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***The Rio Chagres:
A Multidisciplinary Profile of a Tropical Watershed***

**Tree species composition and diversity in
the Upper Chagres River Basin, Panama**

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ABSTRACT

Tree species composition at two sites in the Upper Chagres River basin, Panama, were evaluated using rapid inventory methods. At each site, two 40x40 m quadrats were demarcated, and each was thoroughly searched for tree and shrub species. The 40x40 m quadrats had a mean of 155 species each, and the four pooled had 285 species; 29 other species were noted near the quadrats or the camps where we stayed. These inventories were compared to inventories at 85 other sites in the Panama Canal watershed, and forest composition and diversity was evaluated relative to the mean dry season duration. The Chagres sites are wetter than most of the Canal watershed, and have higher diversity; the only area with higher diversity is even wetter. The wettest areas of central Panama -- along ridges near the Caribbean coast and in the Upper Chagres basin -- are extremely diverse. Many tree species are limited to this wet zone, not occurring in drier areas of the Pacific slope of central Panama.

1. INTRODUCTION: β -DIVERSITY OF FOREST TREES IN CENTRAL PANAMA

Central Panama has high β -diversity of forest trees. In ecological jargon, this means that species turnover from site to site is high (Condit *et al.* 2002). Individual sites in the area, however, have only moderate diversity by tropical forest standards. For instance, a single hectare of forest on Barro Colorado Island in the Panama Canal has about 90 tree species (Leigh 1999). By contrast, sites in Amazonia and Southeast Asia can have three times this number (Phillips *et al.* 1994). But Panama's total diversity is as high as anywhere in the world (Barthlott *et al.* 1996), because high β -diversity makes up for low local diversity.

High species turnover in central Panama is at least partly due to the climatic gradient across the isthmus (Pyke *et al.* 2001, Condit *et al.* 2002). The Pacific slope is relatively dry, whereas the Caribbean is wetter. High ridges along the Caribbean coast are especially wet. Tree species composition from dry to wet zones changes markedly. But most of our studies to date (Pyke *et al.* 2001, Condit *et al.* 2002) have been restricted to the corridor of forest adjacent to the Panama Canal. East of this corridor lies a much larger block of forest -- along the Santa Rita Ridge near the Caribbean coast, and in the Upper Chagres Basin (Fig. 1). Both areas are very wet relative to the Canal corridor, but neither area has been studied much. The Upper Chagres region in particular has no roads and is heavily forested, and access is very difficult. As a result, our current knowledge of tree species on the Santa Rita Ridge and in the Upper Chagres are scanty. Because the climate in these two regions is much wetter than the rest of the Panama Canal watershed, it is likely that there are many unusual species there which we have not yet observed.

2. PRECIPITATION PATTERNS IN CENTRAL PANAMA

All of central Panama has a distinct dry season lasting from late December until late April. This dry season is crucial to the forest: many tree species are clearly water-limited at the end of the dry season. This is most evident during unusually long dry seasons, such as in 1983, when many trees wilt and die (Condit *et al.* 1995, Leigh 1999).

In order to evaluate how the dry season affects tree species composition, we needed to gauge its duration. With data made available by the Autoridad del Canal de Panama, we estimated the period during which evapotranspiration exceeds rainfall at 40 different sites within the Canal watershed (Condit *et al.* 1999). The longest dry season is near Panama City on the Pacific coast, averaging more than 140 days. At the other extreme, on the Santa Rita Ridge and in the northern parts of the Upper Chagres basin (Fig. 1), the dry season is 90-110 days long. However, data are scanty from the Upper Chagres.

3. TREE INVENTORIES

We have assembled data on the tree species present at 85 sites in the vicinity of the Panama Canal watershed. This includes large, permanent forest plots at Fort Sherman, Barro Colorado Island, and along the Cocoli River near Panama City (Condit *et al.* in press), an additional 46 plots that are either 0.32 ha or 1 ha (Pyke *et al.* 2001, Condit *et al.* 2002), and 36 more inventories. In the plots, all trees are measured and mapped, but in inventories, species are only recorded as present or absent. Figure 1 shows the location of all sites, both plots and inventories (some inventory sites are so close together that they appear as single points on the map).

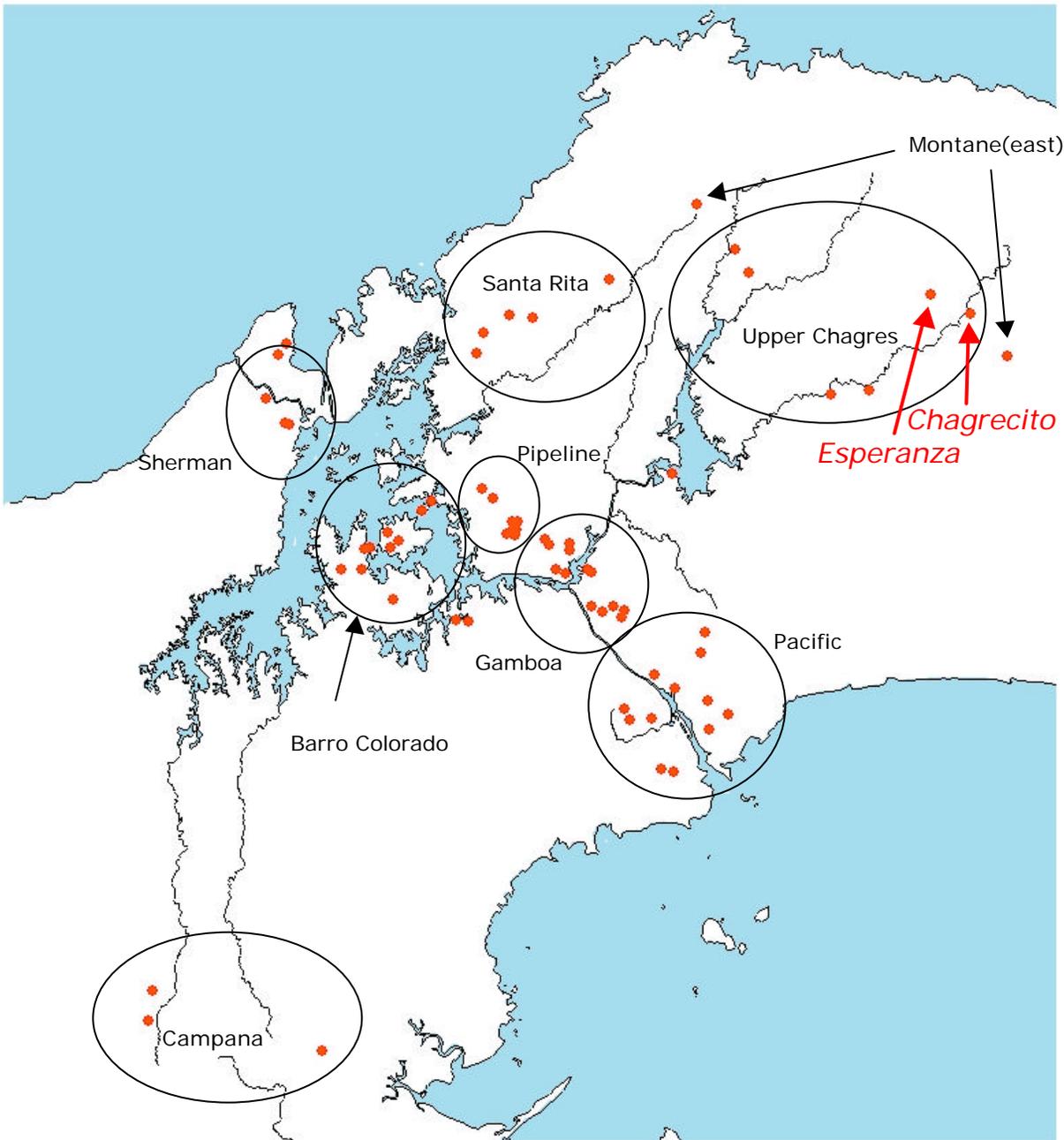


Figure 1. Tree inventories and regions of the Panama Canal watershed. Inventories are solid points; they are grouped into regions as indicated by ovals. The new inventories carried out as part of the U.S. Army Research Office Expedition are labelled: Esperanza and Chagrecito. North is up.

In February and March, 2002, we were able to add four inventories to this dataset in the Upper Chagres River basin, as part of the expedition organized by U.S. Army Research Office. The Upper Chagres is protected in Chagres National Park by Panama's Autoridad Nacional del Medioambiente, and includes more than 150,000 ha or near-pristine old-growth tropical forest (Ibáñez *et al.* 2002). The entire region is roadless, and the eastern section has no human settlements (Condit *et al.* 2001, Ibáñez *et al.* 2002). We had previously established four forest plots in the Upper Chagres region (Fig. 1), but none in the most remote northeastern section.

Two sites we visited as part of the expedition were on the Esperanza River, and the other two at the confluence of the Chagres and Chagrecito Rivers (Fig. 1). At each, we demarcated two 40x40 squares near the campsites (for a total of four such quadrats). We marked each with orange flagging at approximately 5-m intervals, and walked each 5x40 m rectangle systematically. Every tree larger than 1 cm in stem diameter was checked. Any that we could not immediately identify in the field, based on our prior experience throughout central Panama, was collected. Most trees did not have flowers, so leaves were taken; if necessary on tall trees, and slingshot was used to bring down the leaves. All flowers and fruits were collected. Specimens were folded in newspapers for the return trip to Panama City, then dried and eventually compared with herbarium specimens at the Smithsonian Tropical Research Institute and the National Herbarium at the University of Panama.

Lists of every species encountered in each of the 40x40 m quadrats were assembled. These were compared with species lists from all 85 other inventory sites in the Canal watershed. Abundance data were taken from published accounts (Condit *et al.* 1996, in press).

4. TREE SPECIES DIVERSITY IN THE UPPER CHAGRES

The four 40x40 m quadrats at Esperanza and Chagrecito included a mean of 155 tree species ≥ 1 cm in stem diameter (Table 1). On the Santa Rita ridge, in one plot and one inventory, there were an average of 174 species. No other region in the Canal watershed averaged > 100 species per 40x40 m quadrat (Table 1).

The four quadrats at Esperanza and Chagrecito included a total of 285 species when their species lists were pooled. In addition, we recorded 29 more species near the campsites and around the inventory quadrats, bringing the total number of species recorded to 314. Of these 314 species, we have never encountered 50 of them anywhere else in the Canal watershed. A complete list of those 314 species will be made available to anyone contacting the authors.

Table 1. Species diversity in regions of the Panama Canal watershed, per 40x40 m inventory plot. The sample size, *N*, is the number of plots in the region; the number in parentheses is the of plots number fully enumerated.

site	species	<i>N</i>
Santa Rita	174.0	2 (1)
Upper Chagres	155.0	4 (0)
Pipeline	99.7	10 (10)
Sherman	94.9	34 (34)
BCNM	92.6	35 (35)
Laguna	87.5	2 (2)
Gamboia	70.7	12 (6)
Pacific	56.7	25 (22)

Precise locations of the four quadrats are given in Table 2.

Table 2. UTM coordinates of four inventory quadrats, based on GPS. Coordinates refer to the corner of each quadrat furthest to the southwest.

site	UTM east	UTM north	elevation
Chagrecito 1	684333.3	1034639.5	
Chagrecito 2	684397.0	1035202.5	
Esperanza 1	680538.4	1036732.7	
Esperanza 2	680113.2	1036889.2	

5. RANGES IN THE CANAL WATERSHED OF UPPER CHAGRES TREE SPECIES

Besides the inventories at Esperanza and Chagrecito, we had completed four additional tree census plots in the region of the Upper Chagres River (Pyke *et al.* 2001). Two of these were immediately adjacent to the Chagres River downstream of the Esperanza (Fig. 1). The other two were between the Boquerón and Pequení Rivers, north of Lake Alajuela (Fig. 1). Species lists from those for plots were pooled with the list of 314 species recorded at Esperanza and Chagrecito. This produced a total list of 435 tree species for the Upper Chagres region.

Of the regions designated in Figure 1, Santa Rita is the one most similar to the Upper Chagres in terms of tree species composition. The pooled list for 5 Santa Rita sites included 408 tree species, 228 of which were also found in the Upper Chagres. Altogether, Santa Rita and the Upper Chagres inventories included 615 tree species. Including two plots at elevation > 600 m, but immediately adjacent to the Upper Chagres region (referred to as Montane East in Fig. 1), this pooled list reaches 698 tree species.

In 69 inventory sites in the Canal corridor forests -- those immediately adjacent to the Canal -- there were 667 tree species. Only 291 of these species were also recorded in the Santa Rita, Upper Chagres, and Montane East regions.

At all 89 inventory and plot sites throughout the Panama Canal watershed, we recorded 1162 tree species. The largest number of these were restricted to the wet regions (Santa Rita, Upper Chagres, and the few montane inventories at Cerro Campana and the Montane east sites). The next largest number of species were widespread, occurring from the driest to the wettest regions. Only 101 species were restricted to the driest zone (Pacific plus Gamboa).

Table 3. Number of tree species with various geographic ranges in Central Panama. These ranges refer only to local occurrence; most species occur widely throughout the neotropics as well. Wet forest includes the regions of Santa Rita, Upper Chagres, Montane East, and Campana. Intermediate includes Sherman, Barro Colorado (BCNM), and Pipeline Rd. Dry includes Gamboa and Pacific. See Figure 1 for region designations.

Species range in Canal watershed	no. species	% of species
Widespread	198	17.0
Wet forest only	495	42.3
Wet-intermediate	113	9.7
Intermediate only	114	9.8
Dry-intermediate	131	11.3
Dry side only	101	8.7
Wet and dry, not intermediate	10	0.9
TOTAL	1162	100

5. CONCLUSIONS

The biggest break in tree species composition in the Panama Canal area occurs between the Santa Rita region and the forests of the Canal corridor. The wettest zone -- the Santa Rita Ridge along the Caribbean coast, the upper Chagres, and montane sites in the far east and far west of the watershed -- carries the highest number of species which are restricted to a climatic zone. The same zone also has the highest tree species richness.

The region of the Upper Chagres watershed in the far east of the Panama Canal area remains poorly explored botanically. We expect to uncover more species there that are currently not known from central Panama. Further exploration of the region is clearly warranted.

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