The Status of the Panama Canal Watershed and Its Biodiversity at the Beginning of the 21st Century

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Panama is a small Central American country, but it operates a big canal and the world keeps an eye on developments there. Problems with the canal or ecological disasters in its watershed would attract a lot of attention. As Theodore Roosevelt planned, the Panama Canal is a major shipping corridor, transporting 37 ships a day and providing substantial income to the Panamanian government. Yet as Roosevelt could not have recognized—despite his interest in conservation—the canal sits in the center of one of the world's most biologically diverse areas (Myers et al. 2000): Southern Central America has more forest bird species than any other region in the world, except Amazonia and the northern and central Andes, each of which is vastly larger than southern Central America (Stotz et al. 1996); and Panama has as many plant species per 10,000 km^2 as any region in the world, more than Amazonia or the Malay Peninsula (Barthlott et al. 1996). Roosevelt may have suspected, though, that forests are crucial for protecting the water supply of the Panama Canal and for maintaining the plant and animal communities. Fortunately, the year 2000 still found extensive forests around the canal, protected largely thanks to military and shipping interests, but it also found the watershed adjacent to a large and expanding capital city.

LONG-TERM ECOLOGICAL STUDIES REVEAL A DIVERSE FLORA AND FAUNA NEAR THE PANAMA CANAL, HARBORED WITHIN A CORRIDOR OF FOREST STRETCHING FROM THE CARIBBEAN TO THE PACIFIC, BUT DEFORESTATION, LAND DEGRADATION, EROSION, AND OVERHUNTING REMAIN THREATS

Maintaining the ecosystem integrity of the canal will pose a major challenge for conservation in the 21st century. Is urban and economic development compatible with a hydrologically functioning canal and conservation of an extremely diverse flora and fauna?

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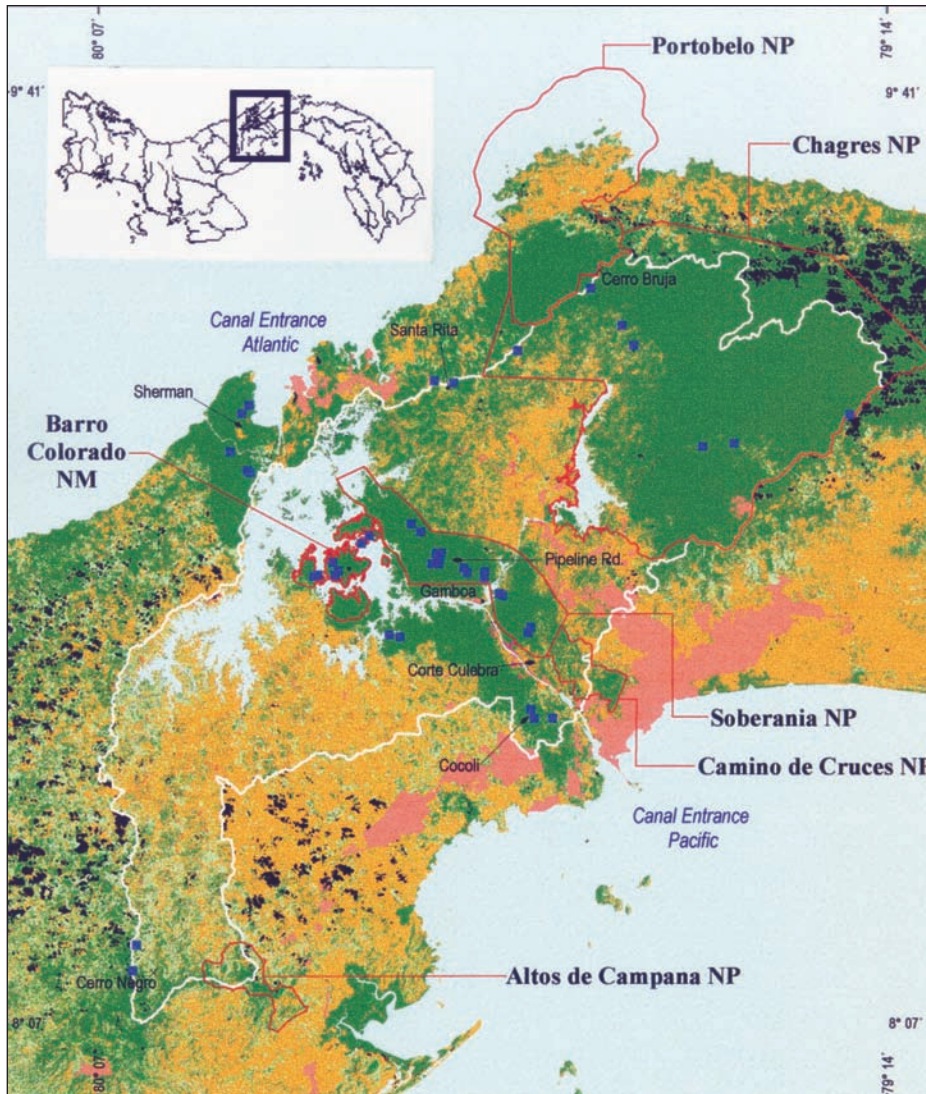
Figure 1. Forest (green) and nonforest (yellow for grass or shrubland, pink for urban, blue for water) near the Panama Canal watershed. Black marks are clouds. The traditional boundary of the watershed is outlined in white (though the Canal Authority recently expanded the official definition of the watershed, we used this earlier boundary in our work). National parks are outlined in red; the convoluted Barro Colorado boundary should not be confused with an urban area. Forest inventory plots are indicated with blue squares. North is up. Lake Alhajuela, the canal's main water source, is east of the canal. Panama City is the large urban area on the Pacific coast just east of the canal entrance. The large green patch on the Pacific coast in the far southern part of the map is mangrove forest; away from the canal corridor, there is no lowland terrestrial forest on the Pacific slope. The canal is about 65 km long from ocean to ocean.

provide a year 2000 summary of the status of the canal's natural resources, the national parks that Panama has created to protect them, and their human inhabitants, based on years of research conducted under the auspices of the Smithsonian Tropical Research Institute and the Panama Canal Commission and collected by a recent in-depth monitoring program sponsored by the US Agency for International Development (Heckadon-Moreno et al. 1999, Ibáñez et al. 1999a). This snapshot of the status of land use, forest communities, hydrology, and human population in the watershed will provide a baseline against which to assess future change. Our analyses of natural communities focus on trees and vertebrates—the best known groups and thus those offering the most useful gauge. Of course, we make no claim that trees and vertebrates represent the entire flora and fauna, and we encourage other researchers to monitor aquatic biota and invertebrates.

The canal's surroundings

The Panama Canal watershed encompasses 2892 km^2 of land area (Figure 1), which is about half the size of the state of Delaware (Heckadon-Moreno et al. 1999, Ibáñez et al. 1999a). It lies in the seasonally moist tropics at 9° north latitude. Rainfall is ample to sustain tall forest throughout the area, but there is a marked dry season from December through April. Rainfall is considerably higher, and the dry season shorter, on the Caribbean side of the isthmus (Condit et al. 2000). Most of the watershed is less than 300 m above sea level, but the fringes to the southwest and east rise to 1000 m in elevation at three peaks. The rainfall gradient across the isthmus and the elevation gradient underlie the region's high diversity and also set the human settlement patterns. At lower elevations and on the drier Pacific slope are most of the cities; much of this area is now grassland, cleared by humans for agriculture (mostly cattle). These grasslands frequently burn during the dry season, but the natural forests do not. In

Much of the news coverage surrounding the year 2000 turnover of the canal to Panama focused on a concern that was raised in the scientific literature 20 years ago: Clearing the forest in the watershed might kill the canal (Wadsworth 1978). Little attention has been paid to the importance of the area in terms of biodiversity, and for the most part the reports ignore the vast quantity of empirical data that exist on the status of the canal watershed and its forests. In this article we

contrast, the wetter Caribbean side of the isthmus is where the largest forest blocks remain.

In terms of general structure, most forests of the canal area are quite similar, except very small areas of mangrove, freshwater swamps, and mountain peaks. Well-drained sites have a closed canopy 20–40 m tall, with emergent trees reaching 50 m in height, and a dense understory of tree saplings, treelets, palms, and many lianas. Large-scale natural disturbances—hurricane or fire—are absent, so small windstorms and individual treefalls are the sole source of canopy turnover. Even the driest sites have a mostly evergreen canopy and thus do not qualify as dry or deciduous forest, and nearly all lowland sites near the canal are called tropical moist forest in the Holdridge (1967) system. However, there is a gradient in deciduousness: Forests near the Pacific coast are about 25% deciduous, whereas Atlantic sites have almost no deciduous trees (Condit et al. 2000). A small area of wet ridges near the Atlantic are classified as wet forest or submontane forest in the Holdridge system, but these forests are structurally not much different from the moist forests.

Forest types in the tropics are most typically defined by climatic zones, and the types found in the watershed—moist and wet forest—are widespread in Central America. Substantial areas are in the national parks of each country. Panama has 12,521 km^2 of land area—16.5% of the country—in national parks, mostly heavily forested (Autoridad Nacional del Ambiente 2000). But these broad forest types belie much more rapid changes in species composition. Moreover, the canal watershed has a substantial share of the protected areas of Panama—10.4% of the nation's national parkland lies in the watershed, which occupies only 3.8% of the nation's land area.

The forests remaining

The first step in evaluating conservation status in the moist tropics is to determine how much land remains forested. In 1998, 54% of the land area of the Panama Canal watershed was forested and 43% was pasture or shrubland (Ibáñez et al.
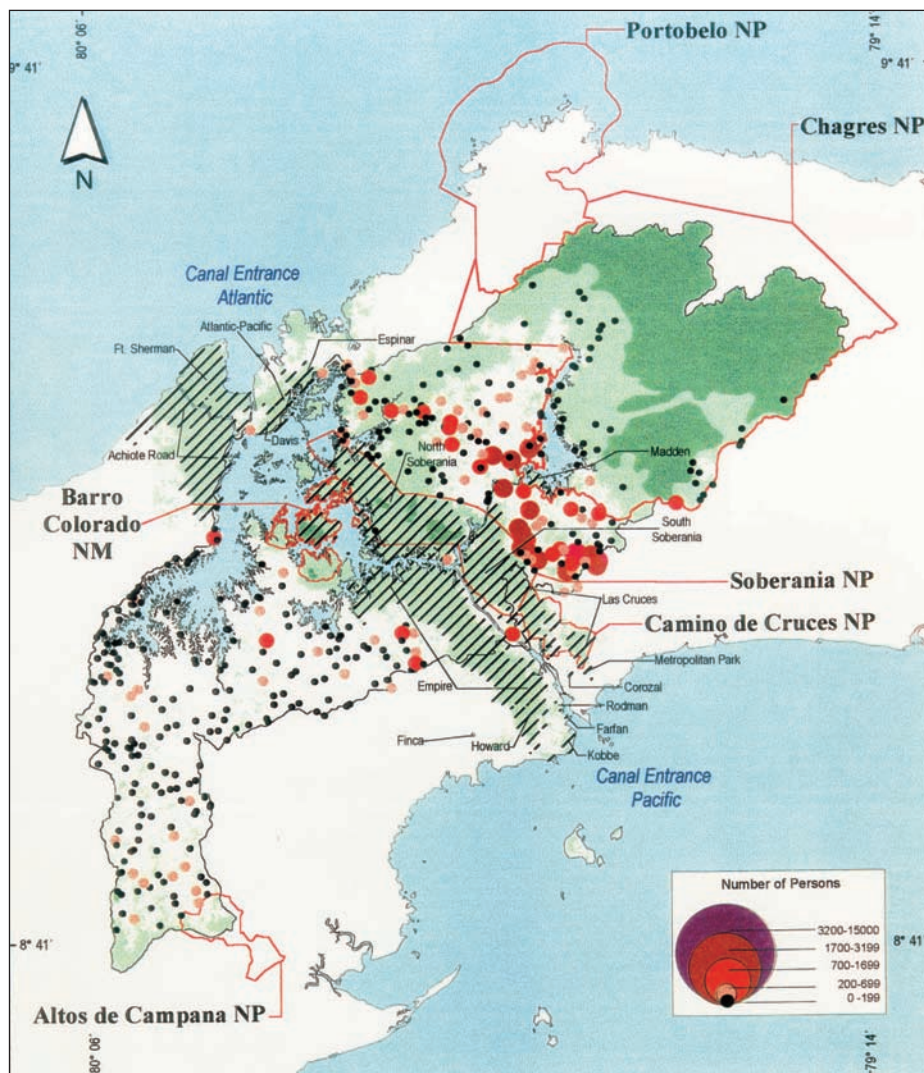

Figure 2. Human communities of the Panama Canal watershed, overlain on the map of forest cover (light green) and old-growth forest (dark green). Each circle represents a single town, according to Panama's 1990 census. All the largest circles (populations greater than 3200) are along the transisthmian highway from Panama City (east of the Pacific canal entrance) to Colon (east of the Atlantic entrance). Chilibre and Las Cumbres include the congregation of towns at the south end of this highway. Also indicated are the bird census regions listed in Table 1 and the area referred to as the canal corridor (hatched).

1999a). The forest is mostly in two large blocks, one east of Lake Alhajuela and one along the canal (Figure 1); we refer to the latter forestland as the canal corridor (Figure 2). The area between the two is a patchwork of forest fragments. Two-thirds of the forest, 108,000 ha, is protected within the three national parks and one nature monument of the watershed. Most of the remaining forest is along the west side of the canal, on land that was used by the US military until the year-2000 turnover. Not all national parkland is forested, however, especially in Altos de Campana National Park, where 50% is anthropogenic grassland or shrubby regrowth; other protected areas are more than 90% forest (Ibáñez et al. 1999a).

The Pacific slope has been settled for about 7000 years by Native Americans and more recently by Spanish colonists. Since the canal was completed in 1914 and the Canal Zone came under the protection of the US government, forests have regrown near the canal, but in the southern half of the isthmus, close to Panama City, they remain fragmented and conspicuously secondary, with few large trees. In contrast, there is extensive forest near the canal in the northern half of the isthmus, in Soberania National Park and Barro Colorado Nature Monument (Figure 1), and old-growth forest remains on Barro Colorado Island and in a few other patches near the canal. The remote forests east of Lake Alhajuela are largely undisturbed, with extensive areas of near pristine old-growth trees (Figure 2). Outside the canal area, Pacific slope forests have been cleared throughout most of Panama and Central America; forests of the Caribbean coast are much more extensive. In terms of global conservation needs, the forests of the Pacific coast near Panama City could be considered the most important in the region, despite their secondary status. Indeed, the canal area is one of the last sites in the world where a corridor of forest stretches from the Atlantic to the Pacific.

Tree species diversity

The most striking feature of the tree communities around the Panama Canal is how variable they are in species composition. Except for sites within 1–3 km of each other, no two forests are similar in terms of their dominant tree species (Ibáñez et al. 1999a, Condit et al. 2001., Pyke et al. 2001). High turnover is illustrated by data from 44 tree inventory plots established throughout the watershed (Condit et al. 2001, Pyke et al. n.d.). In 34 tree inventories in the canal corridor, covering over 90 ha of forest, 561 species were recorded; in just 10 plots in the wet forests, there were 611 species, 422 of which were not recorded in the canal corridor. This abrupt change in species composition—high beta diversity—is why Panama is so rich in total species. The Barthlott et al. (1996) survey reports that Panama has more than 5000 plant species per 10,000 km^2, even though individual sites, such as the Barro Colorado Island 50-ha plot, are not particularly rich (Condit et al. 1996). Wetter sites have higher local diversity, with over 150 species per ha compared with 84 species per ha in the canal corridor (Pyke et al. n.d.), but even these sites are not nearly as rich as the forests of Amazonia or Southeast Asia (Condit et al. 1996). Many tree species are still being discovered: Of the 983 species we tallied in plots, over 200 had not previously been recorded in the watershed, and 19 are newly recorded for Panama (Condit 2001). This tally is based on D'Arcy's (1987) checklist of Panama's flora, which lists the political region of Panama in which each species has been recorded (either Panama's provinces or the former Canal Zone; the canal watershed falls within two provinces and the Canal Zone).

We estimate that the canal corridor has 850–1000 species of trees and shrubs, with 24% to 28% restricted to the wetter section near the Atlantic, 12% to 16% restricted to the drier section near Panama City, and 30% to 45% widespread from coast to coast (Condit 2001). Our inventories on the Santa Rita

ridge and the wetter foothills near Chagres and Altos de Campana National Parks sample a small part of a very large area; our preliminary estimate is that there are 1400–2200 species in these areas, 60% of which do not occur in the canal corridor (Condit 2001). We estimate that the canal watershed holds 1700–2300 tree and treelet species, 60% to 70% of the total for Panama (Condit 2001). Of these, 983 have been identified in our plots, so we know something about their abundance.

Many are exceedingly rare. Of the tree species tallied in plots, 376 appeared in only a single hectare, and 224 were represented by just one individual. Interestingly, however, of the 91 of those that are identified, 87 occur in countries other than Panama; just four are endemic to Panama, and only one—*Pleurothyrium racemosum* in the Lauraceae—is restricted to the area around the canal watershed. *Pleurothyrium racemosum* is known only from a very small area, and it is rare where it is known.

We also tallied all tree species believed to be endemic to central Panama or to the entire nation by consulting the checklist (D'Arcy 1987). We cross-checked each in the Tropicos database from the Missouri Botanical Garden (available at Web site *mobot.mobot.org/W3T/Search/vast.html*), and found that many listed as endemic in the checklist have recently been collected elsewhere. Of the 1555 tree and shrub species that, according to the checklist, occur in the three political regions of the canal watershed, 165 (10.6%) are endemic to Panama and 79 (5.1%) are endemic to the three regions; however, future collecting will presumably reduce these numbers. In plots are 630 species whose names we could match confidently with the checklist and Tropicos; just 27 are endemic to Panama (4.3%) and seven to the three political regions (1.1%). Thus, plot species are less endemic than nonplot species, which suggests that the rarest species are also more likely to be endemic. One plot species is a particularly interesting endemic. *Eugenia nesiotica*, an easy-to-recognize small tree in the Myrtaceae, was described on Barro Colorado Island in the 1930s. It is common on the island, appearing in every one of the 50 individual hectares of the large plot; a few individuals appear in three plots in Soberania National Park 10 km away, and it has been observed at two other sites just west of the canal (Augustín Somoza [Autoridad del Medio Ambiente, Panama], personal communication, 2001). It has not been recorded elsewhere.

In general, the forests of the canal watershed have few species that are narrow endemics, which is a plus in terms of conservation. On the other hand, the forests have high beta diversity and many locally rare species, which makes conservation difficult. No one protected area can capture most of the tree species. However, the broad division between the wet-forest flora along the Atlantic ridges and the main canal corridor flora should be used as a conservation indicator (Pyke et al. n.d.). Large protected areas are located in both regions. However, there is considerable species turnover within each broad floristic region (Pyke et al. n.d.). In particular, there are about 100 species restricted to the drier forests of the Pacific

side of the canal corridor, and there is almost no protected forest in that zone anywhere in Panama. Camino de las Cruces National Park (Figure 1) is the only protected area in Panama in Pacific forest, and it is small and fragmented. The forests just west of the canal on the Pacific coast should be a priority for future protection.

The avifauna

In contrast to botanical checklists, the bird list is near complete: 650 bird species are known from the Panama Canal watershed (Engelman et al. 1995), representing two-thirds of the Panamanian avifauna. Of these, 226 species are restricted to forests and are most at risk from deforestation. The forests of the canal corridor harbor 177 forest species, and the upper Chagres and Campana are home to 168 species, including 49 not known in the canal corridor.

Forest-dwelling bird species richness in the canal corridor increases from the dry Pacific slope forests to the wetter Caribbean slope forests and peaks in Soberania National Park (Figure 1). The diversity in Soberania can be attributed to the habitat heterogeneity in the park—secondary and old-growth forest; swamps, streams, and uplands; and a mixture of floristic elements of dry Pacific forests at the south end of the park and wet Atlantic elements at the north end. Species richness is positively related to annual rainfall, which is in turn positively related to distance from the Pacific Ocean (Table 1).

The impact of forest fragmentation on bird communities is evident in the canal watershed (Willis 1974, Karr 1982).

Small forest patches on both the Pacific and Caribbean slopes lack large fractions of the forest bird community (Table 1) and tend to be dominated by common, widely distributed forest species as well as species of the forest edge. Even common species have disappeared from the largest isolated fragment in the canal area lowlands, Barro Colorado Island, which has failed to sustain populations of 35% of the species originally present on the island's 1567 ha (Robinson 1999). Furthermore, fragmentation on an even larger scale may have disrupted the altitudinal migratory movements of forest birds from the foothills of Chagres National Park to the lowlands of the canal corridor forests. In the decades since construction of the transisthmian highway disconnected lowland forests in the Chagres foothills from those in the canal area, four species of altitudinal migrants that formerly occurred regularly in the canal corridor have rarely been detected: two hummingbirds (*Eutoxeres aquila* and *Phaethornis guy*), a toucan (*Selenidera spectabilis*), and a thrush (*Turdus albicollis*) (Robinson et al. 2000).

Not all bird species of the canal watershed fall within the protection of the national park system. In particular, 14 species are known only from forests along Achiote Road and three species only from Fort Sherman (Figure 2; these species occur elsewhere in the world, but nowhere else in the canal watershed). Since neither of those forests is in a national park, they could be developed in the near future. In contrast, no species are restricted to forests of the drier Pacific slope forests. Although a lack of unique species in drier forests

Table 1. Characteristics of the forested areas in which bird surveys were conducted. The figure in parentheses after the site name is the distance to the Pacific coast (km); Chagres regions are large and the distance is from the approximate midpoint. Rainfall is the annual mean based on a regression surface fitted to data at 29 rainfall stations (Pyke et al. n.d.). The positive relationship between richness and rainfall is significant ($F_{1,16} = 7.37$, p = 0.015), as is a positive relationship between rainfall and distance from the Pacific coast ($F_{1,16} = 168.5$, p < 0.0001).

Forest patch (km distance to Pacific coast)	Location	Area (ha)	Annual rainfall (mm)	Forest-dwelling bird species	Forest-dwellers as percentage of species
Kobbe (0.1)	Canal corridor	432	1750	17	9.6
Farfan (3)	Canal corridor	21	1750	13	7.3
Finca (4)	Canal corridor	37	1750	20	11.9
Rodman (5)	Canal corridor	64	1800	34	19.8
Corozal (7)	Canal corridor	62	1810	39	22.0
Metropolitan Park (5)	Canal corridor	190	1810	51	29.4
Espinar (57)	Canal corridor	867	3105	56	31.6
Madden (30)	Outer watershed	518	2407	64	36.7
Davis (55)	Canal corridor	541	3022	69	39.0
Howard (8)	Canal corridor	1682	1800	71	40.7
Atlantico-Pacifico (57)	Canal corridor	651	3050	75	42.4
Camino de las Cruces NP (19)	Canal corridor	6116	1950	87	49.7
Barro Colorado Island (44)	Outer watershed	1600	2637	104	44.4
Empire Range (18)	Outer watershed	15,020	2100	121	67.8
Soberania NP south (26)	Outer watershed	8800	2150	124	71.2
Fort Sherman (68)	Canal corridor	4795	3200	139	79.1
Achiote Road (67)	Canal corridor	9085	3100	157	88.7
Soberania NP north (46)	Outer watershed	13,145	2500	165	92.1
Altos de Campana NP (11)	Outer watershed	3525	2500	104	unknown
Chagres NP lowlands (38)	Outer watershed	75,000	2850	172	unknown
Chagres NP foothills (38)	Outer watershed	22,000	3500	137	unknown

NP = National Park

might suggest a lesser need to conserve those forests for protection of bird diversity in the canal watershed, important reasons for conservation remain. First, as already indicated for plant conservation, lowland Pacific slope forests in the dry parts of Panama have been almost completely destroyed. Second, several regionally uncommon species have their centers of abundance in Pacific slope forests and are extremely rare in wetter forests; examples include the yellow-green tyrannulet (*Phylloscartes flavovirens*), sepia-capped flycatcher (*Leptopogon amaurocephalus*), lance-tailed manakin (*Chiroxiphia lanceolata*), and rufous-and-white wren (*Thryothorus rufalbus*). Third, the abundance of long-distance Neotropical migratory birds is greater in slope forests of the Pacific than in those of the Caribbean (Karr 1976, Petit et al. 1999). Many long-distance migrants spend more than half of each year in Panama, and the bulk of the populations of Acadian flycatchers (*Empidonax virescens*), bay-breasted warblers (*Dendroica castanea*), chestnut-sided warblers (*D. pensylvanica*), and Kentucky warblers (*Oporornis formosus*) winter in lowland Panama. Fourth, the migratory patterns of year-round resident species between the Pacific and Caribbean slopes have been too little studied. Many insectivorous species are thought to move north to the wetter Caribbean slope during the depths of the dry season when insect abundance is low, whereas some nectarivorous and frugivorous species may instead move south to the Pacific slope to take advantage of a dry season peak in flower and fruit production (Karr and Freemark 1983, Robinson et al. 2000).

Studies in the canal watershed have produced much of the best evidence available on bird densities in tropical forest (Robinson et al. 2000). We know in general that tropical forest birds—like tropical forest trees—are rare. In forests of Soberania National Park, the most abundant species rarely reach densities greater than one pair per hectare, and 80% of species occur at densities less than 10 pairs per 100 hectares (Robinson et al. 2000). Thus, the minimum forest area required to sustain populations of all species over the long-term must be large, on the order of 500 to 1000 km^2 for some of the rarest species (Robinson et al. 2000). Species richness in tracts smaller than several thousand hectares may continue to decline as delayed effects of isolation, such as reduced breeding success, lead to local extinction (Willis 1974, Robinson 1999).

Some birds of the region are globally rare. The canal watershed overlaps three areas of bird endemism, defined as regions where birds with global ranges less than 50,000 km^2 are found (Stattersfield et al. 1998). Eleven of the 226 forest bird species in the watershed (4.9%) have restricted ranges by this definition (Stattersfield et al. 1998). Most of these are common in foothills or highlands, including the higher elevations of the watershed's periphery, and have ranges extending as far as eastern Costa Rica or eastern Panama. But one of the species, *Xenornis setifrons*, the speckled antshrike, is globally threatened (Stattersfield et al. 1998). It is known only from the eastern edge of the watershed to the Colombian border, from only a few sites, and it is never common.

Although only a handful of species are known to have disappeared from the canal watershed and neighboring forests in the decades since the canal's completion (Robinson et al. 2000), failing to protect a significant majority of the remaining forest tracts on both the Caribbean and Pacific slopes will certainly cause further reductions in regional levels of avian diversity. Long-term maintenance of bird species diversity in the canal watershed will therefore require preservation of large forest tracts from ocean to ocean and reestablishment of a forested corridor from the lowlands of the canal area to the Chagres lowlands and foothills.

Amphibians

Amphibians, though less diverse than trees or birds, are known to be indicators of ecosystem alteration. Some of the best long-term data available on tropical amphibians have come from studies in the canal watershed. Ninety-three amphibian species—52% of the amphibian fauna of Panama—have been recorded within the watershed (Ibáñez et al. 1994, 1995, 1996, 1999a, 1999b, n.d.); these amphibians comprise 86 frog, five salamander, and two cecilian species. Species diversity in the lowland forests near the canal increases from the dry Pacific side to the wetter Caribbean side. Diversity peaks in Soberania National Park, where arid and humid tropical amphibian assemblages of lowland Central America mix (Duellman 1966, Myers 1979, Rand and Myers 1990), a pattern that matches that for birds and reflects again the diverse mixture of forest in the park.

Many amphibian species are widely distributed with respect to elevation in the canal area: 54 species occur both in lowland forests (less than 300 m elevation) and higher. But 17 species are restricted to the lowlands, and 22 to the much less-surveyed highlands. Just seven of the canal watershed's 93 amphibian species are found exclusively in nonforest habitat (grassland). The remaining species are all forest dwellers or associated with forests; these include 65 species that occur exclusively in forests and 21 more that occur both inside and outside the forest or at the grassland–forest edge.

All but one of the 93 amphibians in the canal area occur in a protected area. The exception is a dendrobatid, *Phyllobates lugubris*, a species of Costa Rica and western Panama whose range just reaches the western edge of the canal watershed. Five other species with very restricted ranges occur in the watershed. *Atelopus limosus*, *A. zeteki*, and an undescribed species of *Atelopus* are endemic to Panama, all occurring at mid-elevation in a few forests across the country. There are also records from the watershed of two additional species presently considered to be Panamanian endemics, *Bolitoglossa schizodactyla* and *Rana* sp. (*pipiens* complex), though their distributions may extend to Costa Rica.

Amphibians have suffered disappearances and drastic population declines at several sites around the world (Blaustein and Wake 1990, Wake and Morowitz 1991, Houlahan et al. 2000). There has been no clear indication, however, that amphibian abundance has decreased in the Panama Canal watershed. Amphibians were monitored during the 1998, 1999,

and 2000 dry seasons through visual encounters along streamside transects at 10 sites located in the lowlands and highlands, four of them previously surveyed in 1991 through1995 and one in 1976 through 1978. Frogs congregate along streams during the dry season, and thus offer an easy census opportunity. During the 1999 dry season, overall frog abundance was low, but this could be attributed to an unusually wet period that disrupted the concentration of frogs along stream margins. Counts for 2000 were still rather low, although higher than for 1999; dry season rainfall was very close to average. Overall, there is no general, long-term decline, and all species seen in 1991 were present in 2000 (Ibáñez et al. 1999a). Frog populations within the Panama Canal watershed appear not to have been affected by the fungal pathogen that has decimated some species in the highlands of western Panama and in other parts of the world (Berger et al. 1998, Lips 1999).

The impact of hunting

Forests near the Pacific coast are fragmented (Figure 1), secondary, and heavily hunted. Hunting is moderate on the Atlantic side of the canal corridor and low in the remote wet forests of Chagres National Park. The Barro Colorado Nature Monument also suffers little from hunting, thanks to continual, intense patrolling by Smithsonian guards. National parks are no haven from hunting, and protected areas close to large cities (Camino de las Cruces and Soberania National Parks) are heavily hunted. Counts along transects near the canal showed a negative correlation between hunting pressure (as measured by counting shotgun shells and interviewing park guards) and the density of several mammalian species; however, densities of large birds were not correlated (Wright et al. 2000). In general, forests on the Pacific half of the isthmus have few large mammals of any species and are entirely missing several large vertebrates. In contrast, the remote Chagres forests support populations of jaguar (*Panthera onca*), harpy eagle (*Harpia harpyja*), white-lipped peccary (*Tayassu pecari*), and most other large mammals and birds native to the area. This may be due both to less hunting pressure and to the larger areas of intact forest in Chagres National Park (Ibáñez et al. 1999a).

We know from one well-studied system that hunting can have an impact beyond that on vertebrate populations. In particular, seeds of two palm species accumulated beneath tree canopies in hunted areas, whereas seeds were carried away at Barro Colorado. Evidently, hunters have greatly reduced disperser populations of these palms. As a result, the palms recruit far more seedlings in hunted areas (Wright et al. 2000), suggesting that hunting could lead to changes in tree species composition (Robinson et al. 1999). Many plant species have seeds dispersed by large vertebrates, and we suspect that more examples of the impact of hunting on tree recruitment will come to light.

Human population

In 1990 the human population of the Panama Canal watershed was 113,000 and projected to reach 166,000 by the 2000 census (Ibáñez et al. 1999a). The annual rate of population increase in the watershed between 1980 and 1990, 3.8%, was much higher than the population growth of the entire country (2.1%) or the metropolitan area of Panama City (2.7%). The watershed's very high growth is due to a large influx of people into two towns—Las Cumbres and Chilibre—which are at the northern edge of the Panama City urban area and its 1.1 million people (Figure 2).

But rural areas of the watershed are also growing. The western part of the canal watershed consists only of small rural communities (Figure 2), and the population there grew from 15,799 to 19,640 between 1980 and 1990 (2.2% per year). The number of people living inside park boundaries expanded from 1100 in 1980 to 2300 in 1990 (included in the 1980 figure are people who lived in towns now inside Chagres National Park, which was established only in 1984). The number living within 6 km of national parks grew from 23,000 to 35,000 in the same decade, or by 4.2% per year (Heckadon-Moreno et al. 1999, Ibáñez et al. 1999a).

Rural areas are largely deforested, yet very little of the cleared land produces crops. Researchers reported in 1999 that 59% of the land in one rural community east of Soberania National Park was pasture for cattle, 27% was abandoned field of the introduced grass *Saccharum spontaneum*, and less than 1% was used for growing vegetable crops (Heckadon-Moreno et al. 1999, Ibáñez et al. 1999a). This does not include crops grown in gardens immediately adjacent to dwellings, which could not be seen in aerial photographs, but this crop source could not constitute more than 5% of the total land area.

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 dump wastewater directly into the Chilibre River (Heckadon-Moreno et al. 1999, Ibáñez et al. 1999a). Most houses have septic tanks, but there is ample evidence of leakage. Many communities have no waste pickup, and large piles of uncovered garbage accumulate (Heckadon-Moreno et al. 1999, Ibáñez et al. 1999a). Fortunately, most of the streams of the canal watershed have only small human settlements nearby and no industrial establishments, so rivers remain fairly clean except for those near Chilibre and Las Cumbres, which are severely contaminated and unsuitable for any human use (Ibáñez et al. 1999a).

The canal's water supply

Total runoff over the canal watershed is 4.4×10^9 m^3 of water annually. More than half of this, 2.6×10^9 m^3, is used to fill the locks—191,000 m^3 each time a ship passes, 37 times a day. An additional 1.2×10^9 m^3 of water is used to generate electricity at the Gatun Dam for canal operations, and 0.27×10^9 m^3 is processed for drinking water (Ibáñez et al. 1999a).

In 1982, a dry year accompanying a strong El Niño event, the six main rivers feeding the canal carried just 1.8×10^9 m^3 of water, 25% below their long-term average. If the entire watershed suffered a similar reduction (data are available for only those rivers), the 4.4×10^9 m^3 typically available would be

reduced to just 3.3×10^9 m³ of water, less than the 4.1×10^9 m³ needed to fill locks, generate electricity, and produce drinking water. Clearly, the water budget for the canal is tight enough that changes in runoff or sedimentation caused by land use are a serious concern.

The major natural resource concern raised about the canal is whether deforestation will increase siltation, which would reduce water storage capacity and raise the cost of dredging. In view of this concern, the Panama Canal Commission started collecting data on sediment loads in 1981 (Tutzauer 1990) and the watershed monitoring project analyzed those data. The data for 16 years show no trend toward increased sedimentation, supporting Tutzauer's (1990) earlier analysis. Rather, annual sediment loads fluctuate dramatically as a function of rainfall patterns. A model using total rainfall and the number of days of intense storms as independent variables accurately predicts total sediment loads (Ibáñez et al. 1999a). The relationship between rainfall intensity and landslide events, which was documented in Puerto Rico, formed the basis for our model (Larsen and Simon 1993, Larson and Torres Sanchez 1998).

But deforestation has a second, more direct impact on water resources: It alters temporal patterns of flow. We demonstrated this impact in a watershed at the boundary of the north end of Soberania National Park. In a deforested catchment, 26% of incident rain entered streams almost immediately, while only 14% did so in an adjacent forested catchment matching in topography and geology (Ibáñez et al. 1999a). As a result, stream flow during the wet season was higher in the deforested catchment than in the forested one, while the pattern reversed in the dry season. It is likely that further deforestation throughout the watershed would reduce dry season water supplies to the canal; a large-scale hydrological model is being developed that will predict this impact. Since dry season water supply is the major concern for canal operation— the only reason canal use has ever been limited—this issue appears to be far more important than the siltation issue. It is perhaps unfortunate that early papers warning about deforestation (Wadsworth 1978) focused on increased siltation instead of reduced dry season flow.

Greenhouse gases and reforestation

Forests in the canal area of Panama have 280 Mg (megagrams) dry weight per ha of aboveground biomass, whether old-growth or mature secondary forest more than about 100 years old. Annual aboveground production of wood in mature forest is 5 Mg per ha, and an additional 12 Mg per ha is produced as leaf litter and fruit (Leigh 1999). Belowground biomass has not been measured, but it probably adds 25% to these figures. Abandoned fields of tall grass have 50 Mg dry biomass per ha; no one has estimated biomass of farmland, but it is probably a good deal lower. Belowground biomass in grasslands is not known. Mature plantations hold about as much biomass as forests, but because plantation land is harvested, it holds, on average, about half this biomass (Kraenzel 2000).

These estimates allow calculation of the potential value of canal area land in terms of carbon sequestration. The 130,000 ha of grassland and farmland could store another 100–200 Mg of dry weight per ha if reforested. Grasslands are nonproductive or very low in productivity in many areas in central Panama, and conversion to forest would mean little loss in terms of agriculture. However, tree regeneration is inhibited, mostly by anthropogenic fires. In most of the canal region, abandoned grasslands or shrublands burn during the dry season. Even in the absence of fire, though, tree regeneration is slow because of an interaction between seed dispersal and seedling recruitment: Small-seeded species are dispersed into grasslands in abundance, but their seedlings cannot compete with the grass; some large-seeded species can survive in the grassland, but they are rarely dispersed there. Natural restoration of forest and its biomass in Panama grasslands is thus slow or nonexistent and requires some kind of management—at a minimum, fire control. Although restoring forests or growing plantations is thus entirely beneficial in the long run—for carbon storage, commercial wood production, and conservation of the local flora and fauna—it requires short-term investment.

The Panama Canal area has another important role in the greenhouse gas cycle because of the large reservoirs that store water for the canal. Two large dams impound water; one created Lake Gatun in 1910 and provided the water over which ships travel, and the second was built in 1949 to create Lake Alhajuela for water storage. The small lakes and swamps around these two large lakes produce large quantities of methane—a potent greenhouse gas—from decaying aquatic vegetation. Reservoirs are a source of 400–1800 kg • ha • yr, mostly in shallow water (Keller and Stallard 1994). Since forests are slight methane sinks, absorbing about 4 kg • ha • yr, conversion of forest to reservoir provides a large methane source (Keller et al. 1990). But lakes should also be carbon sinks, via eutrophication caused by sediment input from pollution or erosion (Stallard 1998). Accumulation of plant biomass and organic sediment at the lake bottom would store carbon, but calculating how much it would store requires knowing the carbon concentration of the sediments. If spread uniformly over the lake bottoms, the mineral sediment contributed by all the rivers in the watershed would accumulate 23 Mg per ha annually. If this sediment were organic-carbon poor, at about 2% by weight, then 0.46 Mg per ha of carbon would accumulate each year; but if it were richer in organic carbon, at about 25%, there would be 5.5 Mg per ha of carbon. This accumulation of sediment and carbon should continue until the lakes fill, possibly storing more carbon than there was in the preexisting forest.

Conclusions

On the positive side, more than half of the Panama Canal watershed is covered in forest, much in large contiguous blocks, and there a remains a nearly unbroken band of forest connecting the Atlantic and Pacific Oceans. A substantial portion is old-growth forest that is little used by people, where even

the most sensitive species of large mammals and birds persist. The forests protect the water supply, support fisheries and hunting, are valuable in terms of tourism, and conserve the high species diversity of the Panama Canal ecosystem. The high beta diversity of trees, and the need of migratory birds for wet–dry corridors, both underscore the need for extensive areas to be protected—no one protected area can support a high proportion of the tree, bird, or amphibian species now living in the canal watershed.

Fortunately, the existing system of protected areas is extensive and covers a wide range of climate and forests. The weakest link is near the Pacific coast, where the largest block of forest reaching the shoreline is not protected (Figure 1). Since drier forests of Central America are essentially gone, the forests near Panama City should be a top priority for conservation. We also recommend that areas of low human density on the Santa Rita ridge and near Cerro Campana be added to the park system, because these would contribute to a forest corridor that runs the length of Central America. The existing national parks need vigorous protection, because hunting and fishing in parks is a widespread practice.

On the negative side, the human population of the watershed is growing at a high rate, and unless this trend is miraculously reversed, forest loss, hunting, and contamination will spread in the next few decades. Rapid urban development near Panama City will most likely lead to further deforestation near the Pacific side of the canal. Even rural areas are becoming more densely populated. Giving expanding populations, social changes relevant to conservation are even more critical. A better social structure—from regular trash collection to enforcement of land-use regulations—needs to be developed (Ibáñez et al. 1999a). Hunting and fishing need to be managed. Investment in reforesting unproductive grasslands should be encouraged. All of these efforts toward land management would almost certainly lead to long-term payoffs.

The essence of conserving biodiversity and preserving an effectively functioning canal is protection of as much forest as possible. Loss of forests, either through conversion for economic development or pressure from a burgeoning human population, will lead to substantial losses of biodiversity. At this benchmark in the history of the Panama Canal ecosystem, the government of Panama has difficult decisions to make. How will the opportunities for economic development be reconciled with the desire to maintain the natural flora and fauna and preserve clean and functioning ecosystems? The world is watching.

Acknowledgments

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