AN ECOSYSTEM REPORT ON THE PANAMA CANAL: MONITORING THE STATUS OF THE FOREST COMMUNITIES AND THE WATERSHED

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Abstract. In 1996, the Smithsonian Tropical Research Institute and the Republic of Panama's Environmental Authority, with support from the United States Agency for International Development, undertook a comprehensive program to monitor the ecosystem of the Panama Canal watershed. The goals were to establish baseline indicators for the integrity of forest communities and rivers. Based on satellite image classification and ground surveys, the 2790 km^2 watershed had 1570 km^2 of forest in 1997, 1080 km^2 of which was in national parks and nature monuments. Most of the 490 km^2 of forest not currently in protected areas lies along the west bank of the Canal, and its management status after the year 2000 turnover of the Canal from the U.S. to Panama remains uncertain. In forest plots designed to monitor forest diversity and change, a total of 963 woody plant species were identified and mapped. We estimate there are a total of 850–1000 woody species in forests of the Canal corridor. Forests of the wetter upper reaches of the watershed are distinct in species composition from the Canal corridor, and have considerably higher diversity and many unknown species. These remote areas are extensively forested, poorly explored, and harbor an estimated 1400–2200 woody species. Vertebrate monitoring programs were also initiated, focusing on species threatened by hunting and forest fragmentation. Large mammals are heavily hunted in most forests of Canal corridor, and there was clear evidence that mammal density is greatly reduced in hunted areas and that this affects seed predation and dispersal. The human population of the watershed was 113 000 in 1990, and grew by nearly 4% per year from 1980 to 1990. Much of this growth was in a small region of the watershed on the outskirts of Panama City, but even rural areas, including villages near and within national parks, grew by 2% per year. There is no sewage treatment in the watershed, and many towns have no trash collection, thus streams near large towns are heavily polluted. Analyses of sediment loads in rivers throughout the watershed did not indicate that erosion has been increasing as a result of deforestation, rather, erosion seems to be driven largely by total rainfall and heavy rainfall events that cause landslides. Still, models suggest that large-scale deforestation would increase landslide frequency, and failure to detect increases in erosion could be due to the gradual deforestation rate and the short time period over which data are available. A study of runoff showed deforestation increased the amount of water from rainfall that passed directly into streams. As a result, dry season flow was reduced in a deforested catchment relative to a forested one. Currently, the Panama Canal watershed has extensive forest areas and streams relatively unaffected by humans. But impacts of hunting and

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pollution near towns are clear, and the burgeoning population will exacerbate these impacts in the next few decades. Changes in policies regarding forest protection and pollution control are necessary.

Keywords: environmental assessment, forest communities, human population, hydrological aspects, Panama Canal, vertebrate populations, watershed monitoring

1. Introduction

Protection of the watershed of the Panama Canal is a global priority. Fulfilling Theodore Roosevelt's mission, the Canal continues to be an important shipping passage, transporting 37 ships a day and providing substantial income to Panama's government. Besides building the Canal, though, Roosevelt was a prominent conservationist, and perhaps he would have recognized the importance of the natural forest communities around the Canal. Central Panama is one of the most diverse ecosystems on earth, with species richness rivaling or exceeding hotspots such as Amazonia, the northern Andes, or southeast Asia (Barthlott *et al.*, 1996; Stotz *et al.*, 1996; Myers *et al.*, 1999). The forests also protect the water source for the Canal and Panama City and provide resources to rural communities. The Panamanian government recognizes this, and in the past 32 yr has created four parks that protect forests in the Canal's watershed. We report here on a comprehensive monitoring program on the status of these parks and the forest ecosystems around the Panama Canal.

The program was initiated in 1996 by the U.S. Agency for International Development, the Smithsonian Tropical Research Institute, and the Panamanian government's Environmental Authority (Table I). The aim was to monitor natural resources at an ecosystem level – the integrity of the community in a broad sense (Keddy, 1991; Shaw, 1992; Angermeier and Karr, 1994; Karr, 1999; Karr and Chu, 1999). This approach, rather than monitoring rare or important species (Hutchings, 1991), is favored now by managers and ecologists, and it seems particularly appropriate in tropical forest communities, which harbor thousands of species, many of which remain unknown or very poorly known. Because forests dominate the natural ecosystems of the Canal area, our goal was to document not only the integrity of the forests, but also the importance of the forests in terms of conservation, watershed protection, and human society.

The first aim of the 'Proyecto de Monitoreo de la Cuenca del Canal' (PMCC) was to document the area of forest cover in the Canal watershed. From the conservation perspective, this is the key piece of information, since most native species of the moist tropics will not persist after the forest is converted to pasture. Beyond this, though, we wished to document more subtle alterations within the forests. To this end, PMCC established a network of tree plots and censuses of key vertebrate species, aimed at detecting unsuspected changes in forest condition (Palmer, 1992; Shaw, 1992; Condit *et al.*, 1995; Ashton, 1998; Condit, 1998). Tree plots and

TABLE I
Institutions involved with monitoring of the Panama Canal watershed

Acronym	Institution	Supporting country	Mandate (Relevant to Canal watershed)
USAID	United States Agency for International Development	U.S.	Assist Panama protect the Canal watershed
ANAM	National Environmental Authority (formerly INRENARE)	Panama	Manage natural resources, protect the environment
PCC	Panama Canal Commission	Joint U.S.–Panama (solely U.S. prior to 1977)	Operate Panama Canal (before 2000)
PCA	Panama Canal Authority	Panama	Operate Panama Canal (since 2000)
STRI	Smithsonian Tropical Research Institute	U.S.	Carry out ecological research

transects also provided information for locating old growth forest in the watershed, stands that should be a conservation priority (Marcot, 1997). The plots yield species lists and an estimate of total tree species richness in the area. Tree and vertebrate censuses were also aimed at detecting more subtle signs of forest degradation that might be caused by climate change, fragmentation, or the loss of large dispersers due to hunting (Robinson *et al.*, 1999; Curran *et al.*, 1999).

Managing the ecosystem also requires information about activities of human communities, and so PMCC assessed population growth in the watershed and evaluated case studies on the use of forest resources and the degradation and contamination of streams. Finally, the program set out to monitor the status of the water resources of the Canal watershed and to evaluate sedimentation and runoff trends and how forest conversion might be altering them. This last issue is fundamental for the Panama Canal Authority – will the Canal's water supply suffice to let ships pass?

PMCC did not have the resources to monitor all components of the Canal area ecosystem. For example, the biotic component of streams was not evaluated, and this would have provided valuable companion information to the hydrological studies. Also, we made no attempt to set up monitoring programs for the enormously diverse forest arthropod communities (Erwin, 1982, 1995). Despite important progress (Barone, 1998; Ødegaard, 2000), insect species and their role in the forest remain poorly known and broad-scale monitoring methods have not been developed.

Ultimately, the project's goal was to provide baseline data against which to compare future inventories, and thus to document precisely changes in forest communities, vertebrate populations, and water resources. At that future time, it becomes monitoring. Here we provide the initial snapshot of the Panama Canal watershed, its status in the year 2000. An unpublished report to the funding agencies has full details on methods and results (Ibáñez *et al.*, 1999), and there are published executive summary of the report aimed at a non-scientific audience (Heckadon-Moreno *et al.*, 1999). Some of the results summarized here will also be published in a series of shorter papers on specific aspects, and those are cited below where appropriate.

2. The Region

The Panama Canal watershed lies in the moist tropics, at 9°N latitude. Rainfall is well above evapotranspiration, and despite a marked dry season from December through April, the climate and the soils are suitable for sustaining tall, high-biomass forest. But substantial areas are now grassland with scattered trees and small woodlots, cleared by humans for agriculture (mostly cattle). These grasslands frequently burn during the dry season, and fire is a major factor inhibiting natural reforestation. There is no evidence of fires within forest in recent history.

Because wet season storms approach from the Caribbean, the Pacific slope of the isthmus is relatively dry while the Atlantic coast is wet. Annual precipitation near the Pacific entrance to the Canal is 1700 mm, and the dry season lasts an average of 129 days. At the Atlantic mouth of the Canal, rainfall is 3000 mm and the dry season just 102 days long (Condit *et al.*, 2000). Upland areas in the watershed are wetter still. North and east of the Canal runs the Santa Rita ridge (Figure 1), reaching 979 m above sea level at Cerro Bruja. The southwest corner of the Canal watershed has another mountain peak, Cerro Negro, at 984 m elevation. Ridges and peaks near the Atlantic get 3500 mm or more of rain per year, with almost no dry season.

Forests remain near the Panama Canal watershed in five protected areas: Soberanía, Camino de Cruces, Chagres, and Altos de Campana National Parks, and the Barro Colorado Nature Monument (Figure 1). One substantial strip of forest along the west side of the Panama Canal is not in a reserve, but has been protected because it remained until 1999 under the jurisdiction of the U.S. military and the Panama Canal Commission (sites in this forest were used for firing exercises by the military). At the end of 1999, the U.S. military departed Panama and the PCA replaced the binational PCC (Table I). The fate of this unprotected strip of forest is thus still in the balance. A major goal of the monitoring project was to precisely

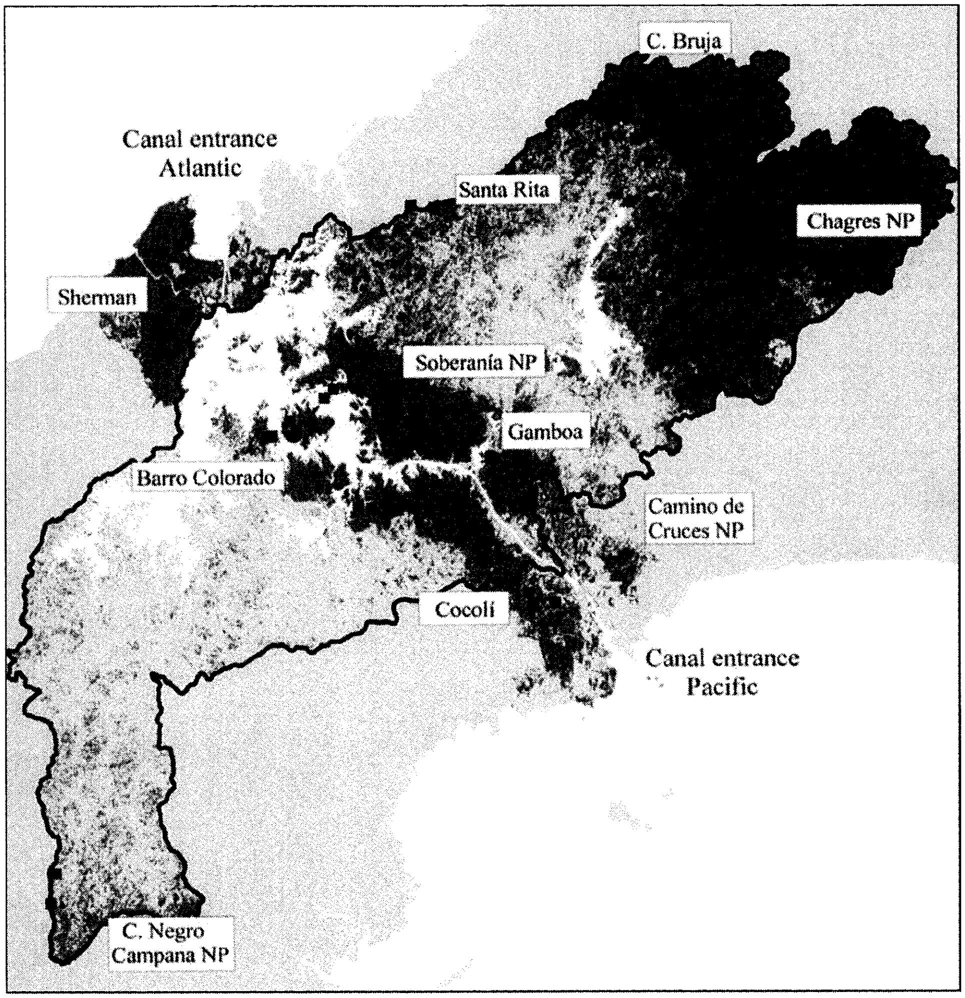

Figure 1. Forest and forest plots in the watershed of the Panama Canal. The solid outline indicates the extent of the Canal watershed. Forest is shown in dark gray, ocean and lakes in white gray; only forest inside the watershed was mapped, except for the regions near both Canal entrances (technically outside the watershed). Plots are indicated by black squares. Location of three national parks (NP) and the Barro Colorado Nature Monument are indicated. The Nature Monument includes Barro Colorado Island, the large island in the Canal, and four peninsulas near the island. Regions discussed in the text are indicated ('C' means Cerro, Spanish for mountain). The forest immediately adjacent to the Canal and all the plots therein (Sherman, Barro Colorado, Soberanía, Gamboa, and Cocolí) are referred to as the Canal corridor in the text. The remaining plots, at Santa Rita, C. Negro, C. Bruja, and in Chagres National Park, are referred to as wet and montane areas. North is up in all maps. The Canal is about 65 km long from ocean to ocean.

delimit forests in the entire watershed, and to determine which are outside protected areas.

The forests of central Panama are very diverse in both plant and animal life. Barthlott *et al.* (1996) report that southern Central America has plant diversity as high as any other site in the world, higher than Amazonia, and Stotz *et al.* (1996) make a similar statement for forest bird diversity of Panama. According to Holdridge's forest classification, there are four life zones in the Canal watershed, but the majority of the land is lowland moist forest (Holdridge, 1967; Croat, 1978). The Santa Rita ridge is lowland wet forest, and small areas at higher elevation are in montane life zones. A main goal of the monitoring project was to delimit forest regions based on tree species composition and document differences in both plant and animal communities between them.

3. The Institutions

The USAID is a U.S. government agency that provides financial support to development projects throughout the world, and has a mandate for protecting natural resources (Table I). The agency has worked in Panama since 1961, and has sponsored many programs in forest protection, restoration, and monitoring. It was USAID that determined the need for monitoring of the Canal watershed and provided funds to initiate the project. They approached STRI in 1995 for assistance in designing and operating the project.

STRI is a Republic-of-Panama-based bureau of the Smithsonian Institution, a trust instrument of the U.S. government operating a museum and research complex (Rubinoff and Leigh, 1990; Table I). STRI has a long history of biological research in the Canal area of Panama, and 30 scientists work full time at the institute. Of particular relevance to USAID's goal with the monitoring program, STRI has a research reserve on Barro Colorado Island in the Panama Canal (Figure 1), where thousands of studies on forest animals and plants, ecology, hydrology, and geology, have been carried out since the 1920s (Leigh *et al.*, 1982; Leigh, 1999). Several scientists at STRI agreed to assist in the design and implementation of the monitoring program.

ANAM is the Panamanian government's natural resource agency, and is responsible for protecting national parks and managing natural resources. It is not a scientific agency, and did not have the resources to carry out a thorough monitoring program. One of USAID's goals was build this capacity in ANAM, so ANAM could continue monitoring in the future without external assistance. STRI was originally charged with designing a program within ANAM that would eventually be taken over by the Panamanian institution. Equipment purchased and personnel trained were to be incorporated into ANAM. In January 2001, this turnover to ANAM did take place, although only about one-quarter of the monitoring personnel were included.

4. Forests of the Panama Canal Watershed

4.1. Forest Cover

The extent of intact forest is crucial to the fate of ecosystems of the Panama Canal area, and the PMCC purchased computer equipment and satellite images to set up a laboratory at ANAM for estimating forest cover remotely. Several LANDSAT images from the 1997 and 1998 dry seasons were found that, jointly, provided cloud-free coverage for 92% of the watershed. Using a supervised and subsequently non-supervised classification (Lillesand and Kiefer, 1987), three vegetation types were mapped: forest, grassland (often with scattered trees), and *rastrojo* (shrubby vegetation <10 m tall). Infrared aerial photos of the entire watershed were acquired in 1997 from the U.S. Army Corps of Engineers to classify the remaining 8% of the watershed, as well as to assess the accuracy of satellite classification.

We estimate that 54% of the land area of the Panama Canal watershed is forest and 43% pasture or rastrojo (Table II). The forest is mostly in two large blocks, one east of Lake Alajuela in Chagres National Park and one along the Canal (Figure 2). The area between the two is a patchwork of forest fragments (Figure 2). Two-thirds of the forest, 108 000 ha, is within the four protected areas of the watershed, while the remaining is mostly along the west side of the Canal, in former U.S. military installations that reverted to Panama in the year 2000. Conversely, the national parks include some deforested land, especially Altos de Campana (Table II).

4.2. Old Growth Forest

Many of the Canal area forests were cleared over the past 200 yr. Particularly since the railroad across the isthmus was completed in the 1850s and work on the Canal was begun in the 1870s, human pressure on the forests has been extensive. We were thus interested in locating areas of old-growth forest – sites that escaped clearing over at least 200 yr. Without precise historical records, identification was based on subjective assessment of the stem diameter and species of large trees. Near the Canal, there are only scattered patches of old-growth forest: about half of Barro Colorado Island (Foster and Brokaw, 1982), along Pipeline Road in Soberanía National Park, and around the Fort Sherman canopy research crane. One small patch across the Canal from Gamboa shows large tree crowns in aerial photos, but remains inaccessible to scientists due to the former military exercises and presence of unexploded shells. All other forests south of Gamboa are secondary. There are probably no more than 3000 ha of old-growth forest near the Canal. But Chagres National Park, distant from the Canal, has extensive, undisturbed, old-growth forest (Figures 1 and 2). Access is difficult, though, as there are only a couple roads at the periphery of the park, and we base this assessment on the few sites where PMCC personnel entered and on evaluation of the aerial photos.

TABLE II

Forest cover in the Panama Canal watershed and its protected areas and major watersheds, and human populations in and around national parks. Total area includes urban areas as well as the three vegetation types; Chagres and Soberanía also include nearly 60 km^2 of open water which are not included in the numbers here. 'Near park' means within 6 km of park boundaty. To compare with figures in and near parks, the population density of the watershed outside national parks is 65.3 persons km^{-2}. The Chagres River watershed refers only to the portion above Lake Alajuela. The number of villages in each watershed was not tallied. NP = national park, NM = nature monument, R = river. A fifth protected area, Camino de Cruces NP (Figure 1), is adjacent to the Canal near Panama City, but less than a square kilometer of the park lies in the watershed, so we did not include it in our analysis

Site	Total land area (km^2)				% Forest	Human population in 1990		
	Forest	Rastrojo	Grass-land	Total		In park (persons km^{-2})	Near park (persons km^{-2})	No. of villages
Chagres NP	869.3	26.8	61.7	964	90.2	2712 (2.8)	14067 (44.7)	39
Soberanía NP	153.4	4.1	9.9	167	91.9	75 (0.4)	19072 (49.0)	4
Campana NP	10.7	5.8	4.5	21	50.3	0	1400 (20.0)	0
Barro Colorado NM	49.2	1.0	0.8	51	96.6	0	466 (2.2)	0
Outside parks	487.3	301.5	826.9	1688	28.9	–	–	389
Chagres R watershed	405.7	4.1	4.1	414	98.0	–	–	–
Pequení R watershed	127.7	2.6	4.6	135	94.6	–	–	–
Boquerón R watershed	76.3	4.4	10.2	91	83.9	–	–	–
Gatún R watershed	73.1	11.3	32.2	117	62.5	–	–	–
Trinidad R watershed	31.7	51.7	88.6	174	20.2	–	–	–
Cirí Grande R watershed	37.6	66.2	79.1	186	18.2	–	–	–
All Panama Canal watershed	1570	339	904	2892	54.3	2787 (2.3)	35005 (35.5)	432

Old-growth forest is mostly restricted to wet and steep sites, those less attractive for cattle pasture or other crops. Human populations have always been densest on the dry Pacific slope, where all the forests have been cleared or heavily cut in the past 100–150 yr.

4.3. Tree Species Composition

To assess tree species richness and to define forest types, the PMCC censused trees in 31 square 1 ha plots, 10 0.32 ha plots (40 × 80 m), and utilized data from 3 larger plots – a 50 ha plot at Barro Colorado Island, a 6 ha plot at Fort Sherman

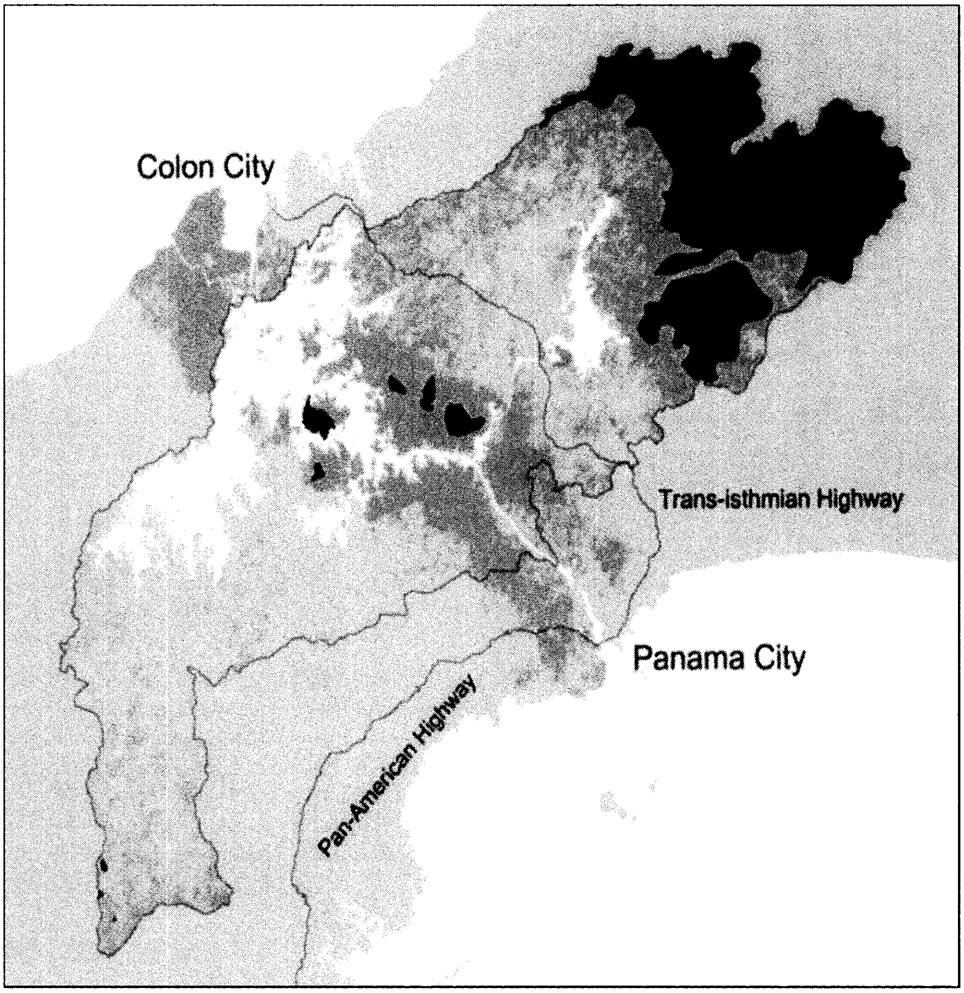

Figure 2. Old growth forest of the Panama Canal watershed. Forest is indicated in dark gray, as in Figure 1, and old growth in black. Small pockets of old growth on Barro Colorado Island and in Soberanía National Park are shown, as well as tiny fragments near Cerro Negro.

near the Atlantic mouth of the Canal, and a 4 ha plot near the Cocolí River not far from Panama City (Condit *et al.*, 2000; see Figure 1). Stems $\geq$ 1 cm diameter were censused in all plots except the 10 small ones (see Condit, 1998; Pyke *et al.*, 2001). The most striking feature of the tree communities documented by these plots was how variable they were in species composition: except for plots within 1–3 km of each other, no two forests were similar in species (Pyke *et al.*, 2001). Adjacent hectares shared 7–9 of their 10 top-ranking species, but at greater distances, rarely more than five of the 10 dominant species were shared. Plots at Cocolí and Sherman, on opposite sides of the isthmus, had no top-ranking species in common. Overall similarity of the 1 ha plots (percent of all species shared) declined from 60–

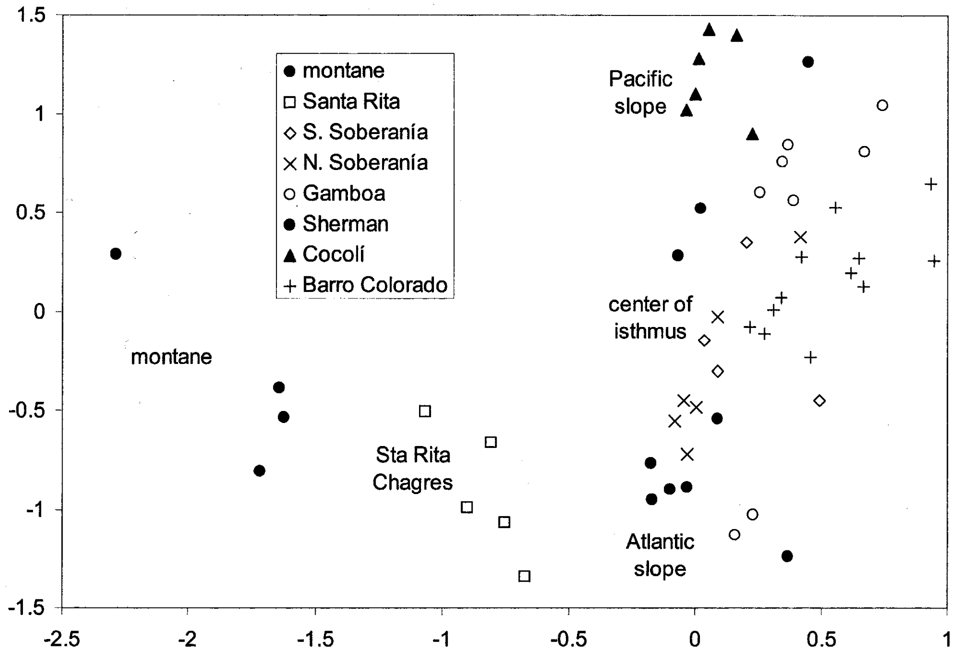

Figure 3. Non-metric multi-dimensional scaling ordination of 1 ha plots, where all trees ≥10 cm dbh were censused. Just six of the hectares of the 50 ha plot at Barro Colorado Island are included. Symbols represent geographic regions, and in general, the ordination closely parallels geography. Conspicuous exceptions are due to geological transitions. One black circle near the Pacific slope (Cocolí group) represents a plot on limestone near Fort Sherman (see text). Two open circles near the Atlantic group represent plots geographically close to Gamboa, on a small outcrop of an andesite formation that mostly occurs in Soberanía and Chagres National Park. This andesite develops a flora characteristic of wet sites (Pyke *et al.*, 2001).

70% in plots separated by 2 km or less, to 35% in plots separated by 10–30 km, and to below 20% in plots separated by 50 km or more (Condit *et al.*, 2002). The total fraction of species shared between single hectares is an underestimate, but the sharp decline with distance and the lack of abundant species in common demonstrates that forests on opposite sides of the isthmus are quite different in tree composition.

Forest plots of the wetter areas, on ridges and peaks along the Atlantic coast in the northeast part of the watershed, and near Cerro Negro in the southwest (Figure 1), were quite distinct in tree species composition from plots near the Canal. Of 599 woody species found in 10 wet forest plots, just 195 were shared with plots in the Canal corridor, (all lowland sites within 5 km of the Canal). Wet sites stand out in an ordination (Figure 3). In the Holdridge system, these wetter sites are classified as wet or submontane forest, while the Canal corridor is moist forest. Thus, the Holdridge classification reflects the primary division in species composition, but it fails to reflect the enormous variation within the moist forest zone, from Atlantic to Pacific within the Canal corridor (Pyke *et al.*, 2001).

Pyke *et al.* (2001) tested for the impact of geology, soil, climate, and geographic separation on forest composition, and Condit *et al.* (2002) examined how dispersal limitation affects tree distributions and forest composition. The rapid change in tree species composition at distances <3 km is probably due to dispersal limitation – most tree species do not spread seeds far (Clark *et al.*, 1999). But the continuous and substantial change in tree species composition across the isthmus and into the upland areas is caused largely by the rainfall gradient – many species are restricted to wet or dry regions. This can be clearly seen by contrasting species turnover across the isthmus of Panama with turnover in Amazonia, where there is no rainfall gradient and where forests hardly change over 50 or 100 km (Pitman *et al.*, 2001; Condit *et al.*, 2002). In Panama, there was also a weak geological impact on tree species composition (Pyke *et al.*, 2001.). For example, a plot on limestone near Fort Sherman shared just 18% of its species with a plot <2 km away on sandstone, but 30% of its species with plots in much drier forest 53 km away at Cocolí (Figures 1 and 3). Conversely, there were cases where communities on similar substrate but 20–30 km apart shared more than 50% of their species, for example the Sherman plots with Soberanía National Park.

4.4. Tree Diversity

The forests around the Panama Canal are remarkably diverse, but mostly in a geographic sense. That is, β-diversity is very high, whereas α-diversity is only moderate by tropical forest standards. Single plots in the Canal corridor averaged 84 tree species ($\geq$10 cm in stem diameter) per ha, whereas those on Santa Rita and montane sites had 145 tree species per ha. For comparison, lowland forests in Ecuador and Malaysia have more than 200 species per ha (Condit, 1995; Romoleroux *et al.*, 1997). But in our entire dataset of 94 ha, we tallied 963 morphospecies (including all free-standing woody plants $\geq$1 cm diameter). The Barro Colorado 50 ha plot had 301 species $\geq$1 cm diameter in 1995; the other 43 plots scattered across the watershed, from dry to wet, from sea level to 800 m elevation, added 662 more species.

The 559 species from the Canal corridor were mostly identified: 86% (480 species) have been named to the species level. The flora of this area has been catalogued for many years (Standley, 1933; Croat, 1978; Foster and Hubbell, 1990; Foster and Brokaw, 1992). In contrast, just 68% of the species at the Santa Rita and montane plots have been fully identified (but 98% are named to the genus level). Nine species not previously known in Panama have been firmly identified, and five more tentatively identified; we suspect that several more of the unnamed species will be new to the Panama flora, and some probably new to science. One genus found by the PMCC, *Lecointea* in the Leguminosae, has never been observed in Panama before.

Two large genera illustrate the diversity of the wet ridges and mountains, as well as the poor state of the knowledge of their flora. The 10 Santa Rita and montane inventories include 31 species in the genus *Inga* (Leguminosae), 7 of which are unidentified, and 28 species in *Pouteria*, 14 of which remain unknown. All plots together have 35 *Pouteria*, while the flora of Panama lists just 25 for the entire country. Thus, if all 35 of those morphospecies prove to be distinct species, the PMCC will have uncovered 11 *Pouteria* species new to the flora of Panama.

4.5. Total species richness

How many tree and shrub species are there in the Canal watershed? We recorded 963 in 44 census plots, but how many are there outside the plots? We gathered data from the checklist of the *Flora of Panama* (D'Arcy 1987) as updated by M. Correa and C. Galdames (pers. comm.). The updated list mentions 863 tree and shrub species as occurring in the Canal Zone, the former designation for an area that corresponds closely with what we define as the Canal corridor. The 33 Canal corridor plots included 83 species not in the checklist, meaning we can name 946 species that have been collected in the corridor; plots include 559 of them. More broadly, the checklist mentions 1555 tree and shrub species as present in the Canal Zone and two adjacent provinces, Colon and Panama. There are 189 species identified in the 44 tree plots but not in the checklist, so we can name 1744 species in those three political zones. But the provinces of Colon and Panama extend well beyond the Canal watershed, so this number can only be used as a guide for estimating total tree and shrub species richness in the watershed.

Still, for the entire Canal corridor and for the watershed, the plots capture no more than 60% of all tree and shrub species present. Even a very intensive network of tree plots is not very effective at identifying species present. There are many rare and localized tree species in tropical forests, which are seldom encountered. It is easy to see this within the plots, for instance, of the 559 species observed in plots in the Canal corridor, 86 were seen in only a single hectare and 55 were represented by a single individual. Including the entire dataset, 208 of 963 species were observed once only.

To estimate total species richness in different regions of the Canal watershed, we extrapolated species counts in plots to larger areas using the diversity index known as Fisher's alpha (Condit *et al.*, 1998), and with species-area curves (Table III). This approach leads to a low estimate of species richness in the Canal corridor, only 800–950 compared to 946 as judged from the checklist of Panama. One source of error may be the distribution of the rarest species, those not sampled in plots. If they tend to be more localized than common species, then it is impossible to accurately estimate species ranges from the plots. For the entire watershed, the estimated total number of species is about 1700–2300, but many more sites where inventories are complete are needed to test modeling approaches and to understand better the abundance and distribution of the rarest species.

TABLE III
Estimated number of species in different regions of the Canal watershed

Region	Observed species in plots	Estimated total species
Pacific slope (Cocolí region)	191	350–450
Central isthmus (Barro Colorado and Soberanía)	302	420–470
Atlantic slope lowland (Sherman region)	252	500–600
Canal corridor non-forest species	0	~100
Total Canal corridor	561	800–950
Chagres/Campana wet forest	599	1400–2200
Total watershed	963	1690–2320

5. Vertebrate Populations

The PMCC carried out two types of surveys to obtain baseline data on vertebrates in the watershed. In five remote areas with difficult access, 10-day intensive inventories were done of all terrestrial vertebrate groups, using mist-nets, small mammal traps, by walking trails, and by talking with local residents and ANAM park wardens, in an attempt to document all species present. At other sites closer to the Canal, three kinds of repeated surveys were carried out. First, large mammals and birds favored by hunters were censused on eight transects, each 5 km long, covering areas differing in hunting pressure (Wright *et al.*, 1999). Second, birds were censused with mist-netting (20 nets for 500 net-hours per site) before and after the breeding seasons, and with point counts during the breeding season (12 points per site). Seven sites were located in six different forest blocks ranging from small fragments (300) to fairly large forests (15 020 ha). Third, frogs were censused using daytime counts along 10 sites (200×1 m transects along streams at most, but 30 m of an entire streambed at Barro Colorado Island), at low elevation (<100 m) at Barro Colorado and Soberanía National Park, and at mid-elevation (360–835 m) in Chagres National Park (Ibáñez *et al.*, 1999). Frogs were counted during the dry seasons of 1998–2000, from mid-December to April, when they congregate near streams.

5.1. Mammals and Large Birds

An important consideration in tropical forest conservation status is the intactness of the large mammal and bird fauna. At the four remote inventory sites in Chagres National Park the observed fauna was largely intact. These sites have jaguar (*Panthera onca*), puma (*Felis concolor*), and white-lipped peccary (*Tayassu pecari*), Central

American spider monkey (*Ateles geoffroyi*), and probably bush dog (*Speothos venaticus*), but this is based largely on information from local residents. Such large mammals are very difficult to census without intensive, long-term efforts. Interestingly, an active harpy eagle (*Harpia harpyja*) nest was found on the surveys – the first nest observed in the Canal watershed. A second harpy nest was subsequently located nearby. In contrast to the four sites with complete fauna, the fifth remote inventory site in Altos de Campana National Park was missing most of these large mammals and birds.

The repeated surveys in forests close to the Canal provided quantitative encounter rates, and will allow future population trends to be documented. Surprisingly, many large game species were observed in the Canal corridor, even in the face of fairly intense hunting pressure. Howler and white-faced monkeys (*Aloutta palliata*, *Cebus capucinus*) and agoutis (*Dasyprocta punctata*) were seen on all transects, and collared peccaries (*Tayassu tajacu*) and white-tailed deer (*Odocoileus virginianus*) were recorded at all but the most heavily hunted site (Wright *et al.*, 1999). Crested guans (*Penelope purpurascens*) were commonly censused on Barro Colorado, and great tinamou (*Tinamus major*), large pigeons (*Columba* spp.), parrots (*Amazona* spp.), and toucans (*Ramphastos* spp.) were recorded on nearly every transect.

Of the 11 species of large mammals censused, nine showed a negative correlation between abundance and hunting pressure, and for five the trend was statistically significant (Wright *et al.*, 1999). In general, it appears that in forests on the Pacific side of the Canal corridor near Panama City and other settlements, hunting pressure is intense and large mammals of any sort are scarce. For large birds, no relation between hunting pressure and sighting frequency were evident. The caliber of most of the shotgun shells observed was too large for birds, suggesting hunters were mainly after mammals. In heavily hunted areas, seed predation by mammals on two palm species was evaluated. Seeds accumulated beneath tree canopies in hunted areas, whereas most seeds are removed at Barro Colorado. As a result, the palms recruit far more seedlings in hunted areas, but mostly very close to adult trees. This indicates that hunting could alter forest composition (Wright *et al.*, 1999).

Several of the largest vertebrates were seldom or never encountered on census transects, so we assembled records of sporadic recent sightings to assess current population status in qualitative terms. The only large mammal that has been entirely lost from the Canal corridor is the white-lipped peccary. Jaguar still occur in Soberanía National Park and the Fort Sherman area, and wanderers occasionally reach Barro Colorado Island. Puma now appear to be regular residents at Barro Colorado Island – there are recent photographic records of three different animals. More unexpectedly, there are two recent reliable sight reports of bush dog from Soberanía National Park. Baird's tapir (*Tapirus bairdii*) and spider monkeys were both extirpated from the Canal corridor by the 1930s, but both were reintroduced to

Barro Colorado Island in the 1960s and have persisted; there are also a few recent records of tapir from the Fort Sherman area.

Among large birds, several species are effectively extirpated from the Canal corridor: harpy and crested (*Morphnus guianensis*) eagles and four species of macaw (*Ara* spp.). There are occasional records of the eagles that are probably wandering birds, and recently the Peregrine Fund attempted to introduce harpies to Soberanía National Park and Barro Colorado. Unfortunately, two introduced birds were killed by hunters, and another bird refused to stay at Barro Colorado and has been recaptured. Finally, the great curassow (*Crax rubra*) is rare but still present in Soberanía National Park and the Fort Sherman area, and there is one recent record from Barro Colorado.

5.2. Birds in forest fragments

Counts of small forest understory birds indicated a clear contrast between small and large fragments: 50–60% of the species in small fragments were birds that typically utilize second-growth habitat, whereas only 10–20% of the species in large fragments were (Condit *et al.*, 2001). That is, small fragments are dominated by birds of the surrounding pastureland, whereas large fragments are dominated by true forest species.

Barro Colorado Island (1567 ha) has provided one of the best documented examples of species loss from forest fragments following isolation. Some 30 forest-interior species have disappeared from the island since its creation in 1914 (Willis, 1974; Karr, 1997; Robinson, 1999). Interestingly, some forest species that have become extinct on Barro Colorado were observed in much smaller fragments on the mainland, so that fragment size is not the sole determinant of survival. Nest predation rates are known to be higher on Barro Colorado Island than in some mainland sites (Karr, 1997), and it also appears that some species are able to recolonize fragments over land, but unable to recolonize over water.

5.3. Diversity and population fluctuations of frogs

Eighty-six species of anurans are known from the Panama Canal watershed (Condit *et al.*, 2001). Nearly all are forest-dwellers, but there is a general division in the fauna between lowland and highland sites: 60% of the species are found at both low and high elevation, while 17% are restricted to lowlands and 22% to uplands (Condit *et al.*, 2001).

Twenty-seven frog species, mainly leaf litter frogs, were observed in the censuses, with an average of 10 species per site (range, 6–13 species/site). A few frog species were present at all or most sites: *Colostethus flotator*, *Bufo typhonius*, *Eleutherodactylus fitzingeri*, *E. vocator* and *Dendrobates auratus* (at 10, 8, 8, 8 and 7 sites, respectively).

The censuses showed clear changes in frog community with elevation, but also with distance at the same elevation (Figure 4). The only transects which shared

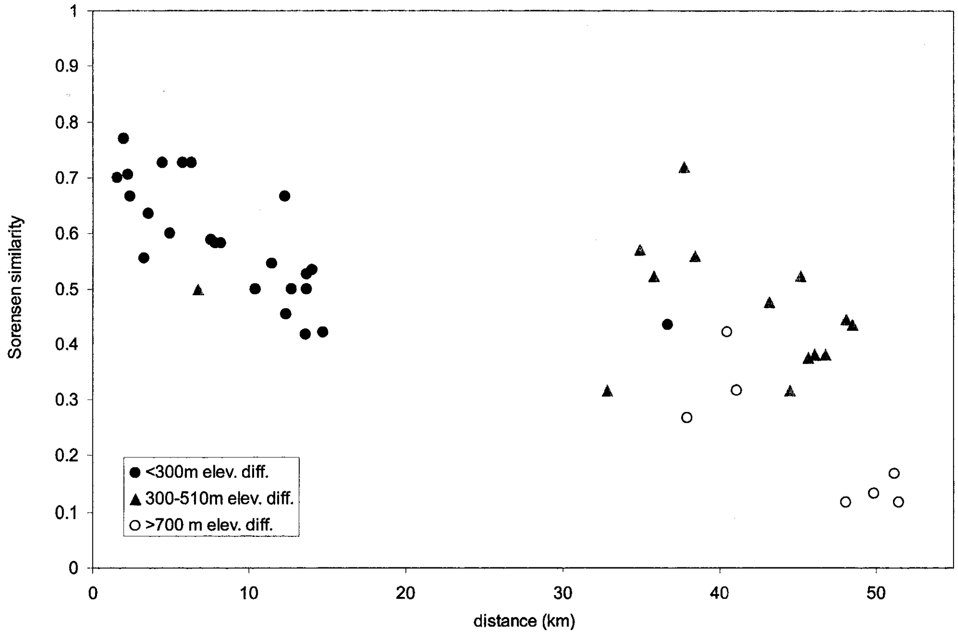

Figure 4. Sorensen similarity in anuran species composition between two transects as a function of distance between the transects. Sorensen similarity is found by dividing the number of species common to two sites by the mean number of species encountered at the two sites.

>70% of the species observed were within 7 km of each other. Among the lowland Barro Colorado and Soberanía sites, the Sorensen similarity in species composition declined quickly with distance. But elevation also had a pronounced impact on frog communities (Figure 4): among sites >30 km apart, similarity was 0.12–0.42 when elevation differed by >700 m; this involved comparisons of the highest elevation site in Chagres National Park (835 m elevation) with lowland sites of Barro Colorado and Soberanía. The other two Chagres sites (360, 540 m elevation) were much more similar to the lowland sites, sharing 32–72% of their species, on a par with similarity among low elevation sites separated by more than 10 km. The turnover in frog communities with distance was remarkably similar to that observed in tree communities, as described above (Pyke *et al.*, 2001). Both frog and tree community similarity declined with distance, even in similar habitat, over the first few kilometers. However, β-diversity was higher in trees, as Sorensen similarity of sites >40 km apart was always less than 20%, considerably lower than in frogs.

The site on Barro Colorado Island was previously censused several times from 1977–1995 using identical methods. The number of frogs counted has fluctuated over 23 yr, but there is no indication of general long-term population change (Figure 5). Some of the variation is probably due to rainfall patterns, because when rain falls during the dry season, fewer frogs congregate along streams. The very dry year of 1977 had high frog counts, whereas the very wet year of 1999 had the lowest (Figure 5). Counts in 2000 were still low, but 1998 counts were high in most species. A multiple regression in which year and dry-season rainfall were included as predicting variables showed no significant effect of year in three of four species (Figure 5). In the last species, *Bufo typhonius*, counts have fallen significantly, even after accounting for rainfall. High variation in all populations underscores the need for long-term monitoring.

Overall, we conclude that frogs in the Canal watershed are not suffering from the drastic population declines caused by pathogenic fungi elsewhere in Central America and the world (Blaustein and Wake, 1990; Berger *et al.*, 1998; Lips, 1999). Only two dead frogs were found during the 1998–2000 counts, none of which showed signs of the fungus in histological preparations from their skins. Although we do not have long-term data at the upland sites, a fairly diverse assemblage of frogs species associated with streams was found, and no dead or dying individuals were observed that could be attributed to a fungal disease (Ibáñez *et al.*, 1999; Heckadon-Moreno *et al.*, 1999).

6. Human Population

6.1. Census

Every 10 yr, the Division of Statistics and Census of the Republic of Panama carries out a national census of the nation, and we acquired the data to analyze in parallel with the information on parks, watersheds, and forests. In 1990, the human population of the Panama Canal watershed was 113 000. The population has been growing substantially – from 22 000 in 1950 and 77 000 in 1980. Assuming the 1980–1990 growth rate – 3.8% yr^{-1} – continues, the population in 2000 would have been 166 000, and in 2010, 241 000. Analyses of the year 2000 census are not yet available, so we cannot test the projections.

The rate of increase from 1980–1990 was much higher in the Canal watershed than in the entire country (2.1%) or the Metropolitan area of Panama City (2.7%). The high growth of the watershed is due simply to its location on the northern outskirts of Panama City, which has 1.1 million people (Figure 6). The majority of the watershed's inhabitants live in Las Cumbres and Chilibre, within the metropolitan area of the capital city. Indeed, 62% of the 113 000 watershed residents live within 1.3 km of the Trans-isthmian Highway running from Panama City to Colon (Figure 4).

Away from this highway, the watershed consists of small rural settlements, many of which have neither paved roads nor electricity (Figure 6). Rural areas have expanded more slowly than the large towns near the Trans-isthmian Highway, but are still expanding. For example, the entire Watershed west of the Canal consists of rural communities, and the population there grew from 15 799 to 19 640 between 1980 and 1990 (2.2% yr^{-1}).

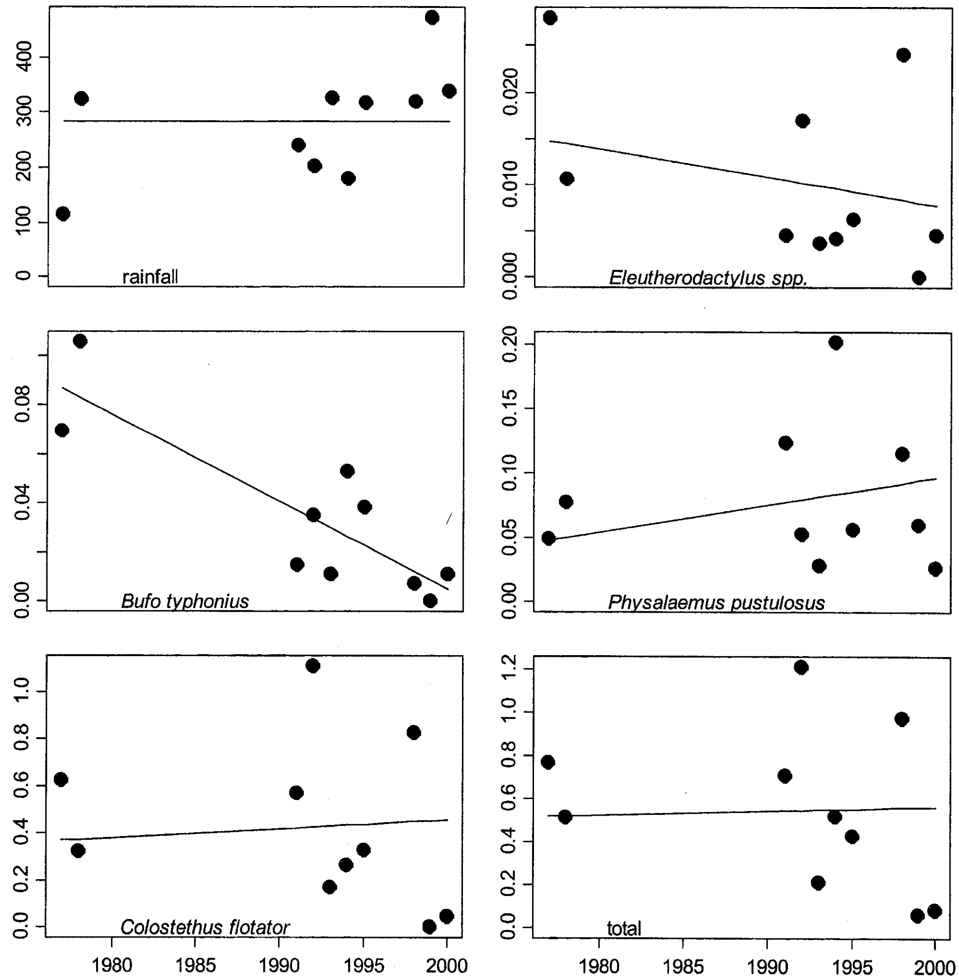

Figure 5. Mean number of frogs m^{-2} per census (9–24 censuses per year) encountered during dry season counts. The upper left panel shows the total rainfall, in mm, recorded at Barro Colorado Island during the dry season months of January to April each year, and the lower right panel is the total frog count (sum of the four species). Frogs in the genus *Eleutherodactylus* were not consistently identified to species, so all are combined here. The lines are from a multiple linear regression, where year and rainfall were separate variables predicting frog count; rainfall was set to the mean of all 10 yr to make the prediction. For example, the regression for the total count was $frogs = 0.0020 \times year - 0.0024 \times rain - 2.77$ ($r^2 = 0.40$, $p = 0.17$), mean rainfall was 283.1, so the line in the lower right panel is $frog = 0.0020 \times year - 3.46$. This suggests what the frog population would have been in a year if rainfall were average, and thus isolates the temporal trend.

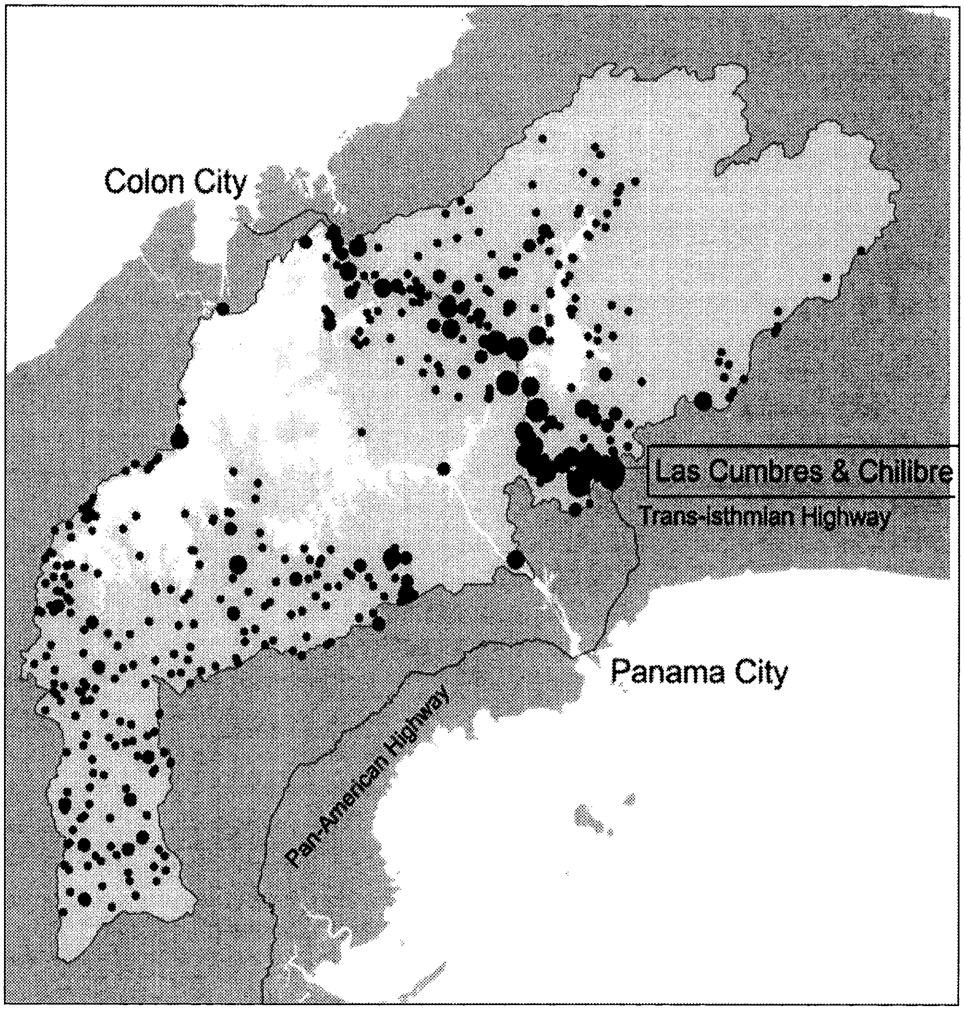

Figure 6. Human communities of the Panama Canal watershed. Each circle represents a single town, according to Panama's 1990 census, and larger circles represent larger towns. All the largest circles (populations >3200) are along the Trans-Isthmian Highway from Panama City to Colon.

We mapped settlements near the national parks of the watershed. There were 43 communities and 2800 people living within national parks in 1990 (Table II); in 1980, these same communities had only 1100 residents. Most of these communities existed before the parks were created (Soberanía in 1977, Chagres in 1984), but people have immigrated into parks. For example, in 1980 there were no communities inside Soberanía National Park, but there were four in 1990.

In 1990, 35 000 additional people lived within 6 km of the watershed's national park boundaries (Table II). Nearly half of these people were in the districts of Las Cumbres and Chilibre, which are adjacent to Soberanía National Park (Figure 6).

The population of these communities in 1980 was 23 000. Thus, population growth in and around parks of the watershed has been very rapid.

6.2. Land use

Rural areas are largely deforested, consisting of pasture land intermingled with small fragments of forest. In the watershed of the Chilibre River, around Las Cumbres and Chilibre, we created a detailed land-use map using aerial photos and extensive field work. The map covered 82.5 km^2 around the communities, excluding land within Soberanía National Park and residential areas. Fifty-nine percent of the area mapped was pasture for cattle and another 27% was abandoned field of the introduced grass *Saccharum spontaneum*. Only 0.8% was commercial tree plantation and 0.4% was used for growing vegetable crops, especially the bean guandú (*Cajanus bicolor*), rice (*Oryza sativa*), maize (*Zea mays*), and various tubers, including manioc (*Manihot escuelanta*), otoe (*Xanthosoma nigrum*), and yam (*Dioscorea alata*). Small gardens around houses were also used for producing food crops, but their extent was difficult to quantify; at most, they included another 5% of the land area. In 1991, 5600 head of cattle were vaccinated in the Chilibre watershed; if this represents all cattle on the 52 km^2 of pasture, there were just over 1 head per ha. This predominance of low-intensity pasture and abandoned grassland is typical of rural areas in the Canal Watershed.

According to our surveys and census figures, most people in Chilibre and Las Cumbres were employed by industrial and commercial enterprises, either locally or in Panama City or Colon; mean salaries ranged from $1200 to $6000 per year ($US). In smaller communities, employment was scarce and irregular, and many people were subsistence farmers. In towns near Chagres National Park, 68% of the people were subsistence farmers, and 64% of the crop production was used by the grower. Most of the land in small settlements was pasture, in many cases owned *in abstentia*. In the community of Santa Rosa, intensively studied by PMCC, 75% of the land area was pasture owned by people who lived elsewhere.

6.3. Sewage and trash

There is no sewage treatment in the watershed of the Panama Canal, with the single exception of the Smithsonian Tropical Research Institute's facility on Barro Colorado Island. Industries in Chilibre were observed dumping waste water directly in the Chilibre River. Most houses have septic tanks, but we observed evidence of leakage. Some of the communities in the Chilibre area have no waste pick-up, and large piles of uncovered garbage accumulate. In the Chilibre watershed, the PMCC documented the location of a number of open garbage dumps and egregious sources of contaminants in the river (Ibáñez *et al.*, 1999).

6.4. Hunting and Fishing

Commercial or sport hunting is always illegal in Panama, but ANAM's laws about subsistence hunting are confusing and contradictory – some is permitted, perhaps even in national parks, perhaps only by indigenous groups. Regardless of the laws, residents of rural areas near national parks commonly hunt in the parks. The park guards of the Barro Colorado Nature Monument patrol 24 hr a day, 365 days per year, and made seven arrests in the first 9 months of 1999. They know many of the regular hunters, and they know which restaurants in Panama City purchase wild meat. Nevertheless, commercial hunters detained by STRI wardens were usually quickly released. During 1997, biologists working at night in Soberanía National Park reported frequent hunting on Friday and Saturday evenings, and Barro Colorado guards report that sport hunting is common.

In Alfajía and Aguas Claras, two small towns adjacent to Soberanía National Park, locals reported that hunting in the park is common. Deer and peccary meat can be sold in Colon for $2 per pound, they reported, and was also eaten locally. Where employment is scarce and salaries $3 to $5 per day, hunting is economically rewarding. In San Juan de Pequení, which includes a small Emberá Indian village in Chagres National Park, hunting with rifles was common, and our survey indicated that wild meat is a staple. The Emberá described hunting terrestrial mammals as well as turtles and crocodiles.

The Emberá also reported fishing in the Pequení River. The community of 218 people consumed an estimated 123 kg/week, according to our interview. The Emberá as well as the Latino community of Nuevo Vigía reported a large commercial fishery for *Tilapia* and *Cichla ocellata* in Lake Alajuela. Local fisherman sold to a buyer from Panama City for $0.40 to $0.60 per pound. The buyers were Asian-Panamanians, and the fish was exported.

Aguilar and Condit (2001) documented the use of plant products collected in a wild state in a small village near the Barro Colorado forest. Overall, we know that animal and plant products collected from the forest are very important for small rural communities near forests. Unfortunately, we have not yet estimated the quantity of forest products extracted or their value, mostly because of the high variation between villages; we did not have the resources to survey large numbers of communities. We estimate that the number of people in the watershed who gather a substantial part of their income from forest products is no more than 10% of the population – those communities near forest that have poor access from outside.

7. Hydrology

7.1. Water budget

The Panama Canal Commission maintained detailed stream flow records for many years, and PMCC assembled data on the annual water budget of the Canal. Total rainfall over the 3300 km^2 watershed averages 9×10^9 m^3 of water per year, of which an estimated 4.6×10^9 m^3 would be lost to evapotranspiration (Leigh, 1999), leaving 4.4×10^9 m^3 to flow into the Canal. With current ship traffic, 37 per day, more than half of this water, 2.6×10^9 m^3, is used to fill the Canal's locks – 191 000 m^3 per ship. An additional 1.2×10^9 m^3 of water is used to generate electricity for Canal operations, and 0.27×10^9 m^3 is processed for drinking water to supply most of the Canal communities and parts of Panama City and Colon.

The three large rivers feeding Lake Alajuela (Chagres, Boquerón, and Pequení, see Figure 7) carried a mean of 1.7×10^9 m^3 of water per year from 1970–1996. The three largest rivers feeding Lake Gatún (Gatún, Trinidad, and Cirí Grande) carried another 0.73×10^9 m^3 of water, so these six rivers contribute 2.4×10^9 m^3, 54% of the Canal's water. In 1982, a dry year accompanying a strong El Niño event, they carried just 1.8×10^9 m^3, a 25% reduction. If the entire watershed suffered a 25% reduction, the 4.4×10^9 m^3 of water typically available would become just 3.3×10^9 m^3, less than the 4.1×10^9 m^3 needed to fill locks, generate electricity, and produce drinking water. A good deal of this can be made up by drawing down Lake Alajuela and the Canal, but in extreme years this means the Canal is too shallow for the largest ships to transit. Clearly, the water budget for the Canal watershed is tight enough that changes in runoff or sedimentation caused by land use are a serious concern.

7.2. Sedimentation

One important concern about maintaining the water supply of the Canal is increased sedimentation caused by deforestation (Douglas, 1990; Bruijnzeel, 1990). Sediments reduce the storage capacity of the lakes, and also require continual dredging so that the Canal is deep enough for large ships. Wadsworth (1978) warned that the Panama Canal would cease to function if deforestation continued unchecked, as Lake Alajuela filled with sediment. Partly in response to Wadsworth's warning, the PCC began detailed data collection on sediments carried by the six main rivers feeding the Panama Canal. Tutzauer (1990) presented an early analysis of these data. In 1999, we updated these analyses and presented a model aimed at predicting erosion and sedimentation.

Sediment volume carried by the six major rivers has shown no tendency to increase since detailed data collection began (1981 for the Chagres, Boquerón, and Pequení; 1987 for the Trinidad, Cirí Grande, and Gatún). The trend for the Chagres is typical (Figure 8). If anything, there is a downward trend in the data, but sediment load had high peaks in 1981, 1987, and 1996.

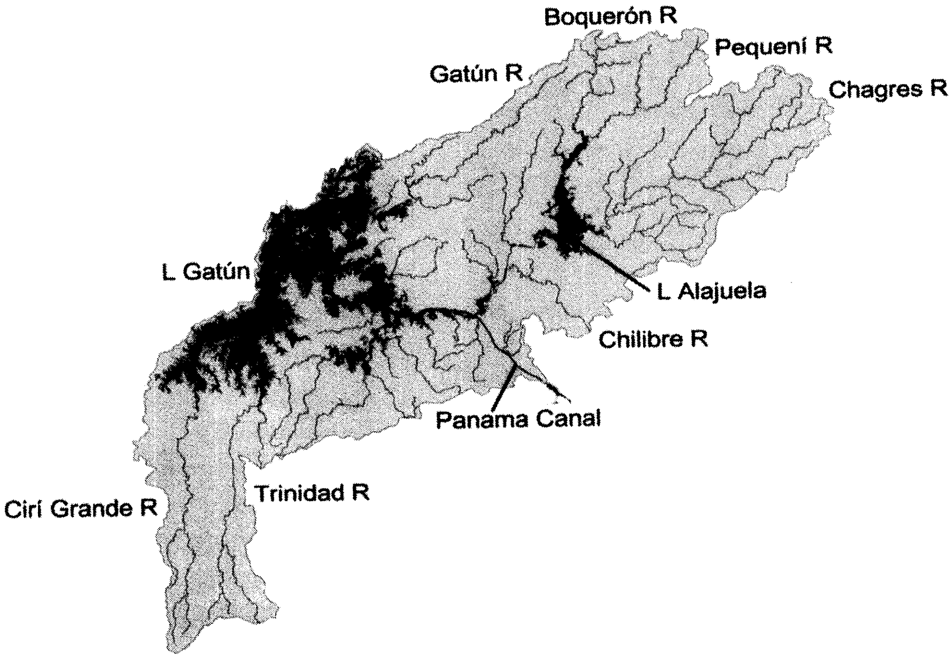

Figure 7. Streams, watersheds, and lakes feeding the Panama Canal. The two lakes were formed by dams in the Chagres River. The six largest rivers as well as the heavily contaminated Chilibre River are indicated; all are discussed in the text. Atlantic and Pacific coasts are omitted from this map, and only the watershed is shown.

The solid line in Figure 6 shows the predictions of a model correlating erosion with total rainfall and with the number of extreme precipitation events. Very heavy rain creates landslides and thus heavy sedimentation. Studies in Puerto Rico indicated that slopes steeper than 12° become prone to landslides on days which get >200 mm of rain (Larsen and Simon, 1993; Larsen and Torres Sánchez, 1998). Thus, the overall erosion model is

$$Y = aR^b + cN \,, \qquad (1)$$

where Y is total sediment load (in Mg per yr per m^2 of the watershed), R is total runoff (precipitation less evapotranspiration) and N is the number of days with >200 mm rain. The parameters a, b, and c were fit from the data, separately for each of the six watersheds. The fit was very good for all six rivers, as illustrated for the Chagres (Figure 8). In five of six, the parameter c was significantly different from 0, indicating that the model was improved by considering days of heavy rain. This can been seen in the Chagres River basin: 1981 had heavier than average rainfall, but no days of high rain, whereas 1987 had average rainfall but 2 days of heavy rain. In both years, the river bore exceptionally high sediment loads. In 1996, rainfall was the highest of the 16 yr, and there were 3 days of heavy rain; sediment loads peaked again (Figure 8). No other years had heavy-rain days.

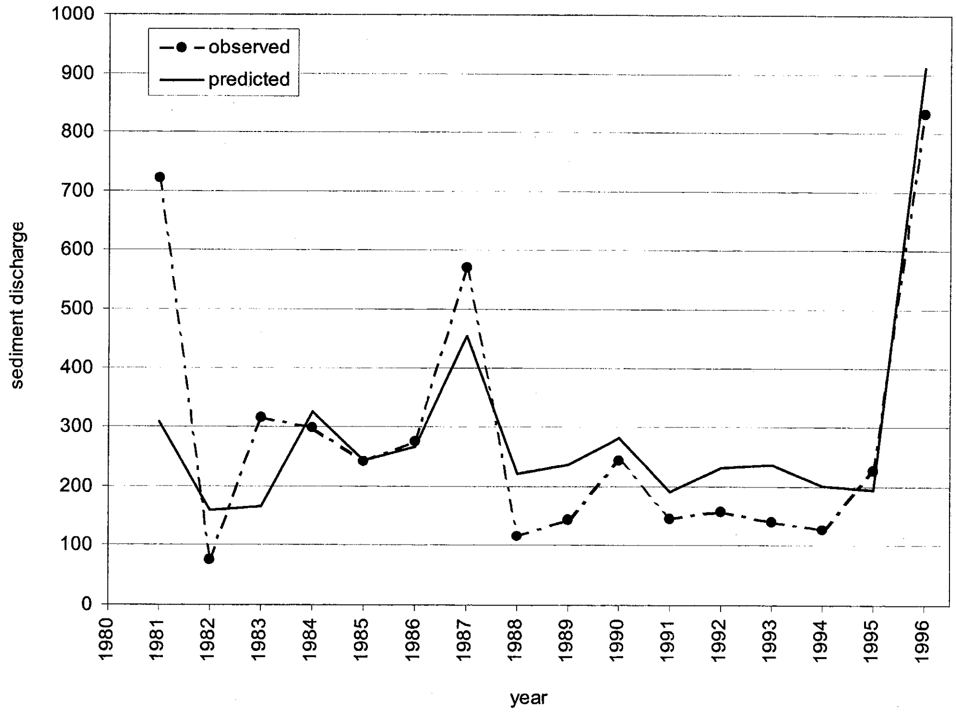

Figure 8. Observed and predicted sediment discharge in the upper part of the Chagres River (the portion east of Lake Alajuela, Figure 7). Observed discharge is based on water samples taken where the river enters the lake. Predicted discharge is from the model described by Equation (1).

Thus, it appears that precipitation is the main driving force behind year-to-year variation in erosion, both the total rainfall and the number of landslide-provoking storms. But we do not reject the role that deforestation might play in causing increased erosion, because there are important problems in evaluating long-term trends in sedimentation. First is the natural year-to-year variation caused by rainfall variation and landslides. Second is the gradual and rather slow pace of deforestation: the Chagres and Pequení watersheds above Lake Alajuela are still mostly forested, while the Trinidad and Cirí Grande Rivers have been largely deforested for decades (Table II). Against the backdrop of high natural variation, detecting slow trends over a 16 yr period is not feasible. Other approaches should be used for assessing the importance of deforestation on erosion. Indeed, work in Puerto Rico (Larsen and Torres Sanchez, 1996, 1998) showed that landslides were least likely where native vegetation remained intact, and most likely around roads and construction, and this will almost certainly hold in Panama, where topography and geology are similar. With experimental studies of the impact of land use on erosion, coupled with the maps of watersheds and forest cover, the PMCC will be able to predict sedimentation for the entire watershed depending on future land-use scenarios.

7.3. Deforestation and Runoff

Another serious hydrological concern about clearing natural forest is that runoff tends to be more rapid from deforested land than from naturally forested land. PMCC resurrected an experimental watershed with three weirs that the PCC operated from 1981–1983. A stream completely within Soberanía National Park passes over one weir, while another stream outside the park in a mix of pasture and forest passes over a second. The third weir is within the park below the confluence of the two. The two upper watersheds are on identical geological substrate, and have similar size and topography. Stream flow at the weirs was monitored with automatic gauges, and precipitation was recorded continuously.

In the deforested catchment, 26% of the water from rainfall events passed directly into the river, while only 14% did in the forested catchment. As a result, stream flow in the forested stream was lower in the wet season, but higher in the dry season, relative to the deforested stream. This difference in runoff may be due largely to soil compaction – permeability of pasture soil was 0.004 cm hr^{-1}, compared to 5.8 cm hr^{-1} for forest soil.

7.4. Stream Water Quality

PMCC evaluated water quality at 52 stations throughout the watershed, in both wet and dry seasons, and at 24 more sites along the heavily settled Chilibre River and its tributaries. At some sites along the Chilibre, fecal coliform counts were 48 000 per 100 mL, and dissolved oxygen fell as low as 2.0 mg L^{-1}; both are levels indicative of high bacterial contamination. But at the mouth of the Chilibre, 5 km below any settlements, fecal coliform counts were <1000 per 100 mL and dissolved oxygen >6 mg L^{-1}. Most other streams had coliform <1000 and dissolved oxygen >5.

Nitrogen and phosphate concentrations were moderately elevated in the Chilibre River, near its mouth, relative to the remaining test sites, but the difference was not dramatic (N and P were not analyzed upstream in the Chilibre, near human settlements, where they would presumably be greatly elevated). The mouth of the Chilibre had 2–2.5 mg L^{-1} N and 0.2–0.5 mg L^{-1} PO_4, whereas most forested streams had $[N] < 1$ and $[PO_4] < 0.25$. The Palenque River, flowing mostly in pasture, also had elevated N and PO_4. But Lutz creek on Barro Colorado Island, entirely forested but flowing through steep calcareous rocks, had N and PO_4 concentrations matching those at the mouth of the Chilibre River.

Overall, most streams in the Canal area are relatively unpolluted, showing no signs of eutrophication or excess bacterial contamination. Clearly, though, the Chilibre River is badly contaminated where it flows through settlements, and where it enters the Chagres River, it shows some signs of this, although largely diluted.

We also evaluated densities of floating aquatic plants in various streams and in Lake Alajuela and Lake Gatún. Plants are a serious concern for the Canal, because in great concentrations they hinder ship travel, and the PCA erects floating barriers where streams enter the Canal to exclude plants. Increasing sedimentation and nutrient pollutants in streams could lead to greater plant concentrations.

The greatest plant concentrations were observed in the Chagres River near where it enters the Canal, and in the Paja River flowing north into Lake Gatún. Important species include *Pistia stratiotes* and *Eichornia crassipes*, but over 50 species were recorded. Operating small boats in either stream is sometimes impossible. The Chagres collects the polluted waters of the Chilibre River above Gamboa, and the Paja River crosses pasture and small towns before entering forest. The Gigantito River in the Barro Colorado Nature Monument has few floating plants, as does the Gatún River, which flows through a mostly forested watershed (Table II). These casual observations suggest there might be a link between deforestation or pollution and floating plant density, but more focused studies are needed.

8. The State of the Environment

On the positive side, more than half of the Panama Canal watershed is covered in mature forest, mostly in large contiguous blocks. A substantial portion of this is old growth forest little used by people, where even the more sensitive species of large mammals and birds persist. The most pristine forests east of Lake Alajuela are protected by their remoteness, but there is old growth forest near the Canal, and protection from hunting can preserve populations of most mammals there, as evidenced at Barro Colorado Island and Soberanía National Park.

On the negative side, the environs of large towns such as Chilibre are extremely degraded and contaminated, and the human population of the watershed is growing at a high rate. Even the smallest rural settlements are surrounded by pastureland, with few forests and limited cropland. Unless there is a miraculous reversal of the population trend, forest-loss, degradation, hunting, and contamination will spread in the next few decades.

We found evidence that forests protect the water supply by reducing runoff and thus storing water through the dry season. Water is in short supply during the dry season, and is critical for the Canal as well as for Panama City, so it seems that preserving forest has an enormous economic payoff for this reason alone. On the other hand, there is no evidence yet, from 16 yr of records, that deforestation is leading to increased erosion in the watershed or sedimentation in the reservoirs.

The forests also support fisheries and hunting, and thus provide protein and direct economic benefits to rural communities. Rural people also use forest products such as firewood, food, and medicines. The fisheries are unmanaged and the hunting is only weakly controlled, with confusing and conflicting laws.

Well-protected forests, with substantial mammal and bird populations, are also valuable in terms of tourism. Both the Barro Colorado Nature Monument and Soberanía National Park attract large numbers of tourists, many of whom are birdwatchers. Both sites harbor substantial populations of large birds and mammals, and are also easily accessible from Panama City. The extensive forests east of Lake Alajuela hold an even more complete fauna, but their remoteness reduces tourism opportunities.

Finally, the forests conserve the extraordinarily high species diversity of the Panama Canal ecosystem. Preserving species diversity is now the subject of an international convention, and we considered the documentation of species present in the Canal watershed to be a main priority of the monitoring program. Vertebrate species are for the most part well documented (Ridgely and Gwynne, 1989; Rand and Myers, 1990; Engleman *et al.*, 1995; Ibáñez *et al.*, 1999). We made the first estimate of total tree species richness in the Canal watershed - about 2000 species – and documented the range of nearly 1000 of them. A species list for the arthropods, although useful, would require decades more work.

The diversity of tree species and the rapid spatial changes in species composition seem to preclude any simple classification system that might be used in conservation planning. Since nearly every forest has a different set of dominant tree species, one cannot simply document 'forest types' by the dominant species and use this to preserve the full range of species composition. But climate and geology predict species composition in a broad sense, and lead to some recommendations for conservation.

In the Canal watershed, the driest climate near the Pacific coast supports only remnants of forest, and these forests harbor a number of unusual tree species (Condit *et al.*, 2001). Several rare bird species have population centers in the drier forests, and a number of bird species migrate from drier to wetter zones during the year (Condit *et al.*, 2001). Because the Pacific slope forests are nearly gone in drier parts of Central America, the few forests near the Canal's Pacific entrance warrant attention. Unfortunately, these forests are near Panama City and thus likely to be cleared soon, now that the U.S. military control is gone. A larger number of species are restricted to wetter zones such as Fort Sherman near the Canal, and especially the very wet forests of Atlantic ridges and mountaintops. The latter sites also harbor the largest number of birds and amphibians with restricted distributions. However, wet forests of Central America are still widespread, far more so than the dry, Pacific slope forests, and the mountain forests are not under immediate threat.

High species turnover and migratory birds underscore the need to protect forests across the climatic gradient of Panama's isthmus in order to preserve populations of most native species. The area of the Panama Canal is one of the few sites where a corridor of forest reaches from Atlantic to Pacific Ocean. From a conservation perspective, if we have just one main message, it is the importance of maintaining this corridor. In addition, we offer the following specific recommendations:

(1) Trash collection, sewage treatment, and enforcement of rules about land use and soil protection need to be widely established. Given expanding human

populations, failure to implement these basic practices will lead to extreme degradation of water resources and loss of their benefits to society.
(2) Deforestation within parks and near streams outside parks should be curtailed.
(3) Fisheries should be monitored and managed.
(4) Hunting in national parks near large towns should be reduced, and restaurants using poached meat should be fined.
(5) Natural regeneration of the forest should be promoted in Altos de Campana National Park. This is an area of very low human population, and there is extensive abandoned grassland and shrubland within the park.
(6) A corridor between Soberanía and Chagres National Parks should be protected and reforested. Again, this is an area of low human population, with a matrix of forest fragments.
(7) Forests near Panama City, in the driest part of the watershed, should be added to the national park system.

The other fundamental goal of the Panama Canal watershed monitoring program was to set a baseline against which future inventories can be compared. We have provided a precise estimate of forest cover, and USAID, the PCA, and the Panamanian government will thus be able to get firm statistics on ecosystem change. Forest plots and vertebrate censuses provide species lists and community descriptions, which can be used for revealing future changes in the integrity of the forests, and population changes of some prominent species. Maps of human population will allow precise assessment of where growth is occurring, and our hydrological models and water quality assessment can be used for projections about how the Canal's water supply will be affected by future development.

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