or west of the northern Andean cordilleras for species with a southern limit in Colombia or Ecuador.
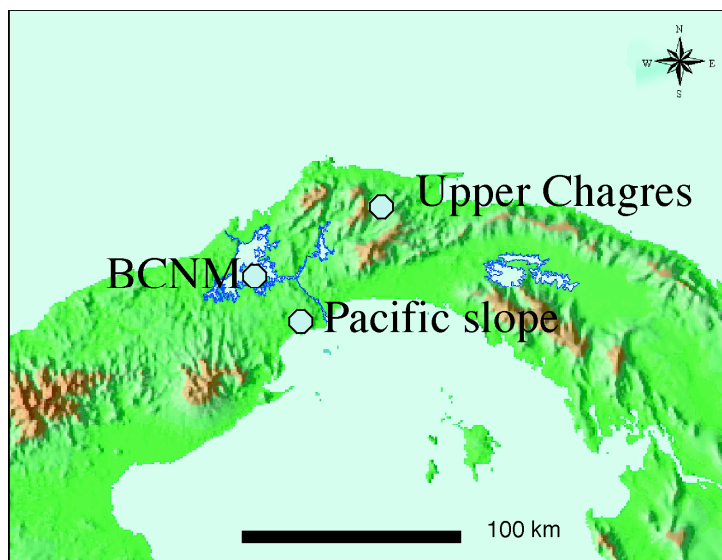

Figure 6-1. Geographic locations of the three study sites along the N-S gradient of central Panama.

3.3   Range Classifications

Nine non-overlapping geographic range categories were defined based on the country presence/absence data (Table 6-3). These nine distributions were lumped into four broad categories, based on the approximate center of geographic distribution: (i) The *Mesoamerica* center of distribution included Mesoamerican countries that lie north of the Nicaragua/Costa Rica border, with a southern range limit of Panama or Colombia; (ii) The *Panama* center included species endemic to Panama or extending to Costa Rica or Colombia; (iii) *South America* species occurred in the Amazon basin and did not occur north of Costa Rica;(iv)

Widespread species are those ranging north of Costa Rica, and extending east of the Colombian Andes. It is not possible to infer a continental origin of the widespread species.

Table 6- 3. Nine fine-scale geographic range designations (column 1) and four broad range categories (column 2) applied the presence/absence data in each neotropical country for the 714 tree species of the Panama Canal watershed.

Geographic range	Geographic Center
1. Panama to north of Costa Rica	Mesoamerica
2. Endemic to Panama	Panama
3. Panama and Costa Rica only	Panama
4. Panama, Costa Rica and Colombia	Panama
5. Colombia to north of Costa Rica	Mesoamerica
6. Panama and Colombia only	Panama
7. Panama to beyond Colombia	South America
8. Costa Rica to S. America beyond Colombia	South America
9. North of Costa Rica to beyond Colombia	Widespread

4   RESULTS

Table 6-4 lists the geographic distributions of Panamanian tree communities as percentages. Widespread species made the largest percentage in all sites and ranged from 47% (336 species) in the Canal area as a whole to 63% of species in the upper Chagres. The proportion of Mesoamerican species ranged from 16% to 13% (Upper Chagres), and is comparable to the proportion of South American trees, which ranged from 21% in the Canal area to 16% in the upper Rio Chagres. The proportion of endemics ranged from 16% in the entire area to 8% in the upper Rio Chagres area. Sites within Panama did not have a notably different geographic

composition of their tree floras, although the Canal area as a whole contained fewer widespread species and more endemics than did the other sites. Of note, 85 of the 714 Canal watershed species (12%) have been collected in the Caribbean islands, which suggests the potential for water dispersal, and/or anthropogenic introductions.

Table 6-4. Geographic affinities of Panamanian rainforest tree species from three study sites.

Site	N	Mesoamerica	Panama	South America	Widespread
Canal area	714	16%	16%	21%	47%
Chagres	337	13%	8%	16%	63%
BCNM	275	15%	10%	17%	57%
Pacific	356	16%	9%	17%	58%

The number of tree species documented in the inventory plots in the entire Canal area is provided in the second row. The geographic designations are described in Table 3.

5   DISCUSSION

Despite the limited tree species pool available for their 1975 study (n=53), Croat and Busey (1975) found similar proportions of widespread and South American tree species (Table 3). On the other hand, Croat and Busey (1975) listed over twice the proportion of Panama-centered species observed in this study. This discrepancy may be explained by the greater geographic coverage of botanical collecting since the early 1970's, which has expanded our knowledge of species' ranges. Many of the Croat and Busey (1975) endemics would probably now be placed in the Mesoamerica or South America geographic categories.

Our study indicates that Gentry (1982) was partly correct in his appraisal of Central America as a colonization front for widespread Amazonian species. Approximately 63% of the tree species of the Canal watershed also occur in Amazonia. However, our study indicates that only 21% of the widespread species are primarily Amazonian in distribution.

The other 47% are so widely distributed that, without information about their broader phylogenetic relationships, it would be impossible to infer a North or South American origin.

It is notable that 433 species cross over the Andes. This suggests that these species originated prior to the formation of the Panama isthmus, since the Andes has provided a strong dispersal barrier for lowland rainforest plants since its major emergence and uplift during late Miocene to early Pliocene (*ca.* 11-3.6 Ma) time (Lundberg *et al.,* 1998) (The dispersed islands of proto-Panama coalesced slightly later at about 3.5–3.1 Ma (Coates and Obando 1996)). Raven (1999) noted that approximately 30% of the lowland flora in Ecuador (1,431 species) occur on both slopes of the Andes, implying ages of several million years for those species. Molecular clock analyses of DNA sequences from the cross-Andean tree populations lend support to an Andean vicariance hypothesis (Dick *et al.,* 2003; C. Dick, unpublished data), although some species-rich and cross-Andean tree groups, such as the *Inga*, have probably diversified much more recently (Richardson *et al.,* 2001) and therefore have successfully dispersed across the northern Andes.

Of the various categories of geographic distribution, only the endemic taxa varied proportionally among the three sites. The upper Chagres area, for example, contained only half (8%) the proportion of endemics represented in the Canal watershed as a whole (16%). The higher level of endemism in the overall flora suggests that our study sites do not encompass areas with unique habitats and specialized floras. The unanticipated broad geographic distribution of most species in the Panamanian tree community is positive news for conservation, as it suggests that the loss of local populations will not produce global extinctions. However, although endemics represent a small proportion of the species that were examined, their absolute numbers are high (n=114). Endemic species, along with those that haven't yet received taxonomic descriptions, may be globally threatened by the extirpation of populations in the Canal watershed as it faces growing threats through development and urbanization (Condit *et al.,* 2001).

In conclusion, our distribution data do not provide strong support for an historical explanation for Panama's high β diversity. It was expected that the species from the Pacific site to have greater geographic affinities with Mesoamerica, and the upper Chagres site to have high floristic affinities with the Amazon basin. Our approach did not permit that distinction to be made however, because so many species are widespread and can probably persist at low population densities in suboptimal habitats. Studies that consider the relative abundances of tree species in relation to their geographic distribution – rather than simple presence or absence – may yet reveal a biogeographic signature in the distribution of tree species in central Panama.

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