Wetlands Ecology and Management **12:** 3–55, 2004.

Wetlands of Central America

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Accepted in revised form 25 July 2003

Key words: Central American wetlands, conservation, inventory, management, Ramsar Convention, refugia

Abstract

The wetlands of seven Central American countries – Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, and Panamá – are reviewed. The region's wetlands are classified into five systems: marine, estuarine, riverine, lacustrine, and palustrine. At a minimum, wetlands cover $\approx$40,000 km^2 ($\approx$8%) of the land area of Central America. These wetlands support high levels of biological diversity, especially of invertebrates, amphibians, and migratory birds. Because of intensive deforestation and conversion of forest lands to agriculture, many species of birds and mammals that formerly were abundant in upland forests now are restricted to wetland refugia. Annual primary productivity of some Central American wetlands equals or exceeds that of tropical rainforests, and wetlands also provide essential ecosystem services such as maintaining water quality. Population and development pressures formerly restricted to upland areas are expanding rapidly into wetlands, resulting in losses of wetlands at rates comparable to losses of rainforests. Since 1990, all seven Central American countries have become signatories to the Ramsar convention on wetlands of international importance, but integrated planning for management and conservation of wetlands in the region only began in 2002. A specific set of recommendations for wetland inventory, ecological research, and management is provided that would be feasible and effective within the social and cultural framework of the Central American countries.

Introduction

Wetlands are some of the most productive and widespread ecosystems in the world, yet they have received much less scientific attention in the tropics than have rainforests and other upland forests. As in the temperate zone, tropical wetlands are being lost rapidly, as they are filled, settled, and tilled. Because basic information on extent, flora and fauna, and ecological processes of tropical wetlands is widely scattered in the literature, or folded into studies of upland forests, it is not immediately accessible to new researchers, managers, and policy-makers. In this monograph, I review the available information on the wetland flora and fauna, ecology, and management of the seven Central American countries: Belize, Guatemala, Honduras, El Salvador, Nicaragua, Costa Rica, and Panamá (Table 1). The wetlands to the north and south are somewhat better known and characterized (reviews in Glooschenko et al., 1993; Junk, 1993; Olmsted, 1993; Wilen and Tiner, 1993), but Central American wetlands overall have received little attention from the scientific and management communities (see CCAD, 2002, for the first steps in regional coordination of wetland inventory and coordinated management).

A first step in studying or managing Central American wetlands is to determine where and how large the wetlands are. Yet the total areal extent of wetlands in Central America remains unknown (Davidson and Gauthier, 1993; CCAD, 2002), as ecological studies in Central America have centered primarily on two rain forests: La Selva Biological Station in Costa Rica and Barro Colorado Island in Panamá (Leigh et al., 1982; Gentry, 1990; McDade et al., 1994). The IUCN Directory of Neotropical Wetlands (Scott and Carbonell, 1986) was the first attempt to identify wetlands of international

Table 1. Geographical and demographic information for the seven Central American countries.

Country	Area (km^2)	Coastline (km)		Population	Population growth rate (%)
		Atlantic	Pacific		
Belize	22,963	280	–	263,000	2.7
Guatemala	108,889	110	240	13,314,000	2.6
Honduras	112,088	640	124	6,560,600	2.3
El Salvador	21,200	–	260	6,353,700	1.8
Nicaragua	130,000	541	352	5,024,000	2.1
Costa Rica	50,899	212	1254	3,835,000	1.6
Panamá	77,082	1160	1697	2,888,300	1.3

Population size and growth rates are 2002 figures (CIA, 2002).

importance in Central America. A subsequent inventory of such wetlands did not include Belize (Davidson and Gauthier, 1993). Both of these compendia focused primarily on wetlands known to be important for resident and migratory birds, and therefore gave short-shrift to several other important wetland categories (*sensu* Cowardin et al., 1979), such as coral reefs, seagrass beds, riverine wetlands, and swamp forests. The World Mangrove Atlas (Spalding et al., 1997) includes aereal extent of mangrove forests throughout Central America, but many of the data on which the Atlas is based are more than 20 years old, and 1–2% of the mangroves in the region are lost annually through deforestation and development (Ellison and Farnsworth, 1996; Farnsworth and Ellison, 1997).

In a widely cited review, Aselmann and Crutzen (1989) estimated that Central America possesses 17,500 km^2 of "freshwater wetlands", but they included only forested swamps, herbaceous marshes, and floodplains. Mangrove swamps, which have received more scientific study than any other wetland type in Central America, occupy at least another 6500 km^2 (Groombridge, 1992), and possibly nearly twice that area (Spalding et al., 1997). Lacustrine wetlands also were excluded from Aselmann and Crutzen's (1989) review, although the two large lakes in Nicaragua, Lago Nicaragua and Lago Managua, alone occupy 9313 km^2, and the basin of Lago Nicaragua (including Lago Managua and the Río San Juan) covers ≈40,000 km^2 (Incer, 1976). The addition of other lacustrine wetlands into Central American inventories would increase substantially the estimate of total wetland area for the region. The historical predilection for classifying Central American vegetation according to the Holdridge Life Zone system (Holdridge, 1967; Holdridge et al., 1971), which does not include "wetland" as a vegetation type, also has resulted in serious underestimates of wetland extent and obscures information needed to manage sustainably the wetlands in this region. Thus, the data compiled here are only a preliminary attempt to synthesize available information, and would be best used as a springboard to stimulate more accurate inventories and further ecological studies of the wetlands of Central America.

Geographic setting

The ≈525,000 km^2 Central America isthmus as we know it today is only 3 million years old (Stehli and Webb, 1985a). During the Cretaceous, the margins of North and South America were separated by ≈3000 km of open water. By the late Cretaceous, an arc of volcanic islands ranging from present-day Colombia to southern Nicaragua foreshadowed the formation of the present isthmus (Raven and Axelrod, 1975). The present-day Maya Mountains of northern Belize have been above water for at least 180 million years, and were an oceanic island during the Cretaceous (Hartshorn et al., 1984). The uplifting of the Central American isthmus in the late Pliocene was a singular event in the evolution of the flora and fauna not only of Central America itself, but also of North and South America. The isthmus provided a corridor for the "Great American Interchange" of temperate and tropical terrestrial flora and fauna (Stehli and Webb, 1985b) as well as a barrier between the Caribbean Sea and the Pacific Ocean. While Central America as a corridor permitted gene flow between North and South America, Central America as a barrier resulted in allopatric speciation

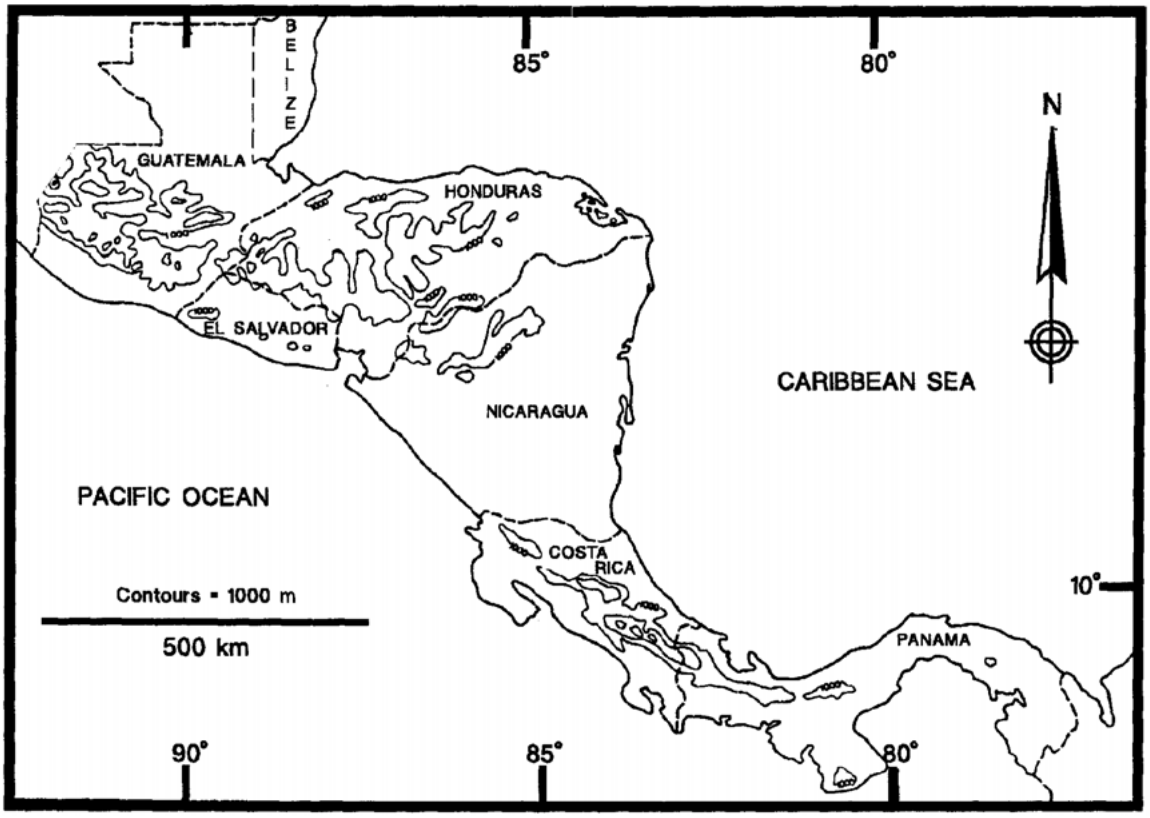

Figure 1. Coarse topography of Central America. Contour lines in 1000 m intervals. Modified from Garcia M. (1983) to include Belize.

of the marine fauna (e.g. Glynn, 1972; Porter, 1972; Knowlton and Jackson, 1994).

Central America lies at the confluence of five tectonic plates: the North American Plate to the north; the Caribbean Plate to the east; the South American Plate to the southeast; the Cocos Plate to the west; and the Nazca Plate to the southwest (Raven and Axelrod, 1975; Coney, 1982; Garcia, 1983; Smith, 1985). This intersection of plates produced several fracture systems within the isthmus, in which many important wetland systems have developed. A large thrust fault cuts east to west across Guatemala from the Gulf of Honduras; Lago de Izabal in Guatemala lies in the eastern basin of this fault. A north–south fault has resulted in the Honduras depression between the southeast corner of Honduras and the large estuary of the Golfo de Fonseca at the border between Nicaragua and Honduras. Lagos Nicaragua and Managua occupy the deepest part of the active geological depression (*graben*) dividing the Central American isthmus from the Golfo de Fonseca at the northwest corner of Nicaragua to the mouth of the Río San Juan on the Caribbean coast (Incer, 1976; Coney, 1982; Smith, 1985; Griesinger and Gladwell, 1993).

Subduction of the Cocos Plate beneath the Caribbean Plate has resulted in active vulcanism across the entire isthmus; at least 20 active volcanoes there have shown signs of activity in the last two decades (Garcia, 1983; Griesinger and Gladwell, 1993). Geothermal groundwater beneath volcanoes modifies stream chemistry and ecology in Costa Rica (Pringle and Triska, 1991), and perhaps elsewhere in Central America. A number of lakes occur in old volcanic calderas (e.g. Lago de Ilopago, Lago de Coatepeque, and Laguna El Jocotal in El Salvador). Mountain ranges in the northern geological province (Belize to northern Nicaragua) trend east-to-west, and include the Maya Mountains of Belize and the central chain in Guatemala. The central cordillera of Costa Rica and Panamá trend from northwest to southeast. The terrain is steeply mountainous on the western side of the isthmus, while the eastern side is a broad coastal plain (Figure 1). These topographic features delineate Atlantic and Pacific climatological and hydrological provinces on either side of the Central American isthmus (Figure 2, Table 2) that differ in their relative extent of wetland systems.

The regional climate is tropical-equatorial, with annual rainfall increasing from north to south, but rarely falling below 1500 mm yr^{-1} anywhere (Figure 2). Both sides of the isthmus have wet and dry seasons, although the Atlantic coastal plain and lowlands receive a more even distribution of monthly rainfall than the Pacific coast, which has a pronounced dry season (Figure 2). The coupling of seasonal rainfall patterns and topography results in a significantly greater volume of surface water run-off into the Caribbean Sea than into the Pacific Ocean (Table 2), and wetland development is more extensive on the Atlantic coastal plains than on the Pacific coast of Central America.

The total population of Central America is $\approx 3.8 \times 10^7$, and it is growing at $\approx 2.1\%$ yr^{-1} (Table 1). Belize is the least populated in the region – it has 0.7% of the population of the entire region, and 4% of the population of similarly-sized El Salvador. Overall, the Central American population is concentrated on the Pacific coasts of Guatemala, El Salvador, Nicaragua and Panamá. The populations of Costa Rica and Honduras are centered in their respective north-central regions, and the population of Belize is densest in the Caribbean port of Belize City.

Wetland classification and wetland types

There is no common classification of wetland types among the countries of Central America (Finlayson and van der Valk, 1995; Scott and Jones, 1995), although all countries have now adopted the 1971 Convention on Wetlands of International Importance, Especially as Waterfowl Habitats (the "Ramsar Convention"). Jurisdiction over wetland resources is commonly split among governmental ministries otherwise dedicated to forestry, agriculture, fisheries, or tourism, among others, each of which classifies wetlands according to its own interests. The widespread use of the Holdridge Life Zone classification system (Holdridge, 1967) in describing vegetation types throughout Central America (e.g. Hartshorn, 1988) has resulted in the placing of many wetland types into broader classifications. Mangrove forests in Belize alone, for example, can occur in "subtropical moist forest," "tropical wet forest," and "tropical wet-transition to subtropical forests" (Hartshorn et al., 1984). *En passant*, it is important to note that Holdridge himself (e.g. Holdridge and Budowski, 1956) was careful to distinguish swamp forests as distinct formations within defined forest life zones.

In this review, I include all habitats that would be considered "wetlands" under the Ramsar convention: "areas of marsh, fen, peatland or water whether natural or artificial, permanent or temporary, with water that is static or flowing, fresh, brackish or salt, including areas of marine water the depth of which at low tide does not exceed six meters" (Lyster, 1985; Sand, 1992). The Ramsar classification is broader than the UNESCO (1973) classification used by Matthews and Fung (1987) and Aselmann and Crutzen (1989) in their reviews of global distribution of wetlands: for example, mangroves are not considered to be wetlands in the UNESCO (1973) classification. In Central America, current regional planning for conservation and management of wetlands uses the Ramsar definition of wetlands as its starting point (CCAD, 2002). However, the Ramsar classification is inadequate as a basis for inventorying wetlands, since it conflates vegetation types with landscape position, and lacks a hierarchy of types. Thus, in each section of this review, I cover the five wetland systems delineated by Cowardin et al. (1979): marine, estuarine, riverine, lacustrine, and palustrine. Within the review's subsections, information is generally ordered from north to south by country.

Geographical distribution and floristics

There has been no complete inventory of Central American wetlands to date (Davidson and Gauthier, 1993; Finalyson et al., 1999; CCAD, 2002) despite attempts to categorize the global extent of freshwater wetlands (Matthews and Fung, 1987; Aselmann and Crutzen, 1989; Finlayson et al., 1999). Thus, the distributional data presented in this section of the various wetland systems throughout the region are bound to be incomplete. Assignment of plants to families follows Mabberley (1993). The generic and specific classification and nomenclature of Gómez (1984) is used for wetland Liliopsida (monocotyledons), while that of Hartshorn et al. (1984) and Wilbur et al. (1994) are used for trees and dicotyledonous shrubs and herbs.

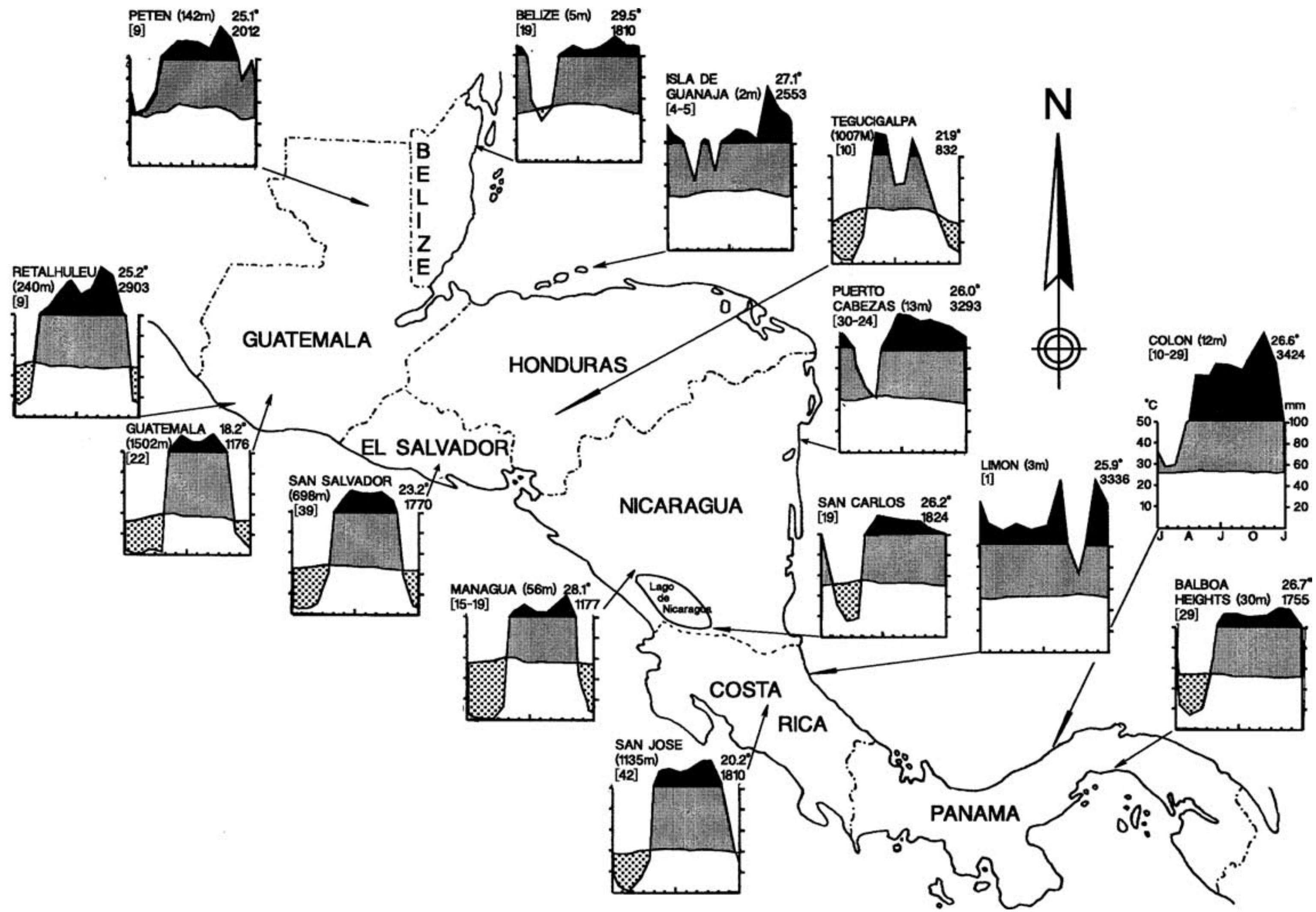

Figure 2. Representative climate diagrams for representative stations within Central American. Each diagram is labelled with its location; elevation above sea level (m); number of years from which data were derived (in brackets; if two numbers, the first is for temperature and the second is for rainfall); mean annual temperature (°C) and mean total rainfall (mm). Plots simultaneously illustrate monthly mean temperature (tick intervals = 10°) and rainfall (tick intervals = 20 mm; above 100 mm, scale is reduced by tenfold; equivalent tick intervals = 200 mm). Dotted fields indicate periods of relative drought (ratio of temerature to precipitation>1:2), and shaded fields indicate periods of relatively humid conditions (temperature to precipitation < 1:2). Measurement scales are shown only for the diagram of Colón, Panamá. Data from Walter et al. (1975), Portig (1976), and Pool et al. (1977).

Table 2. Annual discharge rates of major Central American rivers.

River	Discharge into	Measurement site	Mean annual discharge (m^3/s)
Belize			
Belize	Caribbean	Double Run	155.4
Sibun	Caribbean	Freetown Sibun	50.5
Rio Grande	Caribbean	Big Falls South	24.0
North Stann Creek	Caribbean	Melinda	15.4
Sittee River	Caribbean	Kendall	13.9
Moho River	Caribbean	Blue Creek Village	7.8
Guatemala			
Usumacinta	Gulf of Mexico	Boca del Cerro	1776.0
Salinas	Gulf of Mexico	El Cedro	575.0
Montagua	Caribbean	Morales	181.9
Dulce	Caribbean	Teleman	69.9
Belize	Caribbean	El Arenal	35.9
Maria Linda	Pacific	Agua Caliente	10.9
Los Esclavos	Pacific	La Sonrisa	10.6
Samala	Pacific	Candelaria	9.8
Honduras			
Patuca	Caribbean	Cayetano	209.4
Ulua	Caribbean	Pte. Pimienta	195.5
Chamelecon	Caribbean	Pte. Chamalecon	43.6
Choluteca	Pacific	Los Encuentros	33.7
El Salvador			
Lampa	Pacific	San Marco	377.5
Goascoran	Pacific	near outlet	33.7
Grande San Miguel	Pacific	Vado Mari	27.8
Nicaragua			
San Juan	Caribbean	Los Pilares	563.6
Coco	Caribbean	Guanas	52.2
Grande de Matagalpa	Caribbean	Yacica	20.8
Tamarindo	Pacific	Tamarindo	2.9
Costa Rica			
Grande de Terrabe	Pacific	Palmar	306.4
Parismina	Caribbean	Pascua	132.4
Grande de Tarcoles	Pacific	Balsa	78.4
San Juan	Caribbean	Jabillos	56.5
Grande de Candelaria	Pacific	El Rey	30.3
Panamá			
Changuinola	Caribbean	Bacon Bay	203.9
Chepo	Pacific	Canitas	182.4
Chiriqui	Pacific	David	123.7
Santa Maria	Pacific	San Francisco	87.5
Tabasara	Pacific	Camaron	73.1
Fonseca	Pacific	San Lorenzo	60.8
Chiriqui Viejo	Pacific	Paso Canoa	52.9
San Pablo	Pacific	La Mesa	52.7
Cocle	Caribbean	El Torno	48.4
Lake Gatun	Caribbean	Chico	30.2

Data from Hartshorn et al. (1984) and Griesinger and Gladwell (1993).

Marine wetlands

Coral reefs

Coral reefs are found most extensively off the Atlantic coasts of Belize and Panamá. The ≈257 km long barrier reef off the eastern shore of Belize is the longest barrier reef in the western hemisphere. The reef crest lies only several hundred meters off-shore at its northernmost point at the southern tip of the Yucatán Peninsula. The barrier reef diverges from the mainland towards the south, and is nearly 40 km off-shore at its terminus in the Sapodilla Cays, just north of the Bay of Honduras. The structure of the Belizean reef complex is described in detail in the edited volume by Rützler and Macintyre (1982). Belize also possesses three low coral atolls: Glover's reef, Lighthouse reef, and the Turneffe islands (Stoddart, 1962). Twenty years ago, the flora of Glover's reef was described and included 59 species (Linhart 1980), but complete floristic inventories of the other two atolls have not been conducted since Hurricane Hattie passed over the region in 1961, significantly altering the vegetation structure (Stoddart, 1963, 1969).

Small reefs occur in the Bay of Honduras ($\approx$50 km^2), the Miskito Cays of Nicaragua ($\approx$10 km^2), and southern Costa Rica ($\approx$10 km^2) (Phillips et al., 1982; Scott and Carbonell, 1986; Wells, 1988; Groombridge, 1992). Introductions to the $\approx$250 km of fringing reef complexes on the Atlantic coast of Panamá are provided by Glynn (1972), Porter (1972), and Wells (1988). Species richness of corals in Belize and Panamá are nearly as high as can be found anywhere in the Caribbean (e.g. Porter, 1972), and the application of molecular techniques has resulted in the discovery of new species of corals (e.g. Knowlton et al., 1992). Coral reefs on the Pacific coast of Central America are restricted to southern Costa Rica (and the Cocos Islands of Costa Rica, 500 km SW of the mainland) and Panamá, although they are very limited in extent and species diversity (Glynn, 1972; Porter, 1972; Wells, 1988).

Seagrass beds

The distribution of seagrass beds parallels that of coral reefs in Central America. Five species of seagrass in four genera occur in the tropical western Atlantic: *Halophila decipiens, H. engelmannii, Thalassia testudinum* (Hydrocharitaceae), *Halodule wrightii*, and *Syringodium filiforme* (Cymodoceaceae) (Phillips and Meñez, 1988; Littler et al., 1989; Dawes et al., 1991). Diverse algal communities are associated with coral reefs and seagrass beds. Dawes et al. (1991) reviewed the current status of floristic studies of algae in the tropical Atlantic (including Central America), and an excellent field guide to the marine plants of the Caribbean is available (Littler et al., 1989). The marine algae of the Pacific coast of Central America are less well known, but good species lists are available for Guatemala (Bird and McIntosh, 1979) and Panamá (Earle, 1972).

Estuarine wetlands

Mangrove swamps

Mangrove swamps (mangal) epitomize tropical wetlands in the popular imagination. These vast tidal, estuarine forested wetlands occur on both the Atlantic and Pacific coasts (Figure 3), and account for at least 6500 km^2 (Groombridge, 1992) and possibly as much as $\approx$12,000 km^2, or 2.2% of the total land area of Central America (Spalding et al., 1997; see Table 3). Spalding et al. (1997) estimated that the remaining mangrove forests in Central America, exclusive of Belize, cover 8000–9000 km^2. Belize alone possesses at least 1300 km^2 of mangrove forest (Table 3). Mangrove swamps form narrow bands along the coastal plains of the Atlantic coast of Central America, where tidal amplitude is relatively low ($<$0.9 m), but rarely penetrate inland more than several kilometers along rivers. Dozens of mangrove cays occur within the lagoon complex of the Belizean barrier reef (Stoddart et al., 1982). Tidal amplitude is much greater, and consequently mangroves extend further inland along river courses on the Pacific coast of Central America. On that coast, mangroves also form extensive stands in the major river deltas: Golfo de San Miguel, Río Grande de Térraba, Río Grande de Tárcoles, Golfo de Nicoya, Golfo de Fonseca, and Bahía de Jiquilisco (Figure 3; Golley et al., 1975; Hartshorn, 1988).

More research has been conducted in mangal than in any other Central American wetland type, and as a result there are excellent floristic data for these wetlands. There are four primary mangrove species in Central American mangal: *Rhizophora mangle* (Rhizophoraceae); *Avicennia germinans* (Avicenniaceae); *Laguncularia racemosa* and *Conocarpus erectus* (Combretaceae) (Tomlinson, 1986). *Conocarpus* is often considered a mangrove associate (Tomlinson, 1986) because it is not restricted to mangal, but its ubiquity in Central American mangrove forests has led most authors to include it in floristic lists of true mangrove genera (e.g. Cintron-Molero and Schaeffer-Novelli, 1992; Jiménez, 1992). Two additional *Rhizophora* species, *R. racemosa* and *R.* $\times$ *harrisonii* (a putative hybrid between *R. mangle* and *R. racemosa* [Tomlinson, 1986]), and two additional *Avicennia* species, *A. bicolor* and *A. tonduzii* (= *A. bicolor, sensu* Tomlinson [1986]) occur only on the Pacific coast of Central America (Figure 4). A final species of mangrove, *Pelliciera rhizophorae* (Theaceae), has a very limited distribution on the Pacific coast

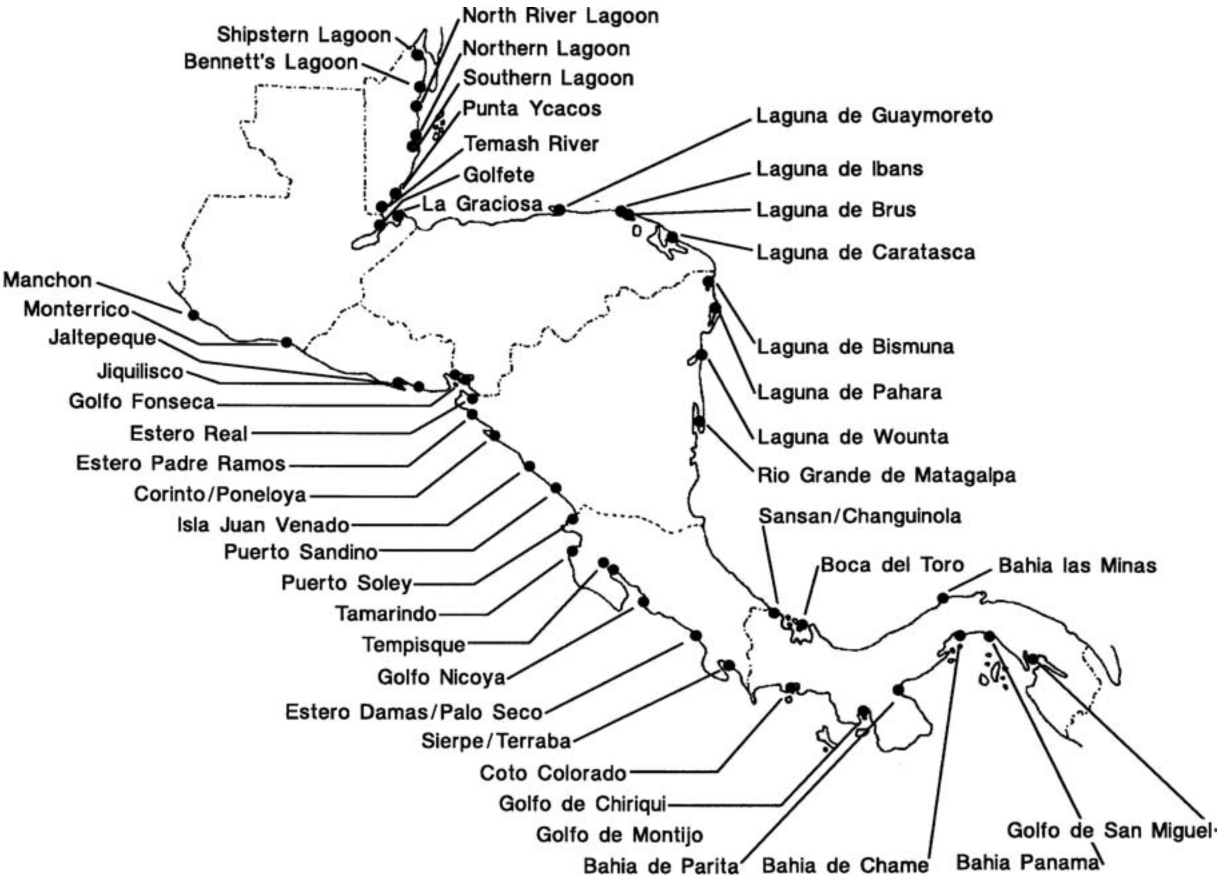

Figure 3. Locations of major mangrove swamps in Central America. Data from Stoddart et al. (1982), Scott and Carbonell (1986), Jiménez (1992), and Spalding et al. (1997).

of southern Costa Rica and Panamá, and has been reported from three sites on the Atlantic coasts of Panamá and Nicaragua (Holdridge et al., 1971; Collins et al., 1977; Jiménez, 1984; Rabinowitz, 1985; Roth and Grijalva, 1991) (Figure 4). *Pelliciera* was more widespread in the Miocene (23 Mya; Figure 4), but its populations had declined dramatically by the early Pliocene (3–5 Mya), probably due to changing climatic conditions and resultant loss of habitat beginning at the end of the Tertiary (Fuchs, 1970; Gentry, 1982; Jiménez, 1984; Graham, 1995).

Although mangal is typified by low species diversity (e.g. Janzen, 1985), there are a number of plants in all major life-forms (herbs, shrubs, trees, vines, lianas, and epiphytes) that occur frequently in both undisturbed and disturbed mangal, along swamp edges, and in the understory of mangroves of relatively short stature (Table 4).

Salt marshes and salt pans

Tidal salt marshes, consisting primarily of perennial herbaceous plants, are relatively uncommon in Central America, and their total areal extent is unknown. With few exceptions, they appear to be confined to leading edges of developing mangrove swamps, in gaps generated by natural disturbance, and in areas where woody vegetation has been cut over (West, 1977; Costa and Davy, 1992; Davy and Costa, 1992). The primary plant species in Central American salt marshes are *Spartina brasiliensis* (= *S. alterniflora*), *S. spartinae*, and *Distichlis spicata* (Poaceae). *Batis maritima* (Bataceae) and *Acrostichum aureum* (Pteridaceae) commonly invade disturbed areas (Tomlinson, 1986; Costa and Davy, 1992), and are common understory species under mangroves in northern Central America. Hypersaline

Table 3. Estimates of mangrove area (ha) for sites indicated in Figure 2.

Belize		*Nicarágua*	
Shipstern Lagoon	4200	Laguna de Bismuna	48,340
Bennett's Lagoon	400	Laguna de Pahara	35,580
N. River Lagoon	800	Laguna de Wounta	36,290
Northern Lagoon	3200	Rio Grande de Matagalpa	74,240
Southern Lagoon	3200	Estero Real	19,410
Punta Ycacos	9000	Padre Ramos	4590
Temash River	20,000	Corinto/Poneloya	10,700
Lagoon cays	≈2000	Peñitas/Juan Venado	2420
Other Atlantic areas	44,517	Puerto Sandion	1990
		Other Pacific areas	200
Guatemala			
Golfete	7600	*Costa Rica*	
La Graciosa	6000	Puerto Soley	200
Manchon	10,850	Tamarindo	400
Monterrico	4325	Golfo de Nicoya	15,176
Other Pacific areas	911	Damas/Palo Seco	2312
		Sierpe/Terraba	17,737
Honduras		Coto Colorado	875
Laguna de Guaymoreto	34,000	Other Pacific Areas	4592
Laguna de Ibans	6600		
Laguna de Brus	11,500	*Panamá*	
Laguna de Caratasca	37,000	Bahía las Minas	4100
Golfo de Fonseca	46,869	Sansan/Changuinola	6500
		Boca del Toro	9800
El Salvador		Other Atlantic areas	112,164
Golfo de Fonseca	4720	Golfo de Chiriqui	44,688
Jiquilisco	19,847	Golfo de Montijo	23,439
Jaltepeque	5004	Peninsula Azeuro	6213
Other Pacific areas	3896	Bahia de Parita	11,553
		Bahia de Chame	5044
		Bahia de Panama	26,192
		Golfo San Miguel	46,489
		Other Pacific Areas	1350

Data for Atlantic sites from Stoddart et al. (1982), Scott and Carbonell (1986), Groombridge (1992), Garrity et al. (1994); and for Pacific sites from Durán (1977) and Jiménez (1992); overall totals checked against Spalding et al. (1997).

salt pans can develop in cleared areas within mangal, and their vegetation is often distinct from adjacent salt marshes. *Sesuvium portulacustrum* (Aizoaceae) and *Salicornia* spp. (Chenopodiaceae) colonize these salt pans. Notable salt marshes and salt pans in Central America occur in Belize on Ambergris Cay (18° N, 87° W) (West, 1977) and Twin Cays (16° 50′ N, 88° 06′ W) (Rützler and Feller, 1987), and in Panamá at the Monjas-Bayano marshes (7° 56′ N, 80° 18′ W), Playa Monagre (8° N, 80° 25′ W), and Aguadulce (8° 15′ N, 80° 30′ W) (Scott and Carbonell, 1986).

Riverine wetlands

Riparian gallery and stream-side forests

Allen (1956) and Gómez (1985) briefly mentioned riparian gallery forests, which form on river banks and gravel bars. These gallery forests are characterized by species with seeds that are dispersed by water or river-dwelling animals, and which are relatively intolerant of even moderate soil–water deficits (Gómez, 1985), but there have been no attempts to distinguish definitively riparian gallery forests in a floristic sense.

In northern and central Belize, lowland gallery forests are dominated by *Spondias mombin* (Anacardiaceae), *Attalea cohune* (Arecaceae), *Ceiba pentandra* (Bombacaceae), *Bursera simaruba* (Burseraceae), *Cassia grandis* (Caesalpiniaceae), *Bucida buceras* (Combretaceae), *Enterolobium cyclocarpum* and *Inga edulis* (Mimosaceae), *Coccoloba belizensis* (Polygonaceae), *Guazuma ulmifolia* (Sterculiaceae), and *Luehea seemanii* (Tiliaceae) (Horwich and Lyon, 1990). MacDougall and Kellman (1993) could not identify

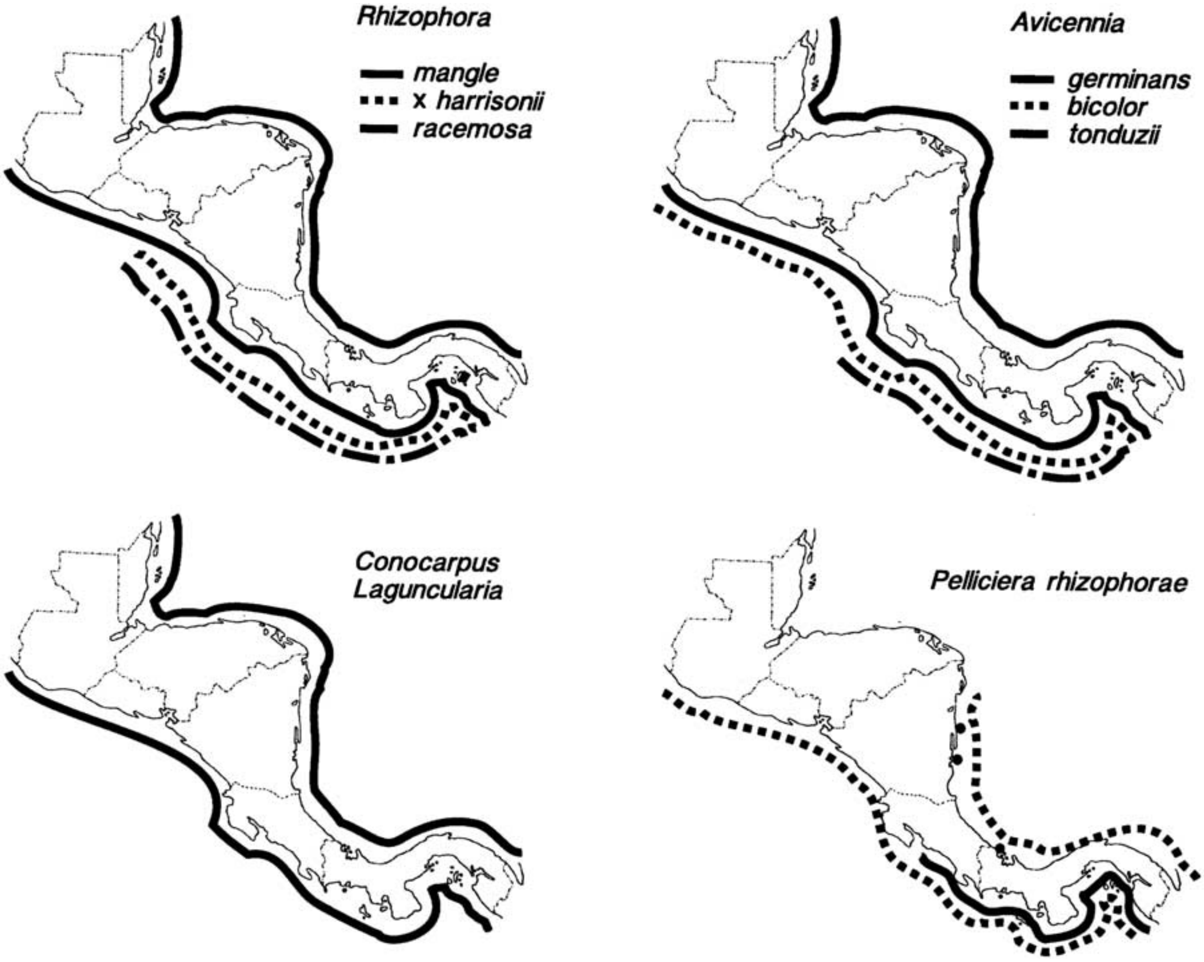

Figure 4. Distribution of mangrove genera in Central America. Distributions of *Rhizophora* spp. from West (1977), Gentry (1982), Jiménez (1987), Cintron-Molero and Schaeffer-Novelli (1992), and Jiménez (1992); of *Avicennia* spp. from West (1977), Tomlinson (1986), and Cintron-Molero and Schaeffer-Novelli (1992); of *Laguncularia* and *Conocarpus* from Tomlinson (1986) and Cintron-Molero and Schaeffer-Novelli (1992). For *Pelliciera rhizophorae*, solid line indicates current distribution along the Pacific coast of Central America (data from Collins et al., 1977; and Jiménez, 1984); solid circles indicate records from the Caribbean coast of Central America (data from Jiménez, 1984; Roth and Grijalva, 1991); dotted lines indicate hypothesized distribution during the Eocene-Oligocene (modified from Fuchs, 1970; Graham, 1977, 1987; Gentry, 1982; Jiménez, 1984).

high elevation (>600 m) riparian forests as clearly identifiable entities based on species composition, but these forests are clearly distinct from the adjacent pine savanna (Meave et al., 1991; Meave and Kellman, 1994). Riparian forest "fragments" occupy <4% of the Mountain Pine Ridge area of Belize (17° N, 89° W), and are bounded on their upland sides by dense swards of *Tripsacum latifolium* (Poaceae). The most abundant tree species in these riparian forests are *Xylopia frutescens* (Annonaceae), *Calophyllum brasiliense* (Clusiaceae), *Licania sparsipilis* (Chrysobalanaceae), *Terminalia amazonia* (Combretaceae), *Alchornea latifolia* and *Hyeronima oblonga* (Euphorbiaceae), *Inga cocleensis*, and *Vochysia hondurensis* (Vochysiaceae) (Kellman et al., 1994). Adults and seedings of three tree species appear to be the best indicators of these riparian forests: *Calophyllum brasiliense, Licania sparsipilis*, and *Sloanea tuerchkeimii* (Elaeocarpaceae).

Other Central American gallery forests were noted in Scott and Carbonell (1986) along the Río María in Guatemala (13° 54′ N, 90° 28′ W) and along the Río Platano in Honduras (15° 35′ N, 84° 20′ W), but there are no vegetation data available for these two sites. Lötschert (1955) recorded *Erythrina glauca* (Papilionaceae) and *Salix chilensis* (Salicaceae) as

Table 4. Associated flora of Central American mangrove swamps.

Species	Country[1]	Coast	Reference[2]
Ferns			
Pteridaceae			
Acrostichum auerum	pantropical	Atlantic; Pacific	1
Acrostichum danaifolium	widespread	Atlantic	1, 2
Herbs			
Araceae			
Montrichardia arborescens	C	Pacific	3
Cyperaceae			
Cyperus planifolius	B	Atlantic	4
Fimbristylis spadicea	widespread	Atlantic; Pacific	4, 5
Mariscus ligularis	C	Pacific	3
Scirpus californicus	C	Pacific	3
Liliaceae			
Crinum erubesceus	widespread	Pacific	6
Hymenocalis littoralis	widespread	Pacific	6
Hymenocalis pedalis	widespread	Pacific	6
Poaceae			
Distichlis spicata	widespread	Atlantic; Pacific	4, 7
Echinochloa polistachia	C (introduced)	Pacific	3
Echinochloa colonum	C (introduced)	Pacific	3
Eragrostis prolifera	B (widespread)	Atlantic	4
Eustachys petraea	B (widespread)	Atlantic	4
Jouvea straminea	C	Pacific	5
Paspalum distichum	B (widespread)	Atlantic	4
Phragmites cf. *australis*	B (widespread)	Atlantic	4
Spartina spartinae	B (widespread)	Atlantic	4
Amaranthaceae			
Blutaparon vermiculare	C	Pacific	5
Aizoaceae			
Sesuvium portulacustrum	widespread	Atlantic; Pacific	5, 8
Asteraceae			
Egletes viscosa	C	Pacific	5
Pluchea symphytifolia	B	Atlantic	4
Tuberostylis rhizophorae	C; P	Pacific	1, 6
Boraginaceae			
Heliotropium curassavicum	C	Pacific	5
Capparidaceae			
Capparis odoratissima	C	Pacific	5
Chenopodiaceae			
Salicornia perennis	B	Atlantic	4, 8
Convolvulaceae			
Ipomoea pes-caprae	widespread	Atlantic, Pacific	5, 8
Euphorbiaceae			
Euphorbia mesembrianthemifolia	widespread	Atlantic	4, 8
Papilionaceae			
Canavalia maritima	C	Pacific	5
Polemoniaceae			
Loeselia ciliata	C	Pacific	5
Turneraceae			
Turnera ulmifolia	C	Pacific	5
Verbenaceae			
Lippia strigulosa	B	Atlantic	4
Shrubs			
Asteraceae			
Borrichia arborescens	B (widespread)	Atlantic	4

Table 4. Continued.

Species	Country[1]	Coast	Reference[2]
Batidaceae			
Batis maritima	widespread	Atlantic, Pacific	1, 8
Bignoniaceae			
Tabebuia palustris	P	Pacific	1, 9
Malvaceae			
Pavonia spicata	C	Pacific	1, 6
Pavonia rhizophorae	P	Pacific	1, 6
Papilionaceae			
Lonchocarpus frutescens	C	Pacific	6
Lonchocarpus moniliformis	C, P	Atlantic, Pacific	9
Rubiaceae			
Erithalis fruticosa	B	Atlantic	4
Surianaceae			
Suriana maritima	B	Atlantic	4
Verbenaceae			
Clerodendrum pittierii		Pacific	6
Trees			
Arecaceae			
Bactris minor	C	Pacific	3
Elaeis oleifera	C	Pacific	3
Raphia taedigera	C, N, P	Atlantic, Pacific	3, 10
Thrinax radiata	B	Atlantic	4
Anacardiaceae			
Metopium brownei	B	Atlantic	11
Annonaceae			
Annona glabra	C	Pacific	3
Bignoniaceae			
Dendrosicus latifolius	widespread	Pacific	3
Caesalpiniaceae			
Mora oleifera	widespread	Pacific	1, 3, 10
Tamarindus indica	C	Pacific	5
Euphorbiaceae			
Hippomane mancinella	widespread	Atlantic, Pacific	4, 8
Malvaceae			
Hibiscus tiliaceaus	widespread	Pacific	3, 6
Meliaceae			
Carapa guianensis	C	Pacific	3
Mimosaceae			
Mimosa pigra	C	Pacific	3
Pithecellobium dulce	C	Pacific	3
Pithecellobium keyense	B	Atlantic	4
Prosopis juliflora	C	Pacific	5
Olacaceae			
Ximenia americana	C	Pacific	5
Papilionaceae			
Pterocarpus officinalis	widespread	Atlantic, Pacific	3, 8, 12
Polygonaceae			
Cocoloba caracasana	C	Pacific	2
Cocoloba uvifera	widespread	Atlantic	4, 8, 13
Rubiaceae			
Randia sp.	C	Pacific	5
Vines and Lianas			
Apocynaceae			
Rhabdadenia biflora	widespread	Atlantic, Pacific	1, 6
Bignoniaceae			
Phryganocidia phellosperma	C	Pacific	3, 6

Table 4. Continued.

Species	Country[1]	Coast	Reference[2]
Caesalpiniacea			
Caesalpinia bonduc	widespread	Atlantic, Pacific	1, 5
Mimosaceae			
Entada polystachia	C	Pacific	3
Papilionaceae			
Dalbergia brownei	C	Pacific	3, 6
Epiphytes			
Bromeliaceae			
Tillandsia dasyliriifolia	G	Pacific	14
Tillandsia caput-medusae	G	Pacific	14
Tillandsia baileyi	G	Pacific	14
Tillandsia festucoides	G	Pacific	14
Tillandsia schiedeana	G	Pacific	14
Aechmea sp.	G (widespread)	Pacific	14
Catopsis sp.	G (widespread)	Pacific	14
Orchidaceae			
Brassavola nodosa	widespread	Atlantic	4, 13, 15, 16
Schomburgkia tibicinis	B	Atlantic	8

[1] Countries: B – Belize; C – Costa Rica; G – Guatemala; H – Honduras; N – Nicaragua; P – Panamá; S – El Salvador.
[2] References: 1 – Tomlinson (1986); 2 – Adams and Tomlinson (1979); 3 – Jiménez and Soto (1985); 4 – Stoddart et al. (1982); 5 – Soto and Jiménez (1982); 6 – Jiménez (1992); 7 – West (1977); 8 – A. M. Ellison and E. J. Farnsworth, *pers. observ*; 9 – Gentry (1982); 10 – Myers (1984); 11 – Hartshorn et al. (1984); 12 – Janzen (1978); 13 – Fosberg et al. (1982); 14 – Gomez and Winkler (1991); 15 – Schemske (1980); 16 – Murren and Ellison (1996).

forming monocultures or mixtures on the borders of rivers in El Salvador. The latter species was almost always covered by the hemiparasitic *Psittacanthus calyculatus* (Loranthaceae). Stream-side evergreen forest communities in a region of Nicaragua otherwise dominated by dry-deciduous forests were noted by Taylor (1959). On particularly wet stream-side sites east of Lake Nicaragua, pure stands of *Bravaisia integerrima* (Acanthaceae), *Annona glabra* (Annonaceae), *Anacardium excelsum, Clusia rosea* (Clusiaceae), *Erythrina glauca*, or *Triplaris melaenodendron* (Polygonaceae) commonly develop (Taylor, 1959).

Allen (1956) claimed that several species assemblages occurred consistently enough to clearly delineate four subtypes of gallery forests in the Golfo Dulce region of Costa Rica: rocky banks of fast-flowing streams dominated by *Pithecellobium longifolium* (Mimosaceae); gravel bars in fast-flowing streams dominated by *Tessaria mucronata* (Asteraceae) or *Albizzia filicina* (Mimosaceae); mudbanks along small, meandering streams dominated by *Gynerium sagittatum* (Poaceae); and old, stable gravel bars dominated by *Ochroma lagopus* (Bombacaceae) and *Cecropia* spp. (Cecropiaceae). Hartshorn and Hammel (1994) identified several species that apparently are restricted to riparian forest habitats at La Selva Biological Station (10° 26′ N, 83° 59′ W): *Cordia lucidula* (Boraginaceae), *Nectandra reticulata* (Lauraceae), *Pithecellobium longifolium, Inga marginata, Ficus insipida* (Moraceae), and *Posoqueria latifolia* (Rubiaceae). Other species common in Costa Rican riparian gallery forests include *Anacardium excelsum* (Anacardiaceae), *Lonchocarpus* spp. (Papilionaceae), and *Ficus* spp. (Gómez, 1985).

Lacustrine wetlands

Freshwater lakes and lakeshores

Lakes occupy at least 11,000 km^2 of Central America (Scott and Carbonell, 1986), although there have been few detailed limnological studies of any of them (see Armitage 1957, 1958, 1971; Brinson and Nordlie, 1975; Brinson, 1976; Thorson, 1976a for notable exceptions). The three largest lakes in Central America, Lago Nicaragua and Lago Managua in Nicaragua, and Lago de Izabal in Guatemala drain directly into the Caribbean. Scott and Carbonell (1986) provide brief descriptions of the other major lakes in Central America. Armitage (1957, 1958, 1971), Armitage and Fassett, 1971) discusses volcanic lakes in El Salvador and Nicaragua.

The floating aquatic vegetation of these lacustrine wetlands is dominated by water ferns (*Azolla* [Azollaceae] and *Salvinia* spp. [Salviniaceae]), water hyacinths (*Eichhornia* spp. [Pontederiaceae]), duckweeds (*Lemna* spp. [Lemnaceae]), and several genera within the Hydrocharitaceae. Emergent vegetation is composed primarily of sedges (Cyperaceae), grasses (Poaceae), cattails (Typhaceae), and pondweeds (*Potamogeton* spp. [Potamogetonaceae]). A list of the more common species of aquatic, emergent, and lakeshore vegetation of Central American lacustrine wetlands is given in Table 5.

Volcanic lakes provide unique habitats for aquatic plants in Central America. These lakes may have extreme pH, such as Lake Nejapa in Nicaragua, with a pH > 10 (Armitage, 1971) and Lake Alegria in El Salvador with a pH of 2–2.5 (Armitage and Fassett, 1971) and have few plant species growing in them. Lake Nijapa has only dense phytoplanktonic assemblages (Armitage, 1971), while Lake Alegria has only one species of aquatic vascular plant, *Eleocharis Sellowiana*, growing in it (Armitage and Fassett, 1971). Several temperate aquatic species reach their southern range limit in the two high altitude lakes in El Salvador, Laguna Verde de Apaneca (1650 m above sea level [a.s.l.]) And Laguna Ninfas (1670 m a.s.l.) (Armitage and Fassett 1971): *Nymphaea odorata* var. *gigantea*, *Proserpinaca palustris* var. *crebra*, *Potamogeton pusillus*, and *Brasenia Schreberi*. The latter is characteristic of lakes in formerly glaciated regions of northern United States and southern Canada (Armitage and Fassett 1971). Similarly, *Eleocharis Sellowiana* is a South American temperate species that reaches its northern range in these two lakes.

Palustrine forested wetlands

Forested wetlands are the most common type of palustrine wetland in Central America. Aselmann and Crutzen (1989) estimated that these cover 15,000 km^2 of land area in the region, with an additional 1000 km^2 of floodplain forests. These forested wetlands are characterized by low plant species diversity; virtual monocultures of the dominant tree species are not uncommon.

Palm swamps

Forested wetlands dominated by palms occur throughout the tropics (Myers, 1990). Wright et al. (1959) found a small (2100 ha) *Manicaria saccifera* palm swamp behind a small mangrove swamp located on the southeastern corner of Belize; Standley (1931) reported a tidal palm-swamp consisting of a mixture of *Bactris minor* and the papilionaceous legume *Pterocarpus officinalis* in Honduras; and Lötschert (1955) mentioned (in a footnote) that *Bactris* swamps could be found occasionally on the southern (Pacific) coasts of Honduras and El Salvador. There have been no further studies of any of these palm swamps.

Palm swamps are more frequent southward from northwest Nicaragua through Panama (Holdridge and Budowski, 1956; Myers, 1984, 1990; Urquhart, 1999), but they have been documented and studied in detail only in Costa Rica (Allen, 1956; Holdridge et al., 1971; Myers, 1984, 1990; Gómez, 1985). There, palm swamps occur in the Atlantic lowlands around Tortuguero (10° 37′ N, 83° 22′ W) (Myers, 1984) and in isolated pockets in the Golfo Dulce region and the Osa Peninsula on the Pacific coast (Allen, 1956). The floristic descriptions of these swamps given below follow Allen (1956), Myers (1984, 1990), and Gómez (1985).

Palm swamps of *Raphia taedigera*, known locally as *yolillales,* account for approximately 600 km^2, or 1.2% of the land area of Costa Rica (Sylvander, 1978). These swamps occur below 300 m a.s.l. as both river- and rain-fed wetlands. Unlike upland tropical forests, palm swamps are striking for their low species diversity. Of the four palm swamps studied by Myers (1990), three were dominated by the palm *Raphia taedigera* (40–70% of stems $\geq$10 cm dbh in 50 m^2 plots). Other common trees in *Raphia* swamps include *Crudia acuminata* and *Prioria copaifera* (Caesalpiniaceae), *Grias fendleri* (Lecythidaceae), *Carapa guianensis* (Meliaceae), *Pentaclethra macroloba* (Mimosaceae), *Pterocarpus officinalis* (Papilionaceae), *Cassipourea guianensis* (Rhizophoraceae), and *Luehea seemanii*. In coastal zones, *Mora oleifera* (Caesalpiniaceae) also occurs in *Raphia* swamps. The understory of *Raphia* swamps is dominated by the palms *Asterogyne martiana* and *Calyptrogyne glauca*, the shrub *Psychotria chugrensis* (Rubiaceae), and a number of herbaceous species, including: *Becquerelia cymosa* and *Calyptrocarya glomerulata* (Cyperaceae); *Calathea lagunae* and *C. lutea* (Marantaceae); and *Spathiphyllum friedrichsthalli* (Araceae).

Table 5. Common plants in Central American lacustrine and non-forested palustrine wetlands.

Species	Habitat			Growth habit		
	Lac	Pal	Floating	Submerged	Emergent	Shoreline
Ferns						
Azollaceae						
Azolla caroliniana	X	X	X			
Azolla filiculoides	X	X	X			
Parkeriaceae						
Ceratopteris pteridoides	X	X	X			
Pteridaceae						
Acrostichum daneaefolium		X			X	X
Salviniaceae						
Salvinia auriculata	X	X	X			
Herbs and shrubs						
Alismataceae						
Sagittaria lancifolia		X			X	
Sagittaria latifolia		X			X	X
Araceae						
Pistia stratiotes		X	X			
Spathiphyllum fridrichstalii		X			X	X
Cyperaceae						
Cyperus luzulae	X					X
Cyperus odoratus		X				X
Cyperus spp.	X	X			X	X
Eleocharis elegans	X				X	X
Eleocharis intersticta	X				X	X
Eleocharis mutata		X			X	X
Eleocharis retroflexa	X				X	X
Fimbristylis spp.		X				X
Fuirena simplex	X	X				X
Scirpus californicus	X	X			X	X
Scirpus spp.	X	X			X	X
Hydrocharitaceae						
Elodea canadensis	X	X		X		
Elodea granatensis	X	X		X		
Hydrilla verticillata	X	X		X		
Vallisneria americana	X	X		X		
Vallisneria spiralis	X	X		X		
Lemnaceae						
Lemna valdiviana	X	X	X			
Lemna spp.	X	X	X			
Liliaceae						
Hymenocalis littoralis		X			X	X
Marantaceae						
Calathea lutea		X			X	X
Thalia geniculata		X				X
Thalia trichocalyx		X				X
Najadaceae						
Najas guadalupensis	X	X		X		
Najas spp.	X	X		X		
Poaceae						
Andropogon spp.	X				X	X
Axonopus capliiaris	X					X
Leptocoryphium sp.		X				X
Panicum purpurascens	X	X				X
Panicum spp.	X	X				X
Paspalum spp.	X	X			X	X

Table 5. Continued.

Species	Habitat			Growth habit		
	Lac	Pal	Floating	Submerged	Emergent	Shoreline
Phragmites australis	X	X			X	X
Pontederiaceae						
Eichhornia crassipes	X	X	X			
Pontedaria cordata	X	X	X	X	X	
Potamogetonaceae						
Potamogeton illinoensis	X	X			X	
Potamogeton pectinatus	X	X		X		
Potamogeton spp.	X	X		X	X	
Typhaceae						
Typha angustifolia	X	X			X	X
Typha domingensis	X	X			X	X
Typha latifolia	X	X			X	X
Asclepiadaceae						
Asclepias curassavica	X					X
Asteraceae						
Spilanthes americana	X					X
Callitrichaceae						
Callitriche sp.	X	X		X		
Ceratophyllaceae						
Ceratophyllum demersum	X	X	X			
Convolvulaceae						
Ipomoea carnea		X				X
Euphorbiaceae						
Acalypha diversifolia		X			X	
Caperonia palustris	X					
Lentibulariaceae						
Utricularia foliosa	X	X		X		
Malvaceae						
Malaviscus arboreus		X			X	X
Menyanthaceae						
Nymphoides sp.		X			X	
Mimosaceae						
Mimosa sp.		X				X
Nelumbonaceae						
Nelumbo lutea	X	X			X	
Nymphaeaceae						
Nymphaea ampla		X			X	
Nymphaea lutea		X			X	
Onagraceae						
Jussiaea spp.	X	X	X		X	
Polygonaceae						
Polygonum spp.	X	X			X	X

An "X" indicates expected habitat (lacustrine or non-forested palustrine), and growth habit of plant.

Palm swamps in the Atlantic lowlands of Costa Rica and Panamá also may be dominated by *Manicaria saccifera*. Myers (1990) described a *Manicaria* swamp (47% of all stems) that was 30% denser, but which had much lower stature and overall stand basal area than nearby *Raphia* swamps. In these swamps, *Manicaria* may be co-dominant with two other palms: *Astrocaryum alatum* and *Euterpe* aff. *oleracea* (Gómez, 1985), while in others, *Astrocaryum* may be the only dominant (Holdridge et al., 1971). Co-occurring hardwood trees and understory species in *Manicaria* swamps are similar to those found in *Raphia* swamps, although their relative abundances differ significantly.

Allen (1956) described an isolated *Raphia* swamp in the Sierpe area of the Golfo Dulce region on the

Pacific side of Costa Rica. There, *Raphia taedigera* was co-dominant with *Symphonia globulifera* (Clusiaceae). Two other palms, *Corozo oleifera* and *Scheelea rostrata*, and one other hardwood, *Pterocarpus officinalis*, were listed by Allen as principal species in the Sierpe *Raphia* swamp. Janzen (1978) and Hartshorn (1988) similarly noted the occurrence of *Raphia* swamps in Corcovado National Park on the Osa Peninsula of Costa Rica.

Other freshwater swamp forests

Like palm swamps, hardwood swamp forests exhibit low species diversity and, in the absence of palms, a preponderance of leguminaceous trees. Forests dominated by *Pterocarpus officinalis* occur throughout Central America (Holdridge and Budowski, 1956; Hartshorn, 1988; Bacon, 1990). *Pterocarpus* swamps occur in a variety of palustrine habitats, ranging from river margins and floodplains (Janzen, 1978; Hartshorn, 1988) to rain-fed upland swamps (Bacon, 1990), as well as on relatively well-drained upland clay soils on Barro Colorado Island in Gatún Lake, Panamá (Knight, 1975). Gómez (1985) considered *Pterocarpus* forests to be the "freshwater swamp forest" referred to throughout tropical floras and vegetation analyses. The apparently wide range of habitats occupied by *P. officinalis* has been attributed to taxonomic confusion and a broad spectrum of morphological and physiological ecotypes (Bacon, 1990), but comparative data on population structure of *Pterocarpus* are lacking for Central America. The understory in some Costa Rican *Pterocarpus* forests ranges from nearly non-existent to virtual monocultures of the lily *Crinum erubescens* (Janzen, 1978; Gómez, 1985).

In coastal regions, *Pterocarpus* forests may grade into swamp forests dominated by the caesalpiniaceous legume *Mora oleifera* (Janzen, 1978; Gómez, 1985; Hartshorn, 1988). This species, often associated with coastal mangrove forests (the *Mora*-mangrove association of Gómez [1985]), is more tolerant of brackish water conditions. Like *Pterocarpus* forests, the understory of *Mora* forests is dominated by *Crinum erubescens*. These swamp forests scarcely have been explored, however, and their extent throughout Central America is unknown.

Belizean swamp forests were divided into four categories by Wright et al. (1959): transitional low broadleaf forests; high marsh and low marsh forests in the north and central parts of Belize (all within the tropical moist forest zone of Holdridge, 1967); and high swamp forest in southern Belize (within the tropical wet forest zone of Holdridge, 1967). Trees characteristic of transitional low broadleaf swamp forests include *Metopium brownei* and *Spondias mombin* (Anacardiaceae), *Stemmadenia* spp. (Apocynaceae), *Tabebuia guyacan* (Bignoniaceae), *Vismia ferruginea* (Clusiaceae), *Quercus citrifolia* (Fagaceae), *Dalbergia Stevensonii* (Papilionaceae), *Coccoloba* spp., *Guettarda combsii* (Rubiaceae), *Guazuma ulmifolia, Vitex* spp. (Verbenaceae), and *Vochysia hondurensis*. High and low marsh forests, distinguished primarily by their canopy height, are characterized by *Metopium brownei, Sabal mauritiiformis* (Arecaceae), *Pachira aquatica* (Bombacaceae), *Bucida buceras, Haematoxylum campechianum* (Caesalpiniaceae), and *Inga edulis*. The high swamp forests are dominated by *Pachira aquatica, Chrysobalanus icaco* (Chrysobalanaceae), and *Pterocarpus officinalis*. The term "marsh forests" was an unfortunate combination, and is no longer used in wetland nomenclature. These forests are more properly considered swamp forests.

Taylor (1959) described semi-seasonal and permanent freshwater swamp woodlands dominated by *Erythrina glauca* (Papilionaceae) and *Pachira aquatica*, and brackish swamp woodlands of *Annona glabra* (Annonaceae) in northeastern Nicaragua. At La Selva Biological Station, Hartshorn (1983) and Hartshorn and Hammel (1994) reported that *Pentaclethra macroloba* is the dominant canopy tree in "primary" swamp forests. Other common canopy species in these swamp forests include *Carapa nicaraguensis, C. guianensis, Luehea seemannii, Pterocarpus officinalis, Otoba novogranatensis* (Myristicaceae), and *Pachira aquatica*. The palms *Iriartea deltoidea, Welfia georgii*, and *Astrocaryum alatum* are the main components of the understory in these swamp forests.

Several other freshwater swamp forest types are of particular interest because of their rarity in Central America. Swamp forests dominated by logwood (*Haematoxylum campechianum*), once common throughout northern Belize, were cut over extensively in the 19th century. The only remaining large stand of *Haematoxylum* remaining in Belize is in the Crooked Tree Wildlife Refuge (17° 45′ N, 88° 32′ W).

Swamp forests of cativo, *Prioria copaifera* (Papilionaceae), occur in isolated patches on the Osa Peninsula of Costa Rica (Holdridge et al., 1971), and were logged extensively for plywood (Mayo

Meléndez, 1965; Hartshorn, 1988). On the Atlantic coast of Central America, *Prioria* occurs southward from northwestern Nicaragua, but in Panamá it occurs only on the Pacific coast (Holdridge and Budowski, 1956; Golley et al., 1975). The understory herb *Calathea longiflora* is endemic to the swamp forests of the Osa Peninsula (Gómez, 1984). Swamp forests dominated by *Mora oleifera* also occur on the Osa Peninsula (Holdridge et al., 1971).

Sajal or *orey* forests, dominated by *Campnosperma panamensis* (Anacardiaceae) occur between Puerto Viejo and the mouth of the Río Sixaola in southeastern Costa Rica, in the Laguna de Chiriquí region of Bocas del Toro, Panamá (Holdridge and Budowski, 1956), and sporadically along the Atlantic coast of Nicaragua (Gómez, 1985; Hartshorn, 1988). Like other freshwater forested wetlands in the tropics, *Campnosperma* can occur in virtual monocultures. However, Gómez (1985) recorded the following trees as co-occurring in sajal: *Dialyanthera otoba* (Myristicaceae); *Symphonia globulifera* and *Calophyllum brasiliense; Carapa guianensis; Grias fendleri; Sacoglottis trichogyna* (Humiriaceae); and occasionally the mangrove associates *Conocarpus erectus* and *Cassipourea* spp.

Non-forested palustrine wetlands

Marshes

Temporary and permanently flooded freshwater and brackish marshes are common in coastal plains, floodplains, and lacustrine overflow regions throughout Central America. At a minimum, they cover $\approx$1000 km^2 (Scott and Carbonell, 1986), while Aselmann and Crutzen (1989) estimated 2000 km^2. These wetlands are critically important habitat for migratory waterbirds (Scott and Carbonell, 1986), as well as locally and globally threatened species (e.g. Jabiru storks, manatees; Appendices 1 and 2). The vegetation of all of these marshes is dominated by water ferns (*Azolla* and *Salvinia*), water hyacinths (*Eichhornia* spp.), arrowheads (*Sagittaria* spp.), grasses, and sedges (Table 5). Rice cultivated in fields adjacent to or carved out of these wetlands provides food for migratory waterfowl (Botero and Rusch, 1994).

Savannas

Although savannas occur pantropically, they are rarely considered when discussing wetlands (Scott and Carbonell, 1986; but see Junk, 1993). Neotropical savannas also are considered rarely in reviews and discussions of global extent of this vegetation formation (e.g. Bourliere and Hadley, 1970; Cole, 1982), and then normally only in the context of South American savannas (Sarmiento, 1984; Junk, 1993). Yet savannas occur widely in Belize, Guatemala, Honduras, and Nicaragua (Lundell, 1937; Beard, 1953; Taylor, 1959; Wright et al., 1959), and sporadically in El Salvador, Costa Rica, and Panamá (Beard, 1953; Lötschert, 1955; Gómez, 1985). Early investigators of these savannas asserted that they formed following anthropogenic activity in the area, such as intentional fires and *milpa* agriculture (Lundell, 1937; Taylor, 1959), but savannas are a "natural" formation occurring under specific climatic and edaphic conditions (Beard, 1953; Sarmiento, 1984; Gómez, 1985). There are no reliable estimates of the regional extent of savannas in Central America (Wright et al. [1959] estimated $\approx$2500 km^2 in Belize), and many of them have been modified for agriculture and livestock production.

Savannas in the Central America should be considered as seasonal wetlands. They occur only in regions with pronounced dry seasons, such as the Atlantic coastal plains in Belize, Honduras, and Nicaragua; the central Petén region of Guatemala; and plains on the Pacific coasts of El Salvador, Costa Rica, and Panamá (Beard, 1953; Lötschert, 1955; Wright et al., 1959; Sarmiento, 1984; Gómez, 1985). Savannas in this region are not confined to low elevations; the Mountain Pine Ridge of Belize consists of pine savanna occurring on poorly drained soils overlying granitic intrusions (Beard, 1953). In general, Central American savannas occur on relatively poor soils overlying impermeable clays that are waterlogged during the rainy season. Standing water may accumulate to depths of 1 m or more (Sarmiento, 1984), but they dry out completely during dry seasons. The majority of Central American savannas are "tall bunch-grass savannas" (*sensu* Beard, 1953), although "short bunch-grass savanna" occurs in Costa Rica (Gómez, 1985), and pine-oak savannas ("orchard savanna", "broken ridge", or "oak and pine ridge" *sensu* Beard, 1953; Wright et al., 1959) occur throughout the region on somewhat better-drained soils.

Grasses in the genera *Andropogon*, *Axonopus*, *Bambusa*, *Leptocoryphium*, *Panicum*, *Paspalum*, and *Trachypogon*, and sedges in the genera *Alvilgaardia*, *Bulbostylis*, *Cyperus*, and *Rhynchospora* dominate the herbaceous vegetation of Central American savannas (Lundell, 1937; Beard, 1953; Taylor, 1959; Wright et al., 1959; Gómez, 1985). The Caribbean pine, *Pinus caribea* (Pinaceae) is the dominant tree in the more wooded savannas. Several species of oaks, primarily *Quercus oleoides* and *Q. hondurensis* (Fagaceae), are sub-dominants. In Belize, the palmetto *Acoelorraphe wrightii* (Arecaceae) is also a common sub-dominant. It is replaced by the palm *Scheelea rostrata* in many open woodlands in Costa Rica. The wooded savannas of Belize's Mountain Pine Ridge exhibit a shrub layer dominated by Melastomataceae.

Temporary and permanent ponds often occur within the savannas (Gómez, 1985). The vegetation of these "aquatic savannas" (*sensu* Gómez, 1985) is generally different from the surrounding grasslands. In Costa Rica, some of the more common species in these ponds are the aquatic fern *Marsilia deflexa* (Marsiliaceae), and the herbs *Alisma plantago-aquatica*, *Echinodorus botanicorum* (Alismataceae), and *Eichhornia costaricana* (Pontederiaceae) (Gómez, 1985). The latter is endemic to Costa Rica's Guanacaste Province (Gómez, 1984).

Bogs

Ombotrophic bogs are known from high altitudes (>1500 m) in the Talamancan Cordillera of Costa Rica (Gómez, 1985). Like their temperate counterparts, the vegetation of these bogs consists primarily of small ericaceous shrubs, ferns, grasses, sedges, and mosses (*Sphagnum*). Gómez (1985) reports the following species as dominants: the ferns *Blechnum buchtieni* and *B. loxense* (Blechnaceae); the grass *Chusquea subtesselata*; *Rapanea ferruginea* (Myrsinaceae); a number of species of *Vaccinium* (Ericaceae); and the bromeliad *Puya dasylirioides*. The lycopsid genus *Isoetes* (Isoetaceae) is abundant in the acidic ponds that occur within these bogs. There have been no detailed systematic or ecological studies of these bogs and their occurrence in other high-altitude regions of Central America is unknown. Lötschert (1955) reported dwarf, wind-blown ericaceous forests above 1700 m a.s.l. in El Salvador. The vegetation of these high-altitude forests, which may be bogs, is composed primarily of *Gaultheria odorata* (Ericaceae). *Lycopodium pithydoides* (Lycopodiaceae), *Blechnum falciforme* and "other sporangiate plants" were reported to grow beneath the *Gaultheria* (Lötschert, 1955).

Wetland soils

Wetland soils, usually considered simply as muds, mucks, or swamp soils, are surprisingly diverse in origin, chemistry, and structure. Quantitative characterization of wetland soils in Central America is just beginning, although there have been historical attempts at other fine-grained classifications. Only Sollins et al. (1994) has applied standard soil taxonomy (USDA Soil Survey Staff, 1975) to wetland soils in Central America, and then only as part of the soil survey at La Selva Biological Station.

Estuarine wetlands

Soils in estuarine and coastal mangrove swamps normally are characterized broadly as Peaty Swamp and Muck Soils (e.g. Golley et al., 1975; Hartshorn et al., 1984). Quantitative characterizations of mangrove soils in Central America are available for Twin Cays, Belize (McKee et al., 1988; McKee, 1993) and Puerto Soley, Costa Rica (11° 36′ N, 85° 40′ W) (Soto and Jiménez, 1982). The mangrove mucks at Twin Cays sampled by McKee et al. (1988) had relatively high pore-water sulfide concentrations (1.6–3.7 mM), pH (6.73), and salinity (40‰), and very low redox potentials (−45 to −204 mV). Soto and Jiménez (1982) illustrated substantial variation in the pH and organic matter content of mucks at Puerto Soley. There, pore-water salinity varied with distance to nearby streams and a canal connected to the sea. Nearest the canal, salinity approximated that of seawater (35‰). The freshwater streams reduced pore-water salinity to as low as 8‰, while in the salt pans in the center of the Puerto Soley swamp, salinity reached 177.4‰. The organic matter content in these mucks ranged from 20.8% in the *Rhizophora mangle* swamp nearest the sea to 2.25–5.4% in the *Avicennia/Conocarpus* stand nearest the canal. The organic matter content of the salt pans was 3.7%.

Meaningful comparisons between these mangrove mucks and those elsewhere in Central America require additional data that are not available. For example, Taylor (1959) described Nicaraguan mangrove mucks simply as "saline soils" with high organic matter content and pore-water salinity slightly higher than seawater.

Riverine and palustrine wetlands

Sollins et al. (1994) identified the soils of the palustrine (forested and non-forested) swamps at La Selva

Biological Station, Costa Rica as Tropaquepts derived from old lava flows ("residual" soils). Three types occur within the Pantano (swamp) consociation: Histic Tropaquepts, where the water table is generally above the soil surface and large amounts of organic matter has accumulated; Typic Tropaquepts, where the water table is lower, normally below the soil surface; and Lithic Tropaquepts, where streams have cut through the valley floor, exposing the underlying bedrock. These swamp Tropaquepts are mottled in color, have a high organic matter content (7–10%), are variably acidic pH (4.2–5.0), and highly reducing and anoxic (gleyed). The Taconazo consociation, which occurs along the margins of the Quebrada El Taconazo at La Selva, is also a Typic Tropaquept (Sollins et al., 1994).

Quantitative comparisons between La Selva swamp and river-margin soils and those of similar wetland soils elsewhere in Central America are impossible, due to the absence of comparable data for any other Central American location (Sollins et al., 1994). However, the La Selva palustrine soils appear qualitatively similar to the Chucum, Caway, and Sibal series described for Belize (Wright et al., 1959; Hartshorn et al., 1984), and the Grumosols, Humic Gleys, and Hydromorphic soils described for Nicaragua (Taylor, 1959). Myers (1990) described the soils of several Costa Rican palm swamps only as permanently flooded alluvial clays low in organic matter (river-fed *Raphia* swamps) or hydromorphic clays derived from deposition during delta formation and coastal regosols (rain-fed *Manicaria* swamp).

Savannas

Soils in Central American savannas are complex and have been characterized differently by various authors. In his classic monograph, Beard (1953) referred to four soil types underlying Belizean savannas that represent four late stages in a developmental series. All four soil types are derived from weathering of alluvial material over limestone bedrock. The Pelly soil, the youngest of the four, consists of a moderately deep sandy loam on top of an impermeable red and white mottled sandy clay. The vegetation associated with this Pelly soil is "broken ridge with cohune" – *Pinus caribea* with cohune palm (*Attalea cohune*). As this soil ages to Roaring Creek soil, the depth of the loam and sand layer decreases, and the mottled sandy clay appears to move up the profile. Cohune palm drops out of the vegetation, and the savanna is characterized by *Pinus caribea* and some oaks. At this point, the impermeable clay layer is sufficiently near the soil surface that most standing water is lost as run-off. The increased run-off removes much of the sandy loam and some clay, leaving behind a sandy layer (as much as 30 cm deep) on top of the clay, and forming Belize soil. The vegetation on Belize soil, which can be observed readily south of Dangriga, Belize, is "oak ridge" (predominantly *Quercus* spp. and *Byrsonima crassifolia* [Malpighiaceae]) or "pine ridge" (predominantly *Pinus caribea*). Finally, the Belize soil is levelled by sheet erosion, run-off is minimal, surface water deposited during the rainy season is lost principally through evaporation, and Baker soil is formed. The vegetation on Baker soil is primarily sedges and grasses, with occasional palmetto and isolated trees such as *Crescentia cujete* (Bignoniaceae) and *Cameraria latifolia* (Apocynaceae).

The soils of the Mountain Pine Ridge are similar to the Belize soil, and occur over granitic intrusions. These soils were studied intensively by Kellman (1979, 1984, 1985a), Kellman and Sanmugadas (1985), and Kellman et al. (1985). Savanna vegetation on the Mountain Pine Ridge is restricted to nutrient-poor, highly weathered, infertile, acidic (pH 4.7–5.0) ultisols of granitic origin. These ultisols have low cation exchange capacity (2–20 meq $\times$ 100 g^{-1}) and low base saturation (2–10%) (Kellman, 1979).

The soils of the poorly drained *aguada* or sinkhole soils of the water-logged savannas of the Central Péten, Guatemala, are "water-logged clays" over limestone (karstic) bedrock (Lundell, 1937). They are strongly acidic on the surface (pH 4.0–5.0), have an increasing proportion of clay with increasing depth, and crack deeply upon drying. Water may remain on the soil surface for up to 9 months of the year, and is lost primarily through evaporation. Nicaraguan savanna soils were described as "Grumosols and Humic Gleys" (Taylor, 1959), and their description was similar to Beard's (1953) Belize soil.

Costa Rican savannas occur on several residual soil types (Gómez, 1985). The soils of the *Trachypogon* savannas (short bunch-grass savanna, *sensu* Beard, 1953) are characterized as immature residual inceptisols. Those of the more wooded savannas are entisols with a shallow clay layer (<1 m below the surface). Finally, soils of the wet savannas are inceptisols and lateritic ultisols, often with a deep organic layer. There have been no comprehensive quantitative analyses of these, or any other Central American savanna soils.

Fauna

Because of the focus on wetland protection as habitat for resident and migrant avifauna (e.g. Scott and Carbonell, 1986; Davidson and Gauthier, 1993), more information is available for bird species diversity than for any other animal group. However, there are representatives from most animal groups that spend all or part of their lives in Central American wetlands. While the geology, hydrology, vegetation, and soil types define the wetland system, animals move among wetlands of different types. Therefore, I review Central American wetland fauna by large-scale taxonomic groupings rather than by wetland system.

Birds

Central American wetlands support a rich resident avifauna, and serve as critical wintering grounds for hundreds of neotropical migrants. A preliminary list of the wetland avifauna of Central America is given in Appendix 1. Records for Belize (Wood et al., 1986), Costa Rica (Stiles and Skutch, 1989), and Panamá (Ridgely and Gwynne, 1989; Lefebvre and Poulin, 1996, 1997) are excellent. Unambiguous data on wetland use by resident and non-resident birds are scant for Nicaragua, Honduras, Guatemala, and El Salvador (Scott and Carbonell, 1986; Ridgely and Gwynne, 1989).

Mammals

The mammal fauna specific to Central American wetlands is documented relatively poorly, although the mammals of the region are well described overall (e.g. Eisenberg, 1989; Emmons, 1990). A list of mammals expected to occur in these wetlands is given in Appendix 2. Many of these species are listed in CITES Appendices as globally threatened or endangered, and recent attention has been focused on the rapid decline of manatee populations in Belize and Costa Rica (Reynolds et al., 1995; Smethurst and Nietschmann, 1999; Morales-Vela et al., 2000).

Reptiles

Coastal wetlands in Central America are famous for their nesting populations of sea turtles. *Chelonia mydas* (green turtle), *Eretmochelys imbricata* (hawksbill), and *Caretta caretta* (loggerhead) nest on Ambergris Cay and the southern cays of Belize (Hartshorn et al., 1984; Perkins and Carr, 1985; Wells, 1988). The three foregoing species, as well as *Dermochelys coriacea* (leatherback) nest at Tortuguero, on the Caribbean coasts of Honduras (Wells, 1988) and Costa Rica (Bjorndal et al., 1985, 1993; Scott and Limerick, 1983; Wells, 1988). Green turtles, hawksbills, and leatherbacks also nest on the Atlantic coasts of Nicaragua and Panamá (Wells, 1988). Olive ridley sea turtles (*Lepidochelys olivacea*) nest on the Pacific beaches (part of Cowardin et al.'s, 1979 marine system of wetlands) of Costa Rica's Santa Rosa National Park, as well as on the Pacific coasts of Honduras, Nicaragua and Panamá (Scott and Limerick, 1983; Scott and Carbonell, 1986; Wells, 1988). Hawksbill, leatherback, and loggerhead turtles also nest on the Pacific coasts of Nicaragua and Panamá, and the green turtle has been reported nesting on the Pacific coast of Nicaragua (Wells, 1988). *Chelonia mydas* has also been observed to nest in brackish lagoons and marshes on the southern Pacific coast of Guatemala (Scott and Carbonell, 1986). A study of the global population structure of *Chelonia mydas* indicated that the Atlantic populations are phylogenetically distinct from Pacific populations, and that within oceans, there are clear geographic population substructures indicating a strong tendency for females to return to their natal beaches to breed (Bowen et al., 1992).

Freshwater turtles in three families occur in Central American wetlands: snapping turtles (Chelydridae); semiaquatic mud turtles (Kinosternidae), and sliders (Emyldidae). Little is known of the distribution of the tropical snapping turtle, *Chelydra serpentina*, although it is listed as occurring in southern rivers and palustrine non-forested wetlands of Belize by Scott and Carbonell (1986) and (without reference to habitat) in Costa Rica (Scott and Limerick, 1983).

The described freshwater turtle fauna of Belize is richer than in any other Central American country, a regional pattern of increasing diversity (south to north) in opposition to that of most other animal and plant taxa of the region. Eight species are listed by Hartshorn et al. (1984): the Central American river turtle *Dermatemys mawei* (Dermatemyidae); *Claudius angustatus*, *Kinosternon acutum*, *K. leucostomum*, *K. scorpioides*, and *Starutypus triporcatus* (Kinosternidae); *Rhinoclemmys areolata* and *Pseudemys scripta* (Emydidae); and *Chelydra serpentina* (Chelydridae). All but the last species are known to occur in Belize's Crooked Tree Wildlife Refuge (Scott and Carbonell, 1986). *Dermatemys mawei* occurs in rivers and lakes throughout the country (Moll, 1986, 1989), and is exploited widely as a food source (Moll, 1986) in spite of its legal protection (Polisar and Horwich, 1994).

The aquatic tropical slider *Chrysemys ornata* occurs throughout Central America, primarily in slow-moving rivers and streams with dense submerged vegetation (Moll and Legler, 1971; Scott and Limerick, 1983; Scott and Carbonell, 1986). Two additional species in this family, *Rhinoclemys funerea* and *R. pulcherrima*, spend at least part of their lives in Costa Rican wetlands. *R. funerea* is found in rivers of the wet Atlantic lowlands of Costa Rica, and *R. pulcherrima* spends the wet season in temporary marshes in the dry lowlands of Guanacaste, Costa Rica. Three species of *Kinosternon* are recorded from Costa Rica: *K. angustipons, K. leucostomum*, and *K. scorpioides* (Scott and Limerick, 1983). Habitat information is available only for *K. leucostomum* (Moll and Legler, 1971; Scott and Limerick, 1983), which frequents swamps, temporary ponds, and slow-moving streams.

The freshwater turtles of the remaining Central American countries are not well known. Scott and Carbonell (1986) record freshwater turtles from Panamá only generically; *Kinsoternon* spp. and *Chrysemys* spp. occur in palustrine and riverine wetlands on both sides of the isthmus.

Two species of crocodile, Morelet's crocodile (*Crocodylus moreleti*) and the American crocodile (*C. acutus*) occur in Central American estuaries and rivers. Morelet's crocodile occurs only in Guatemala and Belize, and the Belizean population is severely threatened (Abercrombie et al., 1980). The American crocodile occurs throughout Central America (Scott and Limerick, 1983; Scott and Carbonell, 1986; Wells, 1988). The caiman, *Caiman crocodilus* (often *C. c. fuscus*) also occurs in wetlands along the Atlantic coast of Central America (Scott and Limerick, 1983; Scott and Carbonell, 1986).

Few snakes occur in Central American wetlands, in contrast to wetlands of both North and South America, which have a significantly higher diversity of snakes (Cadle and Greene, 1984; H.W. Greene, *pers. comm.*, 3/3/2003). In Guatemala and Belize, *Boa constrictor, Drymarchon corais* (indigo snake), *Coniophanes quinquevittatus* (five-striped snake), and *Tretanorhinus nigroluteus* (black water snake) occur in mangrove and freshwater swamps, oxbows, and marshes (Lee, 1996, 2000). *Coniophanes bipunctata* (two-spotted snake) also occurs in freshwater wetlands of these countries, but has not been recorded from mangroves (Lee, 1996). In Costa Rica, the arboreal snakes *Leptodeira* spp. and *Oxybelis* spp. occur in mangroves (Savage, 2002). Frog-eating snakes (*Leptodeira*) forage in freshwater marshes, but breed in the surrounding upland wet forests (Savage, 2002). *Hydromorphus concolor*, a semi-aquatic snake, is found in small streams, while *Tretanorhinus* is more common in or near larger rivers (Savage, 2002).

Amphibians

The amphibian fauna of Central America is very well described (Savage, 1966, 1975, 1982, 2002; Duellman, 1970, 1988, 1990; Scott and Limerick, 1983; Donnelly, 1994; Lee, 1996, 2000). Overall, the neotropics has the greatest species richness of anuran amphibians (frogs and toads) in the world, and at least 325 species occur in Central America (Duellman, 1988). The Central American herpetofauna overall likely evolved in relative isolation (Savage, 1982), and the majority of amphibians found in Central America occur nowhere else in the neotropics. The majority of Central American amphibian taxa rely on wetlands for at least part of their life cycle (Duellman, 1966, 1988; Savage, 1975; Scott and Limerick, 1983; Donnelly, 1994). However, the swamp-inhabiting frogs – those that spend their entire lives in palustrine wetlands – are the least studied of all Central American frog groups (Donnelly, 1994). Accurate inventories of amphibian species diversity are available only for La Selva Biological Station in Costa Rica and Barro Colorado Island in Panamá (Myers and Rand, 1969; Scott et al., 1983; Duellman, 1988; Donnelly, 1994). Given the apparent decline in amphibian populations worldwide (e.g. Wake, 1991), there is a clear need for more information on wetland use by and populations of amphibians in this region.

Fish

Fish occur in every wetland system in Central America. Coral reefs are famous for their spectacular diversity of fish, and attract hundreds of thousands of tourists annually to the region. At least 109 shore-fish families have been recorded from the Caribbean (Montgomery, 1990). Greenfield and Johnson (1981) reviewed the systematics and distribution of blennioid fish associated with coral reefs in Belize and Honduras; Wellington (1974) provided a checklist for many of the fish taxa associated with coral reefs at Cahuita National Park, Costa Rica (9° 40′ N, 82° 45′ W); and the biology of Panamanian coral reef fish was reviewed by Robertson et al. (1990). A comprehensive field guide to coral reef fishes of the Western

Atlantic and Caribbean is available (Humann, 1989). Important commercial species that are associated with the barrier reef in Belize include the Nassau grouper *Epinephelus striatus*, the yellowfin grouper *Mycteroperca interstitialis*, jacks (*Cranax* and *Seriola* spp.), snappers (*Lutjanus* spp.), barracuda (*Sphyraena barracuda*), and bonefish (*Albula vulpes*) (Hartshorn et al., 1984; Wells, 1988).

Despite the acknowledged importance of mangroves worldwide as nursery grounds and refugia from predation for many fish species (e.g. Saenger et al., 1983; Robertson and Duke, 1987), there are surprisingly few data on the fish fauna of mangroves in Central America. Saenger et al. (1983) claimed that 212 species of fish are associated with mangroves in the Western Atlantic. In 15 months of intensive surveying, Phillips (1981) captured 61 fish species representing 27 families in the mangrove embayment at Jiquilisco Bay, El Salvador. This assemblage was dominated by Ariidae, Gerreidae, Sciaenidae, Engraulidae, Clupeidae, and several families of flatfish. Studies in the Gulf of Nicoya, Costa Rica (Ramirez et al., 1990; Rojas et al., 1991) have shown that the ichthyoplankton in this estuary is composed primarily of Engraulidae, Gobiidae, Clupeidae, Sciaenidae, and Haemulidae. The Gulf of Nicoya is economically important as a spawning and nursery area for corvina (*Micropogon altipinnis*) (Araya, 1984). Mangroves are important for Panamanian fisheries (D'Croz and Kwiecinski, 1980), as they host a number of commercially important species, including snappers (*Lutjanus aratus*, *L. argentiventris*), corvina, anchovy (*Cetengraulis mysticetus*), snook (*Centropomus* spp.), *pez congo* (*Galeichthys jordani*), and *mojarra* (*Eucinostomus californiensis*).

The freshwater fish fauna (≈500 species) of Central America is dominated (≈75%) by representatives of three families, the Cyprinodontidae, Poeciliidae, and Cichlidae (Miller, 1966). Cichlids are well represented in Lake Nicaragua (Thorson, 1976a), and at least 70 species of *Cichlasoma* are known to occur in Central America (Miller, 1966; Lowe-McConnell, 1987). Bull sharks (*Carcharhinus leucas*) and sawfish (*Pristis perotteti*) frequently migrate into Lago Nicaragua and the Río San Juan drainage from the Western Atlantic Ocean and Caribbean Sea (Thorson et al., 1966b; Thorson, 1971, 1976b). Overall, good data on distribution and abundance of freshwater fish are available only for La Selva Biological Station, where at least 43 species occur (Bussing, 1994). The most speciose region for fish in Costa Rica is the Río San Juan drainage system, in which 54 species are known to occur (Bussing, 1994).

Invertebrates

Invertebrates generally are neglected in discussions of wetland ecosystems. As noted previously, coral reefs in Belize and Panama attain levels of coral species diversity comparable to the richest sites in the West Indies (Porter, 1972; Cairns, 1982; Muzik, 1982; Humann, 1993), and new species continue to be described (e.g. Knowlton et al., 1992). Diversity of other invertebrates on Central American coral reefs is similarly high (e.g. papers in Rützler and Macintyre, 1982a; see Sterrer, 1986; Humann, 1992, for useful field guides) and new species are continually discovered. Spiny lobster (*Panulirus argus*) and queen conch (*Strombus gigas*), which occur on reef flats throughout the region, are important export species in the Belizean economy (Hartshorn et al., 1984), although their abundance is declining due to over-harvesting (Perkins and Carr, 1985). There is a remarkable 30-year record of polychaete diversity for the Jaltepeque estuary in El Salvador (Lara and Zamora, 1995) that shows significant changes in polychaete species composition related to changes in salinity in the estuary.

Mangroves in Central America host astonishingly speciose marine epibenthic and pelagic invertebrate faunas. At least 200 species of invertebrates, dominated by sponges, ascidians, and bivalves, live epibenthically on submerged mangrove roots in Central America (Rützler, 1969, 1987; Rützler and Feller, 1987; Perry, 1988; Ellison and Farnsworth, 1990, 1992; de Weerdt et al., 1991; Rützler and Smith, 1992; Levings et al., 1994; Farnsworth and Ellison, 1996). The mangrove oyster, *Crassostrea rhizophorae*, is harvested and cultivated throughout the Caribbean (e.g. Hagberg, 1970), and has been investigated for mariculture in Costa Rica (Cabrera et al., 1983; Alfaro et al., 1985; Quesada et al., 1985). Grapsid and sesarmid crab larvae occur commonly in mangrove estuaries (Dittle et al., 1991). Adult crabs are abundant in mangrove swamps and may affect plant community structure in mangal (Smith et al., 1989). Commercially important penaeid shrimp abound in mangrove estuaries throughout Central America, although quantitative data on their abundance and species composition are scarce (D'Croz and Kwiecinski, 1980). Insects are also a conspicuous component of mangrove ecosystems.

There are few complete records of insect species groups associated with Central American mangal (Farnsworth and Ellison, 1991, 1993; Feller, 1995; Feller and Mathis, 1997), although new species are continually described (e.g. Chemsak and Feller, 1988; Mathis, 1989).

Full species inventories of major invertebrate groups associated with freshwater wetlands have yet to be done. The endemic bivalve, *Nephronias tempisquensis* occurs in the Río Tempisque adjacent to the seasonal freshwater lake, Laguna Mata Redonda (10° 19′ N, 85° 25′ W), in Guanacaste Province, Costa Rica (Scott and Carbonell, 1986). Detailed studies on river and stream insect fauna of Central America are rare (e.g. Stout, 1982), although tropical streams generally host more species of aquatic insects than do temperate streams (Stout and Vandermeer, 1975). Janzen and Schoener (1968) noted that riparian forests strips can provide insects with a refuge from the drier, brighter, and hotter surrounding dry deciduous forest.

Table 6. Average net primary productivity (g C m^{-2} yr^{-1}) of coral reefs, seagrass beds, and mangrove forests, and comparisons with some other natural and cultivated ecosystems.

Riverine mangrove swamps	1025–2750
Island mangrove swamps	475
Tropical seagrass beds	520–1971
Coral reefs	2,500
Savannas	900
Tropical rain forests	2200
Temperate salt marshes	1500–3300
Pine plantation (UK)	2190
Rice (world average)	496
Wheat (world average)	343

Data from Lugo and Snedaker (1974), Zieman and Wetzel (1980), and Stiling (1992).

Ecological characteristics: populations, communities, and ecosystems

Marine and estuarine wetlands: coral reefs, seagrass beds, and mangrove swamps

Although ecologists traditionally have studied coral reefs, seagrass beds, and mangrove swamps separately, they are linked in biologically meaningful ways (e.g. United Nations Environment Program, 1985; Twilley et al., 1992). Associated fauna, including commercially important fish, crustacean, and mollusk species move between mangroves, seagrass beds, and coral reefs throughout their life cycles (e.g. D'Croz and Kwiecinski, 1980; McRoy and Helfferich, 1980; Zieman and Wetzel, 1980). As sinks for terrigenous sediments (Twilley et al., 1992), mangroves minimize the amount of sediment transferred to near-shore seagrass beds and coral reefs. Coral reefs, on the other hand, reduce wave energy and help to establish conditions in which mangroves can establish successfully (e.g. Thom, 1982). These three coastal ecosystems are among the most productive on the planet, in terms of average net primary productivity (Table 6), although specific data for primary productivity of Central American coral reefs, seagrass beds, and mangrove swamps are lacking from even the most comprehensive reviews (Birkeland, 1987; Twilley et al., 1992; Twilley, 1995; Lee, 1999; Ellison and Farnsworth, 2001; Kathiresan and Bingham, 2001). However, the existence of standardized research methods (Stoddart and Johannes, 1978; Snedaker and Snedaker, 1984; Phillips and McRoy, 1990) will allow for reliable comparisons among sites when data are collected.

Extensive ecological research has been conducted on the Belizean barrier reef complex, with efforts centered at Carrie Bow Cay (16° 48′ N, 88° 05′ W) in the central barrier reef province. This reef exhibits classic spur-and-groove formations on the inner fore reef, and a shallow back reef with massive coral growth, seagrass beds, extensive coral pavement, well-developed patch reefs and large coral rubble piles resulting from hurricane surges (Rützler and Macintyre, 1982b). The structure and ecological dynamics of invertebrate and fish communities of this reef complex have been the foci of two programs within the National Museum of Natural History (USA) dating back to 1970: the Investigations of Marine Shallow-Water Ecosystems (IMSWE) (1972–1985) and the Caribbean Coral Reef Ecosystem (CCRE) project (1985–2000). This ecosystem was first described comprehensively in the volume edited by Rützler and Macintyre (1982a). It is beyond the scope of this review to summarize the more than 600 papers published to date by IMSWE and CCRE investigators, and interested readers are referred to the annual project summaries edited by K. Rützler and published by the US National Museum of Natural History (e.g. Rützler, 1999).

A similar history of research into coral reef ecology exists for some of the Panamanian reefs (e.g. Cubit et al., 1988). This proved to be particularly

Table 7. Stand characteristics (for trees >10 cm dbh) of some Central American mangrove forests.

Location	Rainfall (mm yr $^{-1}$)	# of species	Canopy ht (m)	Basal area (m^2 ha $^{-1}$)	Trees (ha $^{-1}$)
Nicaragua					
Isla del Venado	–	4	25	14.88	440
Costa Rica[1]					
Santa Rosa	1800	2	10	22.2	800
Moin	3336	4	16.0	96.4	1180
Boca Barranca	2150	3	9.5	31.8	660
Tivives	1800	1–2	20–25	9.03–41.0	480–769
Puerto Soley	1978	3	17.3	19.7	1701
Tamarindo	2031	5	18.0	37.5	918
Pochote	3029	6	20.0	21.0	1220
Jicaral	1654	5	9.6	7.0	1773
Puntarenas	1501	5	10.0	20.0	2370
Quepos	3827	5	24.0	29.0	1850
Sierpe	3676	5	25.4	27.0	1600
Panamá					
Darien	–	1	24–41	13.6–25.1	313–410

[1] Stand density for Costa Rican sites other than Santa Rosa, Moin, and Boca Barranca is for all trees >2 cm dbh.

valuable for assessing the impact of the 1986 oil spill into Bahía Las Minas (Keller and Jackson, 1991). Detailed analysis of the effects on coral reef structure of the die-off of the herbivorous sea urchin *Diadema antillarum* (Lessios, 1988) indicated that this species was not a keystone predator in western Caribbean reefs (Jackson and Kaufmann, 1987). Coral reefs have also provided important insights into the evolution of plant chemical defenses against herbivores (reviewed in Hay, 1984, 1991; Hay et al., 1987). Research on ecology and behavior of reef invertebrates in Panamá have revealed that taxa previously considered to be a single species are in fact species swarms (e.g. Knowlton et al., 1992; Knowlton and Jackson, 1994), although this does not appear to be true for fish species (Sale, 1994). Annual reports of the Smithsonian Tropical Research Institute, Balboa, Panamá should be consulted for up-to-date summaries of ecological research in the Panamanian reefs.

Seagrass beds associated with these coral reefs have received surprisingly little attention in Central America, and Phillips and Meñez (1988) identified this region as a key area in need of basic research. Seagrass beds are highly productive, detritus-based ecosystems (Table 6), and are important habitats for over 100 species of fish (Weinstein and Heck, 1979). The plants themselves are significant food sources for sea urchins (e.g. *Strongylocentrotus purpuratus*, *Diadema antillarum*, *Lytechinus variegatus*, *Tripneustes ventricosus*), fish, green turtles, and manatees (Mortimer, 1981; Tribble, 1981; Thayer et al., 1984), although data from Central American sites are scarce in recent reviews (McRoy and Helfferich, 1980; Zieman and Wetzel, 1980; Thayer et al., 1984). The fish fauna of Panamanian seagrass beds is much richer than those further north in the Gulf of Mexico (Weinstein and Heck, 1979), but latitudinal studies comparing other seagrass fauna similarly have included few Central American sites (Zieman and Wetzel, 1980; Virnstein et al., 1984).

There have been hundreds of ecological studies of Central America mangal. The majority of these have been descriptive, with emphasis on floristics, stand structure, and primary productivity (see Lugo and Snedaker, 1974; Golley et al., 1974; Cintron et al., 1985; Jiménez, 1990, 1992; Cintron-Molero and Schaeffer-Novelli, 1992 for recent reviews). Floristic diversity and stand structural properties of Central American mangrove forests, in terms of true mangrove taxa (*sensu* Tomlinson, 1986) and mangrove associates (Tables 4 and 7), increase from north to south, as seasonal and annual rainfall increases (Pool et al., 1977; Lugo, 1986; Jiménez, 1992). Fauna associated with mangroves – insects and marine epibionts – significantly affect mangrove primary productivity in Belize (Ellison and Farnsworth, 1990, 1992; Farnsworth and Ellison, 1991, 1993; Ellison et al., 1996) and Costa Rica (Perry, 1988).

One of the most conspicuous patterns of vegetation patterns in mangrove forests is the characteristic zonation of species across tidal and/or salinity gradients (e.g. Snedaker, 1982; Ellison and Farnsworth,

Table 8. Number of tropical storms and hurricanes crossing the seven Central American countries between 1871 and 2001.

Country	Tropical storms	Hurricanes
Belize	22	20
Guatemala	9	2
El Salvador	0	1
Honduras	18	10
Nicaragua	11	12
Costa Rica	1	0
Panamá	0	1

Data from Neumann et al. (1992; with 1993 addendum), and NOAA (2002).

1993, 2001). Edaphic factors have been invoked as causal mechanisms determining species zonation patterns in Central American mangal, but the mangroves themselves may alter the edaphic properties of the swamp (McKee et al., 1988; McKee, 1993). Within zones, individual species of mangroves often exhibit gradients in tree size. This variability is related to exposure (Lugo and Snedaker, 1974), hydrology and exposure (Twilley, 1995), and complex gradients in nutrient availability and limitation (Feller, 1995; Feller et al., 2003). Additional mechanisms contributing to species zonation in mangal include tidal sorting of the differently-sized mangrove seedlings (Rabinowitz, 1978a, b, c; Jiménez and Sauter, 1991) and selective predation of seedlings by herbivorous grapsid crabs (Smith et al., 1989). Although studies of community ecology of tropical forests in general have been influenced profoundly by conceptual frameworks based on disturbance, or "gap-dynamics" (Connell, 1978; Denslow, 1987), the role of disturbance in structuring mangrove forests has been ignored until recently (Roth, 1992; Ellison and Farnsworth, 1993; Smith et al., 1994). Tropical cyclonic storms are the primary large-scale natural disturbance agent affecting mangal (Jiménez et al., 1985; Roth, 1992; Smith et al., 1994) and other coastal wetlands in the region, but they rarely cross the coast of Central America south of Honduras (Neumann et al., 1992; Table 8). The importance of small-scale natural disturbance, such as lightning strikes and treefalls (Smith et al., 1994) has been considered only in Belize (Ellison and Farnsworth, 1993; Feller and McKee, 1999) and Panamá (W.P. Sousa, *unpubl. data*). There, small gaps release suppressed understory seedlings, but do not increase species diversity (A.M. Ellison, *pers. observ.*).

Investigations into the population biology and life-history of mangrove plant species in Central America are surprisingly rare (Collins et al., 1977; Jiménez and Soto, 1985; Jiménez, 1988; Duke and Pinzón, 1992; Roth, 1992; Ellison and Farnsworth, 1993), and the data are insufficient to allow for cross-site comparisons or ecological generalizations. Population dynamics of associated marine invertebrates have been documented by numerous investigators in Belize associated with the National Museum of Natural History's (USA) Smithsonian Western Atlantic Mangrove Project (SWAMP; 1980–1995) and CCRE. These studies recently were reviewed (Rützler, 1999).

Riverine wetlands

Ecology of rivers and streams

Ecological studies of rivers and streams are rare in Central America. The notable exceptions are the rivers and streams flowing through La Selva Biological Station in Costa Rica (e.g. Stout, 1981, 1982; Pringle and Triska, 1991; see Sanford et al., 1994 for a review). Near their sources, the streams at La Selva are narrow, rocky-bottomed, and acidic. Downstream, they are broader, siltier, and more pH neutral. The stream waters are relatively rich in phosphorus, nitrate and ammonium, and these nutrients are not generally limiting to growth of algae (Pringle and Triska, 1991; Sanford et al., 1994). Where streams flow through swamp forests, they receive additional inputs of both P and NO_3 from the saturated soils. The levels of total phosphorous (232 ppb) and nitrate (98 ppb) of surface waters in these swamp forests are among the highest measured at La Selva. The algal communities in these streams are very diverse ($\approx$70 species), and a few angiosperms grow on emergent rocks (*Dicranopygium* spp. [Cyclanthaceae] and *Cuphea* spp. [Lythraceae]) (Sanford et al., 1994).

In contrast to the detailed work on the La Selva plant communities (Hartshorn and Hammel, 1994 and references therein), the animal communities of La Selva streams have received scant attention. Stout's papers on Naucoridae (Hemiptera) illustrated the importance of seasonal changes in water level and attendant changes in stream flow and water chemistry on the distribution and abundance of *Limnocoris insularis* and *Cryphocricos latus*. Comparisons of aquatic insect species richness in streams at four Costa Rican sites, with similar samples from temperate North America and Colombia, indicate that species richness of tropical streams is significantly higher than in temperate streams (Stout and

Vandermeer, 1975). Trophic diversity and community structure of La Selva fish communities are broadly concordant with other tropical streams of similar physiognomy. Fish in Costa Rican streams include herbivores, insectivores, piscivores, and omnivores, and food specialists (Bussing, 1994). An example of the last category is the machaca, *Brycon guatemalensis* (Characidae), which is an important consumer of figs (*Ficus glabrata*) and aids in dispersal and germinability of fig seeds. Unfortunately, the most recent global review of the ecology of freshwater fish communities (Lowe-McConnell, 1987) included no comparable information from any other location within Central America, and again, cross-site comparisons and regional generalizations on trophic and community structuring of regional fish assemblages are not yet possible.

Riparian gallery forests

Ecological studies in Central American gallery forests have focused on the riparian forest fragments within the pine savannas of Belize's Mountain Pine Ridge (Meave et al., 1991; Kellman et al., 1994; Meave and Kellmanm, 1994). Forest stands in these fragments are short in stature (20 m) compared with lowland tropical wet forests. Total stem density (plants $\geq$0.5 m tall) averages $\approx$11,000 ha^{-1}, while tree density ($\geq$10 cm dbh) averages 766 ha^{-1} and stand basal area (trees $\geq$10 cm dbh) averages 21.9 m^2 ha^{-1} (Meave and Kellman, 1994). Species richness is high (292 species $\geq$0.5 m tall), comparable to continuous rain forests elsewhere in Central America. The predominant species generally are not restricted to riparian forests, although they are uncommon in the surrounding savanna (Meave and Kellman, 1994). The relatively high species richness in these forests is not well correlated with edaphic factors. Rather, it appears to result from a combination of changes in atmospheric variables (mean and variance in temperature, humidity, and light availability) associated with forest-savanna edges, and disturbances caused by floods, landslides, and fire (Kellman et al., 1994). Meave et al. (1991) and Meave and Kellman (1994) have suggested that riparian forest fragments could have been refugia for tropical wet forest floras during Pleistocene aridity. This hypothesis is supported with comparative data from Belizean gallery forests and similar forests in the Venezuelan savannas (Kellman et al., 1994), and palynological evidence from Guatemalan lakes (Leyden, 1984). Janzen and Schoener (1968) and Janzen (1976) noted that evergreen riparian forest strips are cooler and moister than adjacent (<100 m) areas in the dry deciduous forests of Guanacaste Province, Costa Rica. These riparian forest strips have unique trees (for the area), and also provide refugia for insects intolerant of conditions in the nearby dry forests (Janzen and Schoener, 1968). Even in the absence of additional comparative studies in other neotropical sites (e.g. Honduras and Nicaragua), Meave and Kellman's Pleistocene refugium hypothesis appears broadly applicable throughout Central America, and could be used to identify unique relictual sites appropriate for conservation.

Lacustrine wetlands

The Lago de Izabal ecosystem and surrounding catchment basin (6860 km^2) is a prime example of a Central American lacustrine system. Its ecosystem dynamics were studied intensively by Brinson (1976, Brinson and Nordlie, 1975). This moderate-sized (717 km^2) shallow lake ($\leq$16 m deep near the center) lies on the Atlantic coastal plain of Guatemala, and most of its volume is actually below sea level. The lake drains to the northeast into the Gulf of Honduras via the Río Dulce (Brinson, 1976). Two large rivers, the Río Polochic and the Río Cahabón drain into the lake from the surrounding highlands (Brinson, 1976). The lake is temperature-stratified at $\approx$12 m depth during the wet season, but otherwise is isothermal (25.5–30.4°C). Annual gross primary productivity of Lago de Izabal during 1972, measured as oxygen production by phytoplankton, was estimated at 1400 g O_2 m^{-2} (Brinson and Nordlie, 1975).

Phytoplanktonic assemblages in Lago de Izabal are dominated by diatoms, cyanobacteria (especially *Lyngbya* sp.), and green algae (especially *Staurastrum* spp.), and copepods predominate in the zooplankton. Brinson and Nordlie (1975) reported two annual peaks in plankton abundance: during the dry season in March, and another increase in July–September, following the onset of the rainy season. Marked monthly, seasonal, and annual variability in species composition and abundance were observed between 1969 and 1972.

Lago de Izabal is connected directly to the Caribbean Sea via the Río Dulce. As such, brackish and marine species have been observed occasionally in the lake itself. Thorson et al. (1966b) reported bull sharks (*Carcharhinus leucas*) and sawfish (*Pristis* spp.) in the lake, and marine catfish occur as well (Brinson and Nordlie, 1975). Miller (1966) in summarizing the fish fauna of Central America, reported that species richness of primary and secondary fresh-water species north of Costa Rica was poor compared with southern Central America and South America, but there have been no recent comprehensive studies of fish populations or communities in Lago de Izabal.

In contrast, the limnology and ichthyology of Lago Nicaragua and Lago Managua in Nicaragua have been extensively studied; a summary of basic information is given in Thorson (1976a). Like Lago de Izabal in Guatemala, Lago Nicaragua drains into the Caribbean (via the Río San Juan, which forms the border between Nicaragua and Costa Rica). With an estimated surface area of 7500 km^2 and a drainage basin of $\approx$40,000 km^2, Lago Nicaragua is the largest lake occurring between Lake Titicaca in Bolivia–Perú and the Great Lakes of North America (Incer, 1976; Cole, 1976). It is relatively shallow (maximum depth = 43 m; mean depth = 12 m), and has a shoreline of $\approx$400 km, much of which is surrounded by wetlands of international conservation importance (Davidson and Gauthier, 1993). The smaller Lago Managua (area = 1050 km^2; maximum depth = 28 m; mean depth = 9 m; shoreline = 200 km) drains into Lago Nicaragua via the Río Tipitapa, a slow-moving swamp of the water hyacinth *Eichhornia azurea* (Incer, 1976). Neither lake is known to be thermally stratified, and water temperatures vary only between 24 and 28°C (Cole, 1976). The planktonic communities of the two Nicaraguan lakes were also summarized by Cole (1976). This report is not very helpful, however, because many phytoplankton taxa lack accepted binomials and there was dispute on the degree of endemism of the zooplankton (Herbst, 1960; Cole, 1976).

The remaining large lake in Central America is Gatún Lake, a consequence of the Panamá Canal. It was formed in the early part of this century by the damming of the Chagres River (Weers and Zaret, 1975). Gatún Lake (423 km^2) is shallow (maximum depth = 30 m), moderately oligotrophic, and unstratified. The phytoplankton includes at least 150 species of diatoms, cyanobacteria, dinoflagellates, and green algae. Common grazing zooplankton include the cladoceran *Ceriodaphnia cornuta* and the calanoid copepod *Ciaptomus gatunensis*, which rarely occur at densities greater than 10 L^{-1} (Weers and Zaret, 1975). Extensive use of herbicides to control floating aquatic weeds (*Eichhornia*, *Pistia*, and *Hydrilla*) that may be hazardous to shipping traffic through the canal, and the introduction of sport fish (Scott and Carbonell, 1986) may have altered the trophic and ecosystem dynamics of Gatún Lake, but there are no published studies in this area. The forests fringing the lake, and the seasonal forest on Barro Colorado Island in the center of the lake have been studied in great detail by researchers working under the auspices of the Smithsonian Tropical Research Institute. An introduction to this body of work can be found in Leigh et al. (1982).

Palustrine forested wetlands

Palm swamps

Palm swamps have been studied most intensively in Costa Rica (Holdridge et al., 1971; Myers, 1984, 1990). These species-poor forests (e.g. the *Raphia* swamp at Tortuguero in Table 9) exhibit increased species richness with improving drainage. Average stand height (palms only) is $\approx$14 m, although hardwood trees in some of these swamps average 22–24 m in height. Palm stand basal area ranges from 22–39 m^2 ha^{-1} (*Raphia* swamps) to 94 m^2 ha^{-1} (*Manicaria* swamp). Myers (1984) estimated the standing above-ground biomass of a riverine *Raphia* swamp in Costa Rica to be 4428 g m^{-2}, and annual above-ground production to be 1126 g C m^{-2} yr^{-1}, or about half that of a broad-leaved tropical wet forest (Table 6).

Early investigators (Anderson and Mori, 1967) considered palm swamps to be an early successional community in areas of temporarily low drainage, and suggested that they would be replaced by hardwood stands as the palms aged, increased in height, and allowed more light to reach the forest floor. However, Myers' (1990) analysis showed that the structure of Costa Rican palm swamps was controlled by hydroperiod, and whether the swamps were rain-fed or river-fed. The *Raphia* swamps that he studied were topographically isolated, and were not successional. Comparative studies of palm swamps are needed to resolve the issue of whether these palm swamps are successional or steady-state. Comparable research in mangrove swamps along these lines has demonstrated that these coastal wetland ecosystems, once thought to be "pioneer" formations, are in fact relatively steady state, "climax" communities (Lugo, 1980; Urquhart, 1999).

Other forested wetlands

There are few data on ecological characteristics of other forested wetlands in Central America, despite

Table 9. Comparative stand characteristics of four Costa Rican freshwater forested wetlands.

	BA	D	F	IV
Mora forest, Osa Peninsula[1]				
Mora oleifera	95	70	48	71
Amphitecna latifolia	1	15	19	12
Avicennia germinans	2	4	10	5
Tabebuia rosea	1	4	10	5
Luehea seemannii	0.2	2	5	2
Prioria forest, Río Colorado[2]				
Prioria copaifera	95	80	50	75
Stemmadenia donnell-smithii	1	13	29	14
Pithecellobium latifolium	3	3	11	6
Grias fendleri	0.1	2	7	3
Ixora finlaysoniana	0.1	1	4	2
Raphia forest, Tortuguero[3]				
Raphia taedigera	98	84	65	82
Pentaclethra macroloba	1	4	9	5
Grias fendleri	0.3	4	9	4
Crudia acuminata	0.1	3	7	3
Prioria copaifera	0.1	1	4	2
Virgin swamp forest, La Selva[4]				
Pentaclethra macroloba	29.2	17.3	9.05	18.51
Carapa guianensis	19.4	8.8	5.82	11.33
Pterocarpus officinalis	15.5	3.4	3.88	8.01
Astrocarym alatum	1.25	8.6	6.25	5.38
Iriartia gigantea	1.33	4.9	4.96	3.75

Data given are relative basal area (BA), relative density (D), relative frequency (F), and relative importance values (IV) of the five most common species in each wetland. Data from Hartshorn (1983, 1988) and Lieberman et al. (1985a, b).

[1] Stand area = 0.2 ha; total basal area (trees ≥10 cm dbh) = 7.0 m^2; stand height = 26 m.

[2] Stand area = 0.3 ha; total basal area (trees ≥10 cm dbh) = 16.5 m^2; stand height = 47 m.

[3] Stand area = 0.3 ha; total basal area (all stems) = 103.2 m^2; stand height = 15.3 m.

[4] Stand area = 2.0 ha; total basal area (all stems) = 67.91 m^2.

their economic value. Hartshorn (1983, 1988) compiled comparative stand structure data for these low-diversity forests in Costa Rica (Table 9), but there are no data on annual productivity in these same stands. As is the case for palm swamps, hydroperiod and degree of soil waterlogging are correlated with species composition and complexity of broad-leaved forested wetlands in Central America (Holdridge and Budowski, 1956), but the cause-and-effect hypothesis deriving from this correlation has never been tested explicitly.

Lieberman et al. (1985a, b) studied stand turnover rates in a 2 ha plot of swamp forest at La Selva Biological Station. Between 1969 and 1982, 0.69% of the trees died, and basal area was reduced by 8.31% (trees ≥10 cm dbh). They estimated a stand half-life of 34 years for this swamp forest, making it one of the most dynamic "primary" forests studied anywhere in the tropics (Lieberman et al., 1985a).

Non-forested palustrine wetlands

Marshes

Despite their importance to resident and migratory waterfowl (Scott and Carbonell, 1986; Dugan, 1993; Botero and Rusch, 1994), herbaceous marshes have received relatively little ecological attention. One exception is the small (≈6000 ha) swamp within Costa Rica's Palo Verde wildlife refuge (also known as the Refugio Rafael Lucas Rodriguez Caballero), site of one of the field stations of the Organization for Tropical Studies (Hartshorn, 1983; Scott and Carbonell, 1986). The Palo Verde marsh is a seasonal flooded wetland within the floodplain of the Río Tempisque. This marsh normally floods in September–October, and moist areas may remain through March (Hartshorn, 1983). The Palo Verde marshes and nearby riverine mangrove forest are important breeding, feeding, and wintering grounds for migrant and resident waterfowl, including egrets, ibis, anhingas, Jabiru storks, and blue-winged teal (Slud, 1980; Scott and Carbonell, 1986; Botero and Rusch, 1994). Palo Verde in its entirety is considered as tropical dry forest, and is surrounded by large cattle ranches. Cattle are common grazers within the marsh, and Hartshorn (1983) quoted F.G. Stiles as hypothesizing that the cattle maintain areas of open water within the marsh. Removal of cattle from the Palo Verde marsh following its designation in 1979 as a wildlife refuge led to a dramatic decrease in open water and floating aquatic vegetation as *Typha dominguensis* increased in coverage from <5% to >95% of the marsh area (McCoy and Rodríguez, 1994). This change in vegetation was accompanied by a precipitous decline in resident and migratory waterfowl (McCoy and Rodríguez, 1994). Mechanical removal and crushing of *Typha* led to an initial recovery of open water in the marsh area, but it was subsequently colonized by dense stands of the grass *Paspalidium* spp., which may similarly reduce use of the marsh by birds (McCoy and Rodríguez, 1994). The return of intensive cattle grazing (10–15 cows ha^{-1}) to the marsh in the early 1990s has maintained extensive areas of open water and the recovery of the bird populations (McCoy and Rodríguez, 1994).

Savannas
Ecological research on Central American savannas has focused on the commercially important pine savannas of Belize (Kellman, 1979, 1984, 1985a, b; Kellman and Miyanishi, 1982; Kellman and Sanmugadas, 1985; Kellman et al., 1985). As previously mentioned, savannas are thought to form in response to either specific climatic, edaphic, or incendiary conditions (Beard, 1953; Sarmiento, 1984). This single-factor explanation was questioned by Kellman (1984) who argued that synergistic responses of vegetation to soil nutrients and fire regimes determine vegetation structure in the savannas of Belize's Mountain Pine Ridge. The soils of these savannas are relatively infertile, but decaying plant material can act to increase soil nutrient availability in small patches (Kellman, 1979), creating hot-spots of woody plant diversity and seed germination of several species, including mahogany *Swietenia macrophylla* (Meliaceae) (Kellman and Miyanishi, 1982; Kellman, 1985b). Many of the woody species in these nutrient-rich patches are less fire-prone than pines and grasses (Kellman, 1984). Fire, which has an average recurrence interval of 18 years in the Belizean pine savannas, is suppressed as part of the management policies for Caribbean pine. This fire suppression increases recruitment of *Pinus caribea*, which further enhances the nutrient retention characteristics of the soils. Fire suppression and soil nutrient enrichment function in positive feedback loops altering the vegetation structure of the savanna. Kellman (1984) suggested that in "normal" savannas where fire is not suppressed, woody plants would be less common, and fire frequency would be maintained by the somewhat more flammable grasses and sedges. In this latter situation, fire occurrence and soil infertility interact in negative feedbacks, maintaining grassland savannas with only occasional woody plants. Comparable data for other Central American savannas are unavailable. Edaphic conditions are similar in Honduran savannas (Kellman et al., 1982), and it would be fruitful to examine Kellman's nutrient-fire hypothesis there.

Wetland use and environmental impacts

Until recently, there has been little planned management or conservation of wetlands in any of the Central American countries (CCAD, 2002). Population and development pressures in Central America until recently have had more serious impacts on local forests than on wetlands. However, erosion associated with deforestation, fertilizer and pesticide run-off, cutting of mangroves for fuel wood, clearing of mangroves for shrimp ponds and salinas, and overexploitation of the regions fisheries are contributing to rapid and accelerating destruction of the region's wetlands. Development pressures and wetland degradation are most severe along the drier and more populous Pacific coast of Central America (Davidson and Gauthier, 1993). Several prominent examples are given below.

Coral reefs, seagrass beds, and mangrove swamps
Coral reefs in the region have a long history of human use and abuse. The Maya used the coral cays within the lagoon of the Belizean barrier reef for fishing stations, trading posts, ceremonial centers, and burial sites between 300 BC and 1500 AD (Perkins and Carr, 1985). More recently, the reef has provided fish, conch, shrimp, and lobster for local consumption and, increasingly, the export market (Hartshorn et al., 1984). These fisheries are being rapidly depleted, and it is now rare to find conch or lobster at depths shallower than 15 m. Confirmed instances of toxic ciguateric dinoflagellates were reported for the first time in Belizean waters in 1994 (M. Faust, *pers. commun.*, March 1994), which may reflect increasing nutrient loading of the waters around the barrier reef complex. The increase in eco-tourism focused on the reef complex at Ambergris Cay in northern Belize is resulting in rapid degradation of that section of the reef. Sea turtles throughout the Caribbean have been exploited for centuries, and there is increasing evidence that their populations are declining precipitously due to overfishing and egg collection for market (Cornelius et al., 1991; Lagueux, 1991; Bjorndal et al., 1993). Neotropical migrant birds appear to be becoming increasingly dependent on mangrove forests (Lefebvre and Poulin, 1996; Warkentin and Hernández, 1996; Frederick et al., 1997), possibly because of degredation of upland habitats.

Mangroves are important economically in Central America as nursery grounds for commercial fisheries (D'Croz and Kwiecinski, 1980; Phillips, 1981) and for a growing industry in cultivation of edible oysters (Alfaro et al., 1985; Quesada et al., 1985). Mangroves are also used extensively for polewood, firewood, charcoal production, and tannins (Table 10). In a careful economic analysis, Windevoxhel (1992) illustrated that mangroves are being overharvested

Table 10. Common uses of mangroves in Central America.

Use	Amount ($\times$yr $^{-1}$)
Honduras	
Firewood	80,000–120,000 m^3
Bark (tannins)	1260 tonnes
Clearing (shrimp and salt production)	28,000*
Nicaragua	
Firewood	4645 trees (<8 cm dbh)
Polewood	840 trees (8–12 cm dbh)
Wood	106 kg
Large timber	1514 trees (>12 cm dbh)
Fish catch	1361 kg
Conch catch	4332 individuals
Oysters	6818 kg
Costa Rica	
Charcoal	1300 m^3
Bark (tannins)	1840 – 4490 kg ha $^{-1}$
Panamá	
Charcoal	7448 m^3
Polewood	16,125 m^3
Bark (tannins)	437 tonnes

*Total area cleared 1983–1993.
Data from Alfaro et al. (1985), Jiménez (1992), Windevoxhel (1992), and Davidson and Gauthier (1993).

for charcoal, polewood, and timber production in mangroves from Estero Real to Isla Juan Venado on the northern Pacific coast of Nicaragua.

Oil, chemical, and heavy metal pollution has damaged mangrove swamps and coral reefs on the Atlantic coasts of Costa Rica and Panamá (Jackson et al., 1989; Guzmán and Jiménez, 1992). This contamination originates in sewage discharges, overuse and misuse of agricultural chemicals and fertilizers, topsoil erosion, and oil spills from refineries and tankers. In a particularly well-studied case, 8×10^6 L of crude oil spilled from a ruptured storage tank onto the reef complex near the Smithsonian Institution's Galeta marine laboratory (9° 24′ N, 79° 52′ W), oiling fringing reefs, sand beaches, seagrasses, and mangrove forests (Jackson et al., 1989). The ecological environmental consequences of this spill has been the focus of many studies (e.g. Jackson et al., 1989; Garrity and Levings, 1990; Guzmán et al., 1991; Burns et al., 1993, 1994; Burns and Yelle-Simmons, 1994; Garrity et al., 1994; Levings et al., 1994); the overall environmental impact in the Bahía Las Minas region is summarized by Keller and Jackson (1991). Among other effects, persistent oiling of mangrove sediments leads to increased mutation rates and decreased survivorship of *Rhizophora* seedlings (Duke and Pinzón M., 1992; Klekowski et al., 1994a, b).

Lacustrine wetlands

The large lakes in Central America, Lago de Izabal, Lago Managua, and Lago Nicaragua are all severely eutrophied by agricultural run-off from the surrounding watersheds, although quantitative data are lacking on the severity of pesticide pollution and nutrient input. Lago Atitlán in southwestern Guatemala is a major tourist destination with familiar attendant environmental problems, including increased erosion and siltation following deforestation, increased nutrient loading in the lake resulting from domestic sewage. The lake was renowned for the endemic flightless grebe *Podilymbus gigas*. As of 1984, no more than 45 individuals of *P. gigas* were reported at the lake (Scott and Carbonell, 1986). No *P. gigas* individuals were found in resurvey of the population in 1986–1987; the grebe population at Lago Atitlán was composed exclusively of the pied-billed grebe *P. podiceps* (Hunter, 1988). Thus, it appears that *P. gigas* is now extinct, having been replaced by *P. podiceps* through hybridization or competitive exclusion (Hunter, 1988), and having been preyed upon by bass. Nonetheless, a small section of Lago Atitlán's vanishing reed beds have been declared a protected reserve by DIGEBOS (Guatemala's Dirección General de Bosques y Vida Silvestre, or Forest and Wildlife Directorate) (Davidson and Gauthier, 1993).

Lago de Yojoa in northwest Honduras is a small (90 km^2) lake with commercially important (locally) but poorly documented fish communities. The bass *Micropterus salmoides* was introduced into the lake to support sport as well as commercial fishing (Scott and Carbonell, 1986; Davidson and Gauthier, 1993). The consequences to this lacustrine ecosystem following from the introduction of this species, along with increased pressure from recreational resort development are unknown, and there are no pre-introduction baseline data from which comparative analyses could be drawn.

Palustrine wetlands

Like coastal wetlands, inland freshwater wetlands have been used by Central American peoples for agriculture, hunting grounds, and timber for millennia (Bloom et al., 1983; Alcala-Herrera et al., 1994). However, increasing population and development now severely threatens palustrine wetlands throughout the isthmus.

The freshwater marshes and estuaries in Central America provide critical habitat and/or refugia for many endangered species, including the jaguar (*Panthera onca*), manatee (*Trichechus manatus*) and the American Crocodile (*Crocodylus acuta*). There continues to be legal and illegal export and trade in animals and skins of these species. In 1997 alone, for example, Panamá exported 75,000 crocodile skins (WRI, 2002). In the same year, Nicaragua exported 8000 parrots (WRI, 2002). Only El Salvador failed to meet CITES reporting requirements for these species more than 70% of the time (WRI, 2002). Belize, on the other hand, has prohibited trades in hides since the early 1980s. Despite early hopes that crocodile populations would recover (Abercrombie et al., 1980; Hartshorn et al., 1984), they continue to be threatened by opportunistic hunting, drowning in fishing nets, and coastal development (principally for tourism) in critical nesting habitats (Platt and Thorbjarnarson, 2000b). In contrast, populations of Morelet's crocodile (*Crocodylus moreletii*) appear to be stable in Belize (Platt and Thorbjarnarson, 2000a). Although they are protected throughout their range, manatee populations continue to decline precipitously throughout the region (Reynolds et al., 1995; Smethurst and Nietschmann, 1999; Morales Vela et al., 2000) due to continuous hunting and poaching, toxic run-off from banana plantations and cattle ranches, and increases in boat traffic attendant with eco-tourism.

Marshes also are key feeding grounds for many Nearctic migrant birds. Notable among these are the Palo Verde wildlife refuge in Costa Rica, and the Bay of Panamá. The latter supports literally millions of shorebirds during the winter, including half the world's population of western sandpipers (*Calidris mauri*) (Scott and Carbonell, 1986; Davidson and Gauthier, 1993). Many Central American marshes likely have high levels of agrochemicals; indeed, the capacity of the freshwater wetlands on the shores of Lago de Nicaragua to absorb and retain river-laden sediments and agrochemicals from Costa Rica has been identified as a "specific value and function" of this wetland complex (Davidson and Gauthier, 1993). Many other marshes in Central America have been drained and impounded for agriculture and cattle ranching, although without reliable data on the areal extent of these wetlands, it is difficult to assess the consequences of this conversion for species diversity.

Swamp forests have been logged extensively throughout the region. Their low species diversity makes them easy to manage, but also easy to over-exploit. *Carapa guianensis*, a common inhabitant of Central American swamp forests is a valuable timber tree (McHargue and Hartshorn, 1983), and logwood, *Haematoxylum campechianum*, was the *raison d'être* of the British colonization of Belize in the 18th century (Bolland, 1988). The latter species was all but extirpated from Belize by the middle of the 20th century, and as mentioned earlier, extensive stands (the last in Central America) are found only in Belize's Crooked Tree Wildlife Refuge. About 100 km^2 of cativo, *Prioria copaifera*, remain in the Canglon Forest Reserve near the Golfo de San Miguel, Panamá (Davidson and Gauthier, 1993). Elsewhere in Panamá, it has been cut for plywood (Mayo Meléndez, 1965). Orey or sajal, (*Campnosperma panamensis*) still occurs fairly widely in Panamá, and is also valued for its use in plywood. Estimated reserves are $\approx$600 km^2, but are not protected (Davidson and Gauthier, 1993).

High levels of deforestation in Costa Rican swamp forests have sparked concern about loss of genetic diversity among populations of the dominant trees (Hall et al., 1994a, b). *Pentaclethra macroloba* exhibits low within-population genetic variability (heterozygosity) and high between-population differentiation (Hall et al., 1994a). On the other hand, *Carapa guianensis* exhibited higher heterozygosity within populations and lower between-population differentiation (Hall et al., 1994b). These results, along with observations on the mating systems of the two species, suggest that *Pentaclethra* is much more susceptible to loss of genetic diversity through forest fragmentation than is *Carapa*, and that consequently *Carapa* is a better candidate for careful sustainable management (Hall et al., 1994a, b). Similar studies in cativo and orey swamps should be prerequisite to developing sustainable forestry management plans.

Wetland conservation and management

International and regional efforts

All seven Central American countries have become party to the Ramsar convention on wetlands since 1990, and each has designated at least one Ramsar wetland site of international importance (Table 11), as required by the Ramsar convention (Lyster, 1985; Sand, 1992; Ramsar Convention Bureau, 2002). The majority of these sites are coastal, marine, or

Table 11. Ramsar sites in Central America.

Country	Site name	Size (ha)	Wetland types included
Belize	Crooked Tree Wildlife Sanctuary	6637	Freshwater marshes and streams
Costa Rica	Caño Negro	9969	Freshwater marsh
	Cuenca Embalse Arenal	67,296	Man-made lake
	Gandoca-Manzanillo	9445	Coastal lagoon, coral reefs, seagrass beds, mangroves, palm swamp
	Humedal Caribe Noreste	75,310	Lakes, marshes, wooded swamps, streams, estuaries
	Isla del Coco	99,623	Coral reefs, swamps
	Laguna Respringue	75	Freshwater swamp
	Manglar de Potrero Grande	139	Mangrove
	Palo Verde National Park	24,519	Freshwater marshes, seasonally flooded woodlands, mangroves
	Tamarindo	500	Mangrove
	Terraba-Sierpe	30,654	Mangroves and palm swamps
El Salvador	Laguna del Jocotal	1571	Lake
Guatemala	Manchón-Guamuchal	13,500	Mangrove, palm swamps, freshwater marsh
	Laguna del Tigre National Park	335,080	River, marsh, and lagoon complex
	Punta de Manabique	132,900	Seagrass beds, marshes, swamps
	Bocas del Polochic	21,227	Seasonal wetlands
Honduras	Barras de Cureo y Salado	13,225	Coastal, estuarine, and riverine wetlands
	Jeanette Kawas National Park	78,150	Coral reefs, seagrass beds, mangroves
	Punta Izopo	11,200	Savannas, marshes, mangroves, lakes
	Sistema de Humedales de la Zona Sur	69,711	Mangroves and lagoons
Nicaragua	Cayaos Miskitos	85,000	Coral reefs, seagrass beds, mangroves, riverine wetlands, gallery forests
	Deltas del Estero Real y Llanos de Apacunca	81,700	Mangroves
	Lago de Apanás-Asturias	5415	Artificial lake
	Los Guatuzos	43,750	Lakes, ponds
	Río San Juan	43,000	Rivers, estuaries, marsh, lakes, ponds
	Bahía de Bluefields	86,501	Mangroves, freshwater lagoons
	San Miguelito	43,475	Lake
	Lagunar de Tisma	16,850	Lake, marshes, river shores
Panamá	Golfo de Montijo	80,765	Coastal wetlands, mangroves, marshes, seasonally-flooded grasslands
	Punta Patiño	13,805	Coral reefs, mangroves
	San San-Pond Sak	16,414	Coastal plains, mangroves, peat bogs

Data from Ramsar Convention Bureau (2002).

estuarine wetlands (mangroves and coral reefs), reflecting the aereal dominance of these wetlands in Central America, their potential for eco-tourism, and their availability, as most other wetlands long ago were “reclaimed” for agriculture, pasture, or other uses. Several large freshwater marshes have been identified as Ramsar sites because of their importance to migratory birds. Manchón-Guamuchal in Guatemala may be the last marsh in the country for migrating birds along its western flyway (Ramsar Convention Bureau, 2002). Many of Central America’s Ramsar sites continue to be used extensively by humans for subsistence activities (hunting, fishing, wood-gathering, agriculture) and regional planners are attempting to strike a balance between conservation and use of these wetlands (CCAD, 2002).

A number of governmental and non-governmental organizations (NGO’s) work extensively in conservation and management of Central American wetlands. The involvement of the North American Wetlands Council (Canada) and numerous ornithological organizations, notably the Audubon Society, International Waterfowl and Wetlands Research Bureau (IWRB), Ducks Unlimited, and the Western Hemisphere Shorebird Reserve Network (WHSRN), reflects the importance of these wetlands for resident and migratory birds. The Nature Conservancy (TNC), World Wide Fund for Nature (WWF), and IUCN are also actively involved in wetland conservation in the region. The IUCN–Central American Wetlands Programme (IUCN–ORCA) has a number of demonstration projects for promoting wetland conservation through their sustainable use. These projects include: sustainable management of forest and non-forest resources (fish, shrimp, crabs, mollusks) in the mangroves of the Héroes y Mártires de Veracruz region of Nicaragua (Windevoxhel, 1992); development of a cooperative (Coopemangle) for extraction of wood and bark from the mangroves of the Sierpe-Térraba forest reserve in Costa Rica; economic studies on the floodplain wetlands of the Río La Pasión in the Petén region of Guatemala; and preparing conservation strategies for the international SI-A-PAZ (Sistema de Areas Protegidas por la Paz – International System of Protected Areas for Peace) wetland complex on the Costa Rica-Nicaragua border (Davidson and Gauthier, 1993; IUCN–ORCA, n.d.).

Because of their economic value, forested wetlands in the region (mangroves as well as palustrine swamp forests) fall within the scope of the Tropical Forestry Action Plan (TFAP) of the Food and Agriculture Organization. TFAP has identified the Golfo de Fonseca and the forested wetlands within the SI-A-PAZ complex (including Caño Negro and Los Guatusos) as forest resources of regional importance. Although wetlands were not part of its original mission, the Central American Commission on the Environment and Development (Comisión Centroamericana de Ambiente y Desarrollo – CCAD) now focuses intensively on wetland conservation and management (CCAD, 2002). The Centro Agronómico Tropical de Investigación y Enseñaza (CATIE – Tropical Agricultural Centre for Research and Education) works with the IUCN on wetland-related projects in Guatemala, Honduras, Nicaragua, and Costa Rica.

Within-country conservation and management

Within countries, there are wide disparities in levels of management and degree of protection and granted to wetlands (CCAD, 2002). These were reviewed in detail by Davidson and Gauthier (1993), and are not repeated here. Since the publication of that report, Honduras enacted by executive decree a set of general laws concerning the environment (Government of Honduras, 1993). This set of laws includes explicitly as areas of concern and management only mangroves among the identifiable wetland systems. The Government of Belize has focused conservation and management efforts on mangroves and the offshore cays and barrier reef, which support the country's fisheries and are an attraction for substantial numbers of tourists. Since 1989, a permit has been required to cut mangroves in Belize, although the permit fees are extremely low (BZ \$25.00 for 0.1 acre; BZ \$50.00 for 0.1–1.0 acre; BZ \$300 for $>$1.0 acre; BZ \$1.00 = US \$0.50), and permitting requirements are enforced laxly. Many of the cays are *de jure* nature reserves, although jurisdiction for their administration is vague (the Forestry Department has jurisdiction over mangroves, while the department of Fisheries and Agriculture has jurisdiction over reef resources). Belize initiated a Coastal Zone Management Program in 1990 that includes the barrier reef, atolls, lagoon cays, and much of the Atlantic coastal plain. Community conservation efforts initiated since 1986 have also begun to protect and manage the palustrine wetlands at Crooked Tree Wildlife Refuge, and the riparian forest habitat of the black howler monkey (*Alouatta pigra*) at the Community Baboon Sanctuary (Hartup, 1994). Costa Rica has published a map in which all of the wetlands within its borders are identified (Bravo and Ocampo, 1993), but their total area has yet to be measured. The first two workshops to develop national strategies for conservation and sustainable development of Costa Rican wetlands were held in early 1994 (McCarthy, 1994; MIRENEM/DGVS, 1994a, b). Currently, all seven Central American countries are developing maps and databases of their wetlands (CCAD, 2002).

Recommendations

The Wetlands of the World series is intended to provide state-of-the-art synopses of wetland inventory, ecology, and management. The information presented in this review illustrates clearly the need for additional data from Central American wetlands in each of these three areas. Regional coordination of wetland inventories, comparative ecological research, and joint management strategies are resulting in integrated planning and consistent policies across the isthmus (CCAD, 2002). In this section, I suggest several areas of investigation and action that should be high priorities for wetland scientists and policy-makers in Central America.

Inventory

There can be no long-term management plans for, or coordinated research programs in, Central American wetlands without a complete inventory of the regional extent of all wetland systems in the isthmus. The most recent descriptions of many freshwater swamp forests in Central America are over 30 years old, and so their potential utility as forest resources is limited by the absence of data on their current extent. The geographical information system (GIS) database for Costa Rican wetlands (Bravo and Ocampo, 1993) is an excellent model for identifying and illustrating wetland locations throughout Central America. Nicaragua's Instituto de Recursos Naturales de Nicaragua (IRENA) is in the process of identifying all wetlands in that country (Davidson and Gauthier, 1993). Remote sensing technology has been used to quantify the areal extent of seagrass beds, mangrove swamps, and palustrine wetlands in Belize and Florida (Patterson, 1986; Corves et al., 1989; Kelly, 1991; Pope et al., 1994). CCAD (2002) identified such an inventory as a high priority for action.

Biodiversity of wetland flora and fauna are best documented for Belize, Guatemala, Costa Rica, and Panamá. Honduras began to develop a system of conservation areas only in 1993 (Government of Honduras, 1993), and consequently its overall biodiversity is little-known relative to its neighbors. The 1993 legislation regarding the Honduran environment does not, however, explicitly mention wetlands other than mangroves, and therefore the immediate prospects for wetland biodiversity inventories are dim. El Salvador and Nicaragua, still emerging from the twilight of their protracted civil wars, are at least a decade behind the remaining Central American countries in accounting for the extent of biodiversity in all their natural areas, including wetlands. Thus, the following strategies are recommended:

1. The wide use of remote sensing and GIS to inventory and quantify the areal extent of wetlands, with common data formats for each of the Central American countries, should be encouraged and supported by national and international agencies.
2. Rapid assessments of wetland biodiversity should be conducted in all of the Central American countries. These efforts should focus initially on the less studied countries: Honduras, El Salvador, and Nicaragua.

Ecology

Comparative ecological research that will generate meaningful theoretical generalities and cogently inform policy regarding wetlands in the region cannot continue to focus myopically on rainforests in Costa Rica and Panamá, and on the barrier reef complex of Belize. Investigations of wetlands in the region should be of a comparative nature: analogous data should be collected using standard methods from physiognomically similar sites throughout the isthmus.

Ecological studies of Central American wetlands also need to move beyond descriptions of wetland flora and fauna and observations of correlations with edaphic or other environmental factors. Key questions that should be focused on are:

1. *What is the nature and magnitude of the linkages between rivers, mangrove swamps, seagrass beds, and coral reefs*? This question should be addressed in terms of nutrient and sediment deposition and retention rates; their consequences for productivity of each wetland system and for the four systems as a whole; and the expected effects of changing land-use patterns on resources (e.g. fisheries, tourism) derived from each of these wetland systems.
2. *What are predicted consequences for coastal wetlands resulting from rapidly rising sea levels predicted under global climate change scenarios*? Granger (1991) reviewed the impacts on agriculture, water resources, forestry, tourism, and frequency and severity of tropical cyclonic storms in the Caribbean islands. A similar analysis needs to be performed for the Central American isthmus.
3. *Which wetlands or wetland systems in the isthmus provide unique ecological functions or dynamics*? This question could be addressed at the population, community, and/or ecosystem level. Three examples are: (1) do high elevation isolated lakes, such as those that occur in calderas in El Salvador and Guatemala, harbor endemic flora and fauna (such as the now extinct Atitlán grebe). (2) Do wetland-inhabiting anuran amphibians possess life-history strategies and patterns of community structure that differ significantly from other, better-studied anurans across the isthmus? (3) Are palustrine forested wetlands, such as palm swamps and *Pterocarpus* forests "pioneer," early successional formations, or steady-state

ecosystems dependent on local hydrological and topographic conditions?

4. *Are specific wetland "values and functions" compatible with wetland ecology, or will they degrade the valued wetland in the near-term*? For example, Davidson and Gauthier (1993) identified the absorptive capacity for river-laden sediments and agrochemicals of the wetland complex around Lago Nicaragua as a positive value and function. Detailed time-series data focusing on the changes in the population, community, and ecosystem properties of these wetlands concomitant with their receiving this run-off are needed. Otherwise, this positive valuation of these wetlands will encourage further deforestation in the Nicaraguan and Costa Rican portions of the Lago Nicaragua watershed.
5. *What are the current and projected trends in seasonal distribution and abundance of birds dependent on Central American wetlands*? Because many of these species are migratory, this question needs to be addressed in concert with ornithologists and appropriate NGO's in North America.

Despite its historical emphasis on forestry and agriculture, CATIE would be the most appropriate agency within the isthmus to coordinate this research agenda, and should work hand-in-hand with CCAD, which is coordinating regional management policies for wetlands.

Conservation and management

As of 1998, all seven Central American countries had ratified the Ramsar convention on wetlands (Ramsar Convention Bureau, 2002). The Ramsar convention is used most commonly to protect unique or representative wetlands (criterion 1), or wetlands of international importance *especially as waterfowl habitat* (criterion 3; italics added), but their importance to migratory waterfowl also could be considered within the 1979 Bonn convention on the conservation of migratory species of wild animals (Sand, 1992) In addition, the second criterion of the Ramsar convention specifies that a wetland should be considered internationally important if it "supports an appreciable assemblage of rare, vulnerable, or endangered species . . ." (2.a.); if it "is of special value for maintaining the genetic and ecological diversity of a region . . ." (2.b.); if it "is of special value as the habitat of plants or animals at a critical stage of their biological cycle" (2.c.); or if it "is of special value for one or more endemic plant or animal species or communities" (2.d.) (Dixon, 1994).

Jurisdiction over wetland resources often is poorly defined within each Central American country, if wetlands are included explicitly in each country's environmental legislation at all. This has resulted in widespread degradation and outright destruction of wetlands throughout the region. Wetland degradation also is linked to identification of specific values and functions relative to development of nearby uplands, rather than to sustainable functioning of the wetland itself.

The long-term success of community-based conservation initiatives (e.g. Hartup, 1994), as compared with the historically meager record of governmental and international management protection strategies, should be noted. The regional influence of the Catholic Church, although often perceived as antagonistic to environmental protection, could be harnessed to provide strong underpinnings for local conservation programs (DeWitt, 1995).

In closing, therefore, the following recommendations are suggested that could lead to more sustainable management and protection of the region's wetlands:

1. The IUCN should encourage Central American signatories to the Ramsar convention to use broader criteria in designating additional wetlands of international importance. In particular, wetlands should be identified and managed appropriately because of their unique contribution to and reservoir of the region's biodiversity. Specific examples include the riparian forest fragments in Belize's Mountain Pine Ridge, and isolated lakes in the region's volcanic calderas.
2. The IUCN should work to develop regional agreements on Nearctic migratory avifauna within the scope of the 1979 Bonn convention on the conservation of migratory species of wild animals.
3. Jurisdiction for wetland conservation, protection, and sustainable management should be clearly defined in national legislation and consolidated within a single governmental agency or ministry in each country.
4. Wetland values and functions should reflect not only the down-stream consequences of economic development (especially agriculture, forestry, and urbanization), but also the functioning of the wetland ecosystem itself, its flora, and its fauna.

5. Community-based conservation and management initiatives should be fostered and encouraged throughout Central America.

Acknowledgements

This review was begun while the author was supported by grants from the US National Science Foundation (BSR 91-07195; DEB 92-53743). Laura Rowe and Marianne Panuncio assisted with library research. Harry Greene provided useful pointers to newer literature on snakes of Central American wetlands. Mark Brinson, Nick Brokaw, Elizabeth Farnsworth, and Dennis Whigham provided critical comments on draft versions of the manuscript. Dennis Whigham showed remarkable perseverance and tenacity in seeing it through to publication.

Appendix 1. Birds associated with Central American wetlands.

Species	Status[1]	Marine/ estuarine[2]	Riverine[3]	Lacustrine	Palustrine Forested	Palustrine non-forested
Tinamidae (Tinamous)						
Crypturellus cinnamomeus	R					B
Podicipedidae (Grebes)						
Podilymbus gigas[4]	R			G		G
Podilymbus podiceps	R	C	C	G, N, P		B, C, G, N
Tachybaptus dominicus	R	B	C	B, P		B, P
Procellariidae (Shearwaters and Petrels)						
Procellaria parkinsonia	M	C				
Puffinis griseus	V	B, C, G				
Hydrobatidae (Storm-Petrels)						
Oceanodroma leucorhoa	M	C, G				
Oceanodroma melania	M	C				
Oceanodroma microsoma	M	C				
Oceanodroma t. kelsalli	V	C				
Oceanites oceanicus	M	C				
Phaethontidae (Tropicbirds)						
Phaethon aethereus	R, V	C, P				
Phaethon lepturus	V	B				
Pelecanidae (Pelicans)						
Pelecanus erythrorhynchos	M					B, C
Pelecanus occidentalis	R	B, C, G, N, P				
Sulidae (Boobies)						
Sula dactylatra	V	B				
Sula leucogaster	R	B, C				
Sula sula	R	B				
Phalacrocoriacidae (Cormorants)						
Phalacrocorax auritus	R	B				B
Phalacrocorax olivaceaus	R	B, C, G, P	B, G	N, P		C, N, P
Anhingidae (Anhingas)						
Anhinga anhinga	R	B, C, H, N, P	B, C	B, C, G, N, P		B, C, G, N, P
Fregatidae (Frigatebirds)						
Fregata magnificens	R	B, C, H, N, P				
Ardeidae (Herons and Egrets)						
Agamia agami	R	P	B	G	P	
Ardea alba	M	H, N				
Ardea cocoi	M		P	P		P
Ardea herodias	M	B, C, H, N, P	B, C, P	G		B, C, G, N, P
Botaurus lentiginosus	M					B
Botaurus pinnatus	R	N	B			B, N

Appendix 1. Continued.

Species	Status[1]	Marine/ estuarine[2]	Riverine[3]	Lacustrine	Palustrine Forested	Palustrine non-forested
Bubulcus ibis	M, R	B, P	B, C, P	G	B	B, C, N
Butorides striatus	M, R	B, C, P	B, C			B, C
Butorides virescens	R	N, P	B	G, S	B	B, C, G, S
Casmerodius albus	M, R	B, P				B
Cochlearius cochlearius	R	B, N, P	B, C, P		B, C, P	B, C, G, N, P
Egretta alba	R	B, N, P		G		C, G, P
Egretta caerulea	M, R	B, C, N, P	B, C	N		B, C, N, P
Egretta rufescens	R	B, C				
Egretta thula	M, R	B, C, N, P	B, C			B, C, G, N, P
Egretta tricolor	M, R	B, C, N, P	B, C			B, C, G, N, P
Ixobrychus exilis	R	B, N		G, N		B, C, N
Nyctanassa violacea	R	B, C, N, P	B, C	N	B	B, C, G, N
Nycticorax nycticorax	R	B, N, P	C	N	B, C, P	B, C, N, P
Tigrisoma lineatum	R	B, N	B	P		B, C, N, P
Tigrisoma mexicanum	R	B, G, N, P	C, G			B, C, G, N
Trigrisoma fasciatum	R			P	P	P
Ciconiidae (Storks)						
Jabiru mycteria	R	H, N	B, G			B, C, G, N
Mycteria americana	R	B, G, H, N, P	G			C, G, N, P
Threskiornithidae (Ibises and Spoonbills)						
Ajaia ajaja	R	B,G, H, N, P	B, C, G, P			B, G, N, P
Eudocimus albus	R	B, G, H, N, P	C, G	N	P	B, C, N
Mesembrinibis cayensis	R	C, P			C, P	
Plegadis falcinellus	R, V		P		P	C, P
Anatidae (Ducks and Geese)						
Anas acuta	M			N		B, C, N, P
Anas americana	M	G, P	G	G		B, C, G, P
Anas carolinensis	M					B
Anas clypeata	M	N, P		G, N		B, C, G, N, P
Anas cyanoptera	M, V			N		C, N
Anas discors	M	G, H, N, P	C, G	G, H, N, P		B, C, G, H, N, P
Aythya affinis	M	B, C, N		G, N		B, G, N, P
Cairina moschata	R	C, G, H, N, P	B, G	G, H	B, C	B, C, G, H, N, P
Dendrocygna autumnalis	M	N, H, P	B, G	G, H, N, S		B, C, H, N, P, S
Dendrocygna bicolor	R			G, S		C, S
Oxyura dominica	R	P		P, S		C, S
Oxyura jamaicensis	M			G, N		G, N
Sarkidiornis melanatos	R				P	
Cathartidae (American Vultures)						
Cathartes aura	R		B, C, G, H, P, S			B, C, G, H, P, S
Cathartes burrovianus	R					B, G
Coragyps atratus	R	B				B
Sarcorampus papa	R					B
Pandionidae (Ospreys)						
Pandion haliaetus	M, R	B, G, N, P	B, G	G		B, G, N, P
Accipitridae (Kites, Hawks, and Eagles)						
Busarellus nigricollis	R			G		
Buteo magnirostris	R	P				
Buteogallus anthracinus	R	C, G, P	B, C, G, P	G		B, C, P
Buteogallus subtilis	R	P				
Rostrhamus sociabilis	R		G	G		
Spizastur melanoleucus	R		B			B

Appendix 1. Continued.

Species	Status[1]	Marine/ estuarine[2]	Riverine[3]	Lacustrine	Palustrine Forested	Palustrine non-forested
Falconidae (Falcons and Caracaras)						
Falco columbarius	M	B				B
Micrastur semitorquatus	R	P				
Aramidae (Limpkins)						
Aramus guarauna	R	N	B, G		B, G, P	C, G, N
Rallidae (Rails, Gallinules, and Coots)						
Amaurolimnas concolor	R	N, P				N, P
Aramides axillaris	R	B, N, P	B		B	B, N, P
Aramides cajanea	R	B, G, N, P		N, P	B, P	B, G, N, P
Fulica americana	M	C, G, N		G, N, P, S	C	B, C, G, N, P, S
Gallinula chloropus	R			G, S		B, G, S
Laterallus albigularis	R	P		P		N, P
Laterallus exilis	R					N
Laterallus ruber	R	N			B, G	B, G, N
Porphyrula martinica	R	P		N, P, S		B, C, G, N, P, S
Porzana flaviventer	R					B, G, N, P
Porzana carolina	M			G		B, C, G, P
Rallus longirorstris	R	B				
Rallus maculatus	R				B	
Heliornithidae (Sungrebes)						
Heliornis fulica	R		B, G, P			B, G, P
Eurypygidae (Sunbitterns)						
Eurypyga helias	R	N, P				G, N, P
Jacanidae (Jacanas)						
Jacana jacana	R			H		H, P
Jacana spinosa	R	B, G, N, P		G, H, N, P, S		C, G, H, N, P, S
Haematopodidae (Oystercatchers)						
Haematopus palliatus	R	G, P	G			G
Charadriidae (Plovers)						
Charadrius alexandrinus	M	C, G				
Charadrius collaris	M	B, C				
Charadrius semipalmatus	M	B, C, N, P				
Charadrius vociferus	M	B, G	B, G			B, G
Charadrius wilsonius	R	B, C, G, P				C, G
Pluvialis dominica	V	B				
Pluvialis squatarola	M	B, C, P				
Vanellus chilensis	V					P
Scolopacidae (Sandpipers and Snipes)						
Actitis macularia	M, R	B, C, G, N, P		G, N		B, C, G, N, P
Aphriza virgata	M		C			
Arenaria interpres	M	B, C, P				
Calidris alba	R	C, P				
Calidris alpina	M	C, G				
Calidris bairdii	M	G				
Calidris canutus	M	C				
Calidris fuscicollis	M		B			B
Calidris mauri	M	C, G, P				C, G, P
Calidris melanotos	M		B			B, C
Calidris minutilla	M	C, N, P				C, P
Calidris pusilla	R	C, P				
Catoptrophorus semipalmatus	M	B, C, G, N, P				C, G
Gallinago gallinago	R			G		G
Limnodromus griseus	M	C, P	B, C			B, C, P

Appendix 1. Continued.

Species	Status[1]	Marine/ estuarine[2]	Riverine[3]	Lacustrine	Palustrine Forested	Palustrine non-forested
Limnodromus scolopaceaus	M	B				
Limosa fedoa	M	B, C, P				
Limosa haemastica	M	B, C, G				
Micropalama himantopus	M	C				
Numenius americanus	M	B				
Numenius phaeopus	M	B, C, G, N, P				
Philomachus pugnax	V	G, C				
Tringa flavipes	M	B, C				B, C
Tringa melanoleuca	M	B, C				B
Tringa solitaria	M	B, C, G		N		B, C, G, N
Tryngites rubruficollis	M	B				
Recurvirostridae (Stilts and Avocets)						
Himantopus himantopus	R		B, G	G, N, S	B, S	B, C, G, N, P
Himantopus mexicanus	R	B, C				B
Recurvirostra americana	V	B, C				
Phalaropodidae (Phalaropes)						
Phalaropus lobatus	M	C				
Steganopus tricolor	M	C				
Stercorariidae (Jaegers and Skuas)						
Catharacta skua	V	B				
Stercorarius longicaudus	M	B, C				
Laridae (Gulls and Terns)						
Anous stolidus	M, R	B, C				
Chlidonias niger	V	B, C, P				G, N
Gelochelidon nilotica	V	C		P		
Hydroprogne caspia	R	B, G	B		B	B
Larus argentus	M	B, C				
Larus atricilla	M	B, C, N, P		G, N		G, N
Larus delawarensis	M	B, C, P				
Larus pipixcan	M	B, C, P				
Phaetusa simplex	M	P				
Sterna albifrons	M	C, G		P		
Sterna anaethetus	R	B, C				C
Sterna antillarum	R	B				
Sterna dougallii	R	B				
Sterna elegans	M	C				
Sterna fuscata	R	B				
Sterna hirundo	M	B, C		P		
Sterna maxima	M, R	B, C, P				
Sterna sadvicensis	M, R	B, C				
Xema sabini	M	C				
Rynchopidae (Skimmers)						
Rhynchops niger	M	B, C	C			N, P
Columbidae (Pigeons and Doves)						
Columba cayannensis	R, V	P				
Columbina talpacoti	R, V	P				
Leptotila verreauxi	R, V	P				
Zenaida asiatica	R	B				
Cuculidae (Cuckoos and Anis)						
Coccyzus minor	R	B				
Crotophaga ani	R	B				
Crotophaga major	R	P				
Crotophaga sulcirostris	R	B				
Piaya cayana	R	P				

Appendix 1. Continued.

Species	Status[1]	Marine/ estuarine[2]	Riverine[3]	Lacustrine	Palustrine Forested	Palustrine non-forested
Strigidae (True Owls)						
Otus cooperi	R				G	
Nyctibiidae (Potoos)						
Nyctibus griseus	R	B			C	
Trocholidae (Hummingbirds)						
Amazilia tzacatl	R	B	B		B	
Anthracothorax prevostii	R	B				B
Archilochus colubris	M	B	B		B	
Chalybura urochrysia		R, V		P		
Damophila julie	R, V	P				
Florisuga mellivora	R, V	P				
Glaucis hirsuta	R, V	P				
Lepidopyga coeruleogularis	R, V	P				
Phaeochroa cuvierii	R, V	P				
Phaethornis longuemareus	R, V	P				
Phaethornis superciliosus	R, V	P				
Trogonidae (Trogons)						
Trogon melanurus	R	P				
Alcedinidae (Kingfishers)						
Ceryle alcyon	M	B, C, P	B, C, P		B, C, P	B, C, P
Ceryle torquata	R	B, C, P	B, C, P		B, C, P	B, C, P
Chloroceryle aenea	R	B, C, P	B, C, P		B, C, P	B, C, P
Chloroceryle amazona	R	B, C, P	B, C, P		B, C, P	B, C, P
Chloroceryle americana	R	B, C, P	B, C, P		B, C, P	B, C, P
Chloroceryle inda	R	P				
Ramphastidae (Toucans)						
Ramphastos sulphuratus	R	P				
Picidae (Woodpeckers)						
Campephilus melanoleucos	R	P				
Celeus loricatus	R	P				
Colaptes punctigula	R	P				
Dryocopus lineatus	R	P				
Melanerpes rubricapillus	R	P				
Picumnus olivaceus	R	P				
Furnariidae (Ovenbirds)						
Xenops minutus	R	P				
Dendrocolaptidae (Tree creepers)						
Dendrocincla fluginosa	R	P				
Lepidocolaptes souleyetii	R	P				
Sittasomus griseicapillus	R	P				
Xiphorhynchus guttatus	R	P				
Xiphorhynchus picus	R	P				
Formicariidae (Ant-birds)						
Thamnophilus doliatus	R	P				
Tyrannidae (Tyrant flycatchers)						
Contopus virens	M	P				
Elaenia flavogaster	R	P				
Epidonax virescens	M	P				
Myiarchus panamensis	R	P				
Myiobius atricaudatus	R	P				
Myiobius barbatus	R	P				
Myiodynastes maculatus	R	P				

Appendix 1. Continued.

Species	Status[1]	Marine/ estuarine[2]	Riverine[3]	Lacustrine	Palustrine Forested	Palustrine non-forested
Myiozetes cayanensis	R	P				
Myiozetetes similis	R	B				B
Oncostoma olivaceum	R	P				
Pachyramphus polycopterus	R	P				
Phaeomyias murina	R	P				
Philohydor lictor	R	P				
Pitangus sulphuratus	R	P				
Sublegatus arenarum	R	P				
Tityra semifasciata	R	P				
Todirostrum cinereum	R	P				
Tolmomyias sulfurescens	R	P				
Tyrannus melancholicus	R	B, P	B		B	B
Hirundinidae (Martins and Swallows)						
Hirundo rustica	M	B	B	B		B
Progne chalybea	R	B		B, P		B
Progne subis	M	B		B		B
Tachycineta albilinea	R	B		B, P		
Tachycineta bicolor	M	B	B	B		B
Corvidae (Jays)						
Psilorhinus morio	R	B				
Mimidae (Catbirds and Mockingbirds)						
Melanoptila glabrirostris	R	B				
Mimus gilvus	R	B				B
Pipridae (Manakins)						
Chiroxiphia lanceolata	R	P				
Manacus vitellinus	R	P				
Pipra mentalis	R	P				
Schiffornis turdinus	R	P				
Troglodytidae (Wrens)						
Thryothorus leucotis	R	P				
Thryothorus rutilus	R	P				
Troglodytes aedon	R	P				
Turdidae (Thrushes, Solitaires and Bluebirds)						
Catharus minimus	M	C				
Catharus ustulatus	M	C				
Hylocichla mustelina	M	C				
Polioptila plumbea	R	P				
Turdus grayi	R	P				B
Vireonidae (Vireos)						
Cyclarhis gujanensis	R	P				
Vireo flavifrons	M	C				
Vireo flavoviridis	R	P				
Vireo olivaceus	R, M	B, P	B		B	B
Vireo pallens	R	B	B		B	B
Parulidae (Wood warblers)						
Dendroica castanea	M	P				
Dendroica cerulea	M	P				
Dendroica coronata	M	B	B		B	B
Dendroica dominica	M	B	B		B	B
Dendroica fusca	M	P				
Dendroica palmarum	M	B				
Dendroica pensylvanica	M	P				
Dendroica petechia	R, M	B, C, P	B			

Appendix 1. Continued.

Species	Status[1]	Marine/ estuarine[2]	Riverine[3]	Lacustrine	Palustrine Forested	Palustrine non-forested
Dendroica striata	M	P				
Geothlypis poliocephala	R		B		B	B
Geothlypis trichas	M	B	B		B	B
Mniotilta varia	M	B, C, P	B		B	B
Helmitheros vermivorus	M	P				
Oporonis philadephia	M	P				
Parula americana	M	B				
Protonotaria citrea	V, M	B, C, P	B		B	B
Seiurus auricapillus	M	C				
Seiurus noveboracensis	M	C, P				
Setophaga ruticilla	M	B, C, P	B		B	B
Vermivora chrysoptera	M	P				
Vermivora peregrina	M	C, P				
Wilsonia canadensis	M	P				
Icteridae (Orioles, Meadowlarks and Blackbirds)						
Agelaius phoeniceus	R					B
Cassiculus melanicterus	R		G			
Cassidix mexicanus	R	P				
Cassidix nicaraguensis	R					N
Icterus chrysater	R	P				B
Icterus cucullatus	R	B	B			B
Icterus dominicensis	R					B
Icterus galbula	M	B, C, P	B		B	B
Icterus mesomelas	R	B, P	B		B	B
Icterus spurius	M	B	B		B	B
Quiscalus mexicanus	R	B, C, P				B
Thraupidae (Tanagers)						
Cyanerpes cyaneus	R	P				
Euphonia laniirostris	R	P				
Piranga rubra	M	B, C, P				B
Thraupis episcopus	R	P				
Thraupis palmarum	R	P				
Emberizidae (Grosbeaks, Buntings, Sparrows and Finches)						
Ammodramus savannarum	R					B
Arremonopus conirostris	R	P				
Cyanocompsa cyanoides	R	P				
Oryzoborus angolensis	R	P				
Passerculus sanwichensis	V					B
Passerina ciris	M	C				
Passerina cyanea	M	B, C	B		B	B
Sporophila americana	R	P				
Sporophila nigricollis	R	P				
Volatina jacarina	R	P				

For each wetland type, letters indicate countries (as in Table 3) for which unambigous records were available for each wetland type. Data compiled from Dickerman (1975, 1977), Stiles and Smith (1977), Dyrcz (1984), Hartshorn et al. (1984), Caldwell (1986), Scott and Carbonell (1986), Wood et al. (1986), Ridgely and Gwynne (1989), Stiles and Skutch (1989), Botero and Rusch (1994), Lefebvre and Poulin (1996, 1997), Warkentin and Hernández (1996), Butler et al. (1997), and Frederick et al. (1997).

[1] Status: R – resident (non-breeding or breeding); M – migrant; V – accidental or occasional visitor.

[2] Marine/Estuarine wetlands include pelagic, island, and mangrove habitats.

[3] Riverine wetlands include gallery forests.

[4] Likely to be extinct (Hunter, 1988).

Appendix 2. Mammals associated with Central American wetlands.

Species	Marine/ estuarine	Riverine	Lacustrine	Palustrine forested	Palustrine unforested
Didelphidae (Opossums)					
Chironectes minimus		B, G, C, H, N, P			
Didelphis marsupialis	N				N
Metachirus nudicaudatus		C, P			
Micoureus cinereus		B, G, C, H, N, P			
Myrmecophagidae (Anteaters)					
Tamandua mexicana (III)		B, G, C, H, N, P, S			
Emballonuridae (Sheath-tailed bats)					
Rhynchonyctris naso		B, G, C, H, N, P			
Saccopteryx bilineata		B, G, C, H, N, P, S			
Saccopteryx leptura		B, G, C, H, N, P, S			
Diclidurus albus					B, G, C, H, N, P, S
Noctilionidae (Bulldog bats)					
Noctilio albiventris	G, C, N, P, S				G, C, N, P, S
Noctilio leporinus	B, G, C, H, N, P, S				B, G, C, H, N, P, S
Phyllostomidae (Leaf-nosed bats)					
Carollia spp.		B, G, C, H, N, P, S			
Choeroniscus spp.					B, G, C, H, N, P, S
Desmodus spp.		B, G, C, H, N, P, S			B, G, C, H, N, P, S
Macrophyllum macrophyllum				B, G, C, H, N, P, S	
Micronycteris spp.		B, G, C, H, N, P, S			
Phylloderma stenops		B, G, C, H, N, P, S		B, G, C, H, N, P, S	B, G, C, H, N, P, S
Phyllostomus spp.		B, G, C, H, N, P, S			
Trachops cirrhosus			B, G, C, H, N, P, S		B, G, C, H, N, P, S
Vampyrum spectrum					B, G, C, H, N, P, S
Vespertilionidae (Vespertilionid bats)					
Eptesicus spp.		B, G, C, H, N, P, S			
Molossidea (Free-tailed bats)					
Cynomops spp.		B, G, C, H, N, P, S			B, G, C, H, N, P, S
Cebidae (New World Monkeys)					
Alouatta palliata (I)		G, C, H, N, P, S			
Alouatta pigra (II)		B		B	
Canidae (Coyotes etc.)					
Canis latrans	N				
Procyonidae (Raccoons and allies)					
Nasua narica (III)	N	N			
Potos flavus (III)		B, G, C, H, N, P, S			
Procyon cancrivorus	P	P			
Procyon lotor	B, G, C, H, N, P, S	P			N
Mustelidae (Mustelids)					
Lutra anectens		B, G, H, P	P		P
Lutra longicaudis (I)		B, G, C, H, N, P, S			
Felidae (Cats and allies)					
Panthera onca (I)	N	B		B	
Trichechidae (Manatees)					
Trichecus manatus (I)	B, C, H, N	B, C, G, H, P			B, C, G, H, N, P
Tapiridae (Tapirs)					
Tapirus bairdii (I)		B, G		B, G, P	
Cervidae (Cervids)					
Mazama americana (III)		B, G, C, H, N, P, S			
Odocoileus virginianus (III)					N

Appendix 2. Continued.

Species	Marine/ estuarine	Riverine	Lacustrine	Palustrine forested	Palustrine unforested
Dasyproctidae (Cavimorphs)					
Agouti paca (III)	P	B, G, C, H, N, P, S			C, P
Hydrochaeris hydrochaeris					P
Echimyidae (Spiny rats and Tree rats)					
Diplomys labilis	P				

For each wetland type (as in Appendix 1), letters indicate countries (as in Table 3) in which each species is expected to occur. Roman numerals in parentheses following a species name indicates CITES Appendix number. Data compiled from Hartshorn et al. (1984), Scott and Carbonell (1986), Eisenberg (1989), and Emmons (1990).

References

Abercrombie, C.L., III, Davidson, D., Hope, C.A. and Scott, D.E. 1980. Status of Morelet's crocodile *Crocodylus moreleti* in Belize. Biological Conservation 17: 103–113.

Adams, D.C. and Tomlinson, P.B. 1979. *Acrostichum* in Florida. American Fern Journal 69: 42–46.

Alcala-Herrera, J.A., Jacob, J.S., Castillo, M.L.M. and Neck, R.W. 1994. Holocene palaeosalinity in a Maya wetland, Belize, inferred from the microfaunal assemblage. Quaternary Research 41: 121–130.

Alfaro, M.J., Quesada, Q.R., Zamora, M.E., Madrigal, C.E. and Pacheco, U.O. 1985. Análisis comparativo de sustratos para colectar juveniles del ostión de manglar (*Crassostrea rhizophorae*, Guilding 1828) en Estero Vizcaya, Limón Costa Rica. Revista de Biología Tropical 33: 1–6.

Allen, P.H. 1956. The Rain Forests of Golfo Dulce. Stanford University Press, Stanford, CA, USA, 417 pp.

Anderson, R. and Mori, S. 1967. A preliminary investigation of *Raphia* palm swamps, Puerto Viejo, Costa Rica. Turrialba 17: 221–224.

Araya, H.A. 1984. Los sciaénidos (corvinas) del Golfo de Nicoya. Revista de Biología Tropical 32: 179–196.

Armitage, K.B. 1957. Lagos de la Planicie Costera de El Salvador. Comunicaciones del Instituto Tropical de Investigaciones Cientificas, San Salvador 6: 5–8.

Armitage, K.B. 1958. Lagos Volcánicos de El Salvador. Comunicaciones del Instituto Tropical de Investigaciones Cientificas, San Salvador 7: 39–48.

Armitage, K.B. 1971. A highly alkaline lake in Nicaragua. Hydrobiologia 38: 437–439.

Armitage, K.B. and Fassett, N.C. 1971. Aquatic plants of El Salvador. Archiv für Hydrobiologie 69: 234–255.

Aselmann, I. and Crutzen, P.J. 1989. Global distribution of natural and freshwater wetlands and rice paddies, their net primary productivity, seasonality and possible methane emissions. Journal of Atmospheric Chemistry 8: 307–358.

Bacon, P.R. 1990. Ecology and management of swamp forests in the Guianas and Caribbean region. *In*: Lugo, A.E., Brinson, M. and Brown, S. (eds), Forested Wetlands. Elsevier Science Publishers, Amsterdam, The Netherlands, pp. 213–250.

Beard, J.S. 1953. The savanna vegetation of northern tropical America. Ecological Monographs 23: 149–215.

Birkeleand, C. 1987. Comparison between Atlantic and Pacific tropical marine coastal ecosystems: community structure, ecological processes, and productivity. UNESCO Reports in Marine Science 46: 1–262.

Bird, K.T. and McIntosh, R.P. 1979. Notes on the marine algae of Guatemala. Revista de Biología Tropical 27: 163–169.

Bjorndal, K.A., Bolten, A.B. and Lagueux, C.J. 1993. Decline of the nesting population of hawksbill turtles at Tortuguero, Costa Rica. Conservation Biology 7: 925–927.

Bjorndal, K.A., Carr, A., Meylan, A.B. and Mortimer, J.A. 1985. Reproductive biology of the hawskbill, *Eretmochelys imbricata* at Tortuguero, Costa Rica, with notes on the ecology of the species in the Caribbean. Biological Conservation 34: 353–368.

Bloom, P.R., Pohl, M., Buttleman, C., Wiseman, F., Covich, A., Miksicek, C., Ball, J. and Stein, J. 1983. Prehistoric Maya wetland agriculture and the alluvial soils near San Antonio Rio Hondo, Belize. Nature 301: 417–419.

Bolland, O.N. 1988. Colonialism and Resistance in Belize. Cubola Productions, Banco Viejo del Careen, Belize, 218 pp.

Botero, J.E. and Rusch, D.H. 1994. Foods of Blue-Winged Teal in two neotropical wetlands. Journal of Wildlife Management 58: 561–565.

Bourliere, F. and Hadley, M. 1970. The ecology of tropical savannas. Annual Review of Ecology and Systematics 1: 125–152.

Bowen, B.W., Meylan, A.B., Robs, J.P., Limpus, C.J., Balazs, G.H. and Avise, J.C. 1992. Global population structure and natural history of the green turtle (*Chelonia mydas*) in terms of matriarchal phylogeny. Evolution 46: 865–881.

Bravo, J. and Ocampo, L. 1993. Humedales de Costa Rica (map). Universidad Nacional Escuela de Ciencias Ambientales, Programa Uso y Conservacion de Humedales, Heredia, Costa Rica.

Brinson, M.M. 1976. Organic matter losses from four watersheds in the humid tropics. Limnology and Oceanography 21: 572–582.

Brinson, M.M. and Nordlie, F.G. 1975. Lake Izabal, Guatemala. Verhandlungen Internationale Vereingigung für Theoretische und Angewandte Limnologie 19: 1468–1479.

Burns, K., Garrity, S.D. and Levings, S.C. 1993. How many years until mangrove ecosystems recover from catastrophic oil spills? Marine Pollution Bulletin 26: 239–248.

Burns, K.A., Garrity, S.D., Jorissen, D., Macpherson, J., Stoelting, M., Tierney, J. and Yellesimmons, L. 1994. The Galeta oil spill. 2. Unexpected persistence of oil trapped in mangrove sediments. Estuarine, Coastal and Shelf Science 38: 349–364.

Burns, K.A. and Yelle-Simmons, L. 1994. The Galeta oil spill. 4. Relationship between sediment and organism hydrocarbon loads. Estuarine, Coastal and Shelf Science 38: 397–412.

Bussing, W.A. 1994. Ecological aspects of the fish community. *In*: McDade, L.A., Bawa, K.S., Hespenheide, H.A. and Hartshorn, G.S. (eds), La Selva: Ecology and Natural History of a Neotropical Rainforest. University of Chicago Press, Chicago, Illinois, USA, pp. 195–198.

Butler, R.W., Guy Morrison, R.I., Delgado, F.S., Ross, R.K. and John Smith, G.E. 1997. Habitat associations of coastal birds in Panama. Colonial Waterbirds 20: 518–524.

Cabrera, J., Zamora, E. and Pacheco, O. 1983. Determinación del tamaño comercial de la ostra de manglar *Crassostrea rhizophorae* (Guilding, 1929) en sistema suspendido en Estero Vizcaya, Limón, Costa Rica. Revista de Biología Tropical 31: 257–261.

Cadle, J.E. and Greene, H.W. 1984. Phylogenetic patterns, biogeography, and the ecological structure of neotropical snake assemblages. *In*: Ricklefs, R.E. and Schluter, D. (eds), Species Diversity in Ecological Communities. University of Chicago Press, Chicago, IL, USA, pp. 281–293.

Cairns, S.D. 1982. Stony corals (Cnidaria: Hydrozoa, Scleractinia) of Carrie Bow Cay, Belize. *In*: Rützler, K. and Macintyre, I.G. (eds), The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize., I. Structure and Communities. Smithsonian Institution Press, Washington, D.C., USA, pp. 271–302.

Caldwell, G.S. 1986. Predation as a selective force on foraging herons: effects of plumage color and flocking. The Auk 103: 494–505.

Central Intelligence Agency (CIA) 2002. CIA World Factbook 2002: http://www.odci.gov/cia/publications/factbook/index.html

Chemsak, J.A. and Feller, C. 1988. New species of Cerambycidae from Twin Cays, Belize (Coleoptera). Proceedings of the Entomological Society of Washington 90: 179–188.

Cintron, G., Lugo, A.E. and Martinez, R. 1985. Structural and functional properties of mangrove forests. *In*: D'Arcy, W.G. and Correa, M.D. (eds), The Botany and Natural History of Panamá. Missouri Botanical Garden, Saint Louis, Missouri, USA, pp. 53–62.

Cintron-Molero, G. and Schaeffer-Novelli, Y. 1992. Ecology and management of New World mangroves. *In*: Seeliger, U. (ed.), Coastal Plant Communities of Latin America. Academic Press, Incorporated, San Diego, California, USA, pp. 233–258.

Cole, M.M. 1982. The influence of soils, geomorphology and geology on the distribution of plant communities in savanna ecosystems. *In*: Huntley, B.J. and Walker, B.H. (eds), Ecology of Tropical Savannas. Springer-Verlag, Berlin, pp. 145–174.

Cole, G.A. 1976. Limnology of the great lakes of Nicaragua. *In*: Thorson, T.B. (ed.), Investigations of the Ichthyofauna of Nicaraguan Lakes. University of Nebraska–Lincoln, Lincoln, Nebraska, USA, pp. 9–15.

Collins, J.P., Berkelhamer, R.C. and Mesler, M. 1977. Notes on the natural history of the mangrove *Pelliciera rhizophorae* (Tr. & Pl.), (Theaceae). Brenesia 10/11: 17–29.

Comisión Centroamericana de Ambiente y Desarrollo (CCAD). 2002. Política Centroamericana para la Conservación y Uso Racional de los Humedales. CCAD, San José, Costa Rica.

Coney, P.J. 1982. Plate tectonic constraints on the biogeography of Middle America and the Caribbean region. Annals of the Missouri Botanical Garden 69: 432–443.

Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. Science 199: 1302–1310.

Cornelius, S.E., Ulloa, M.A., Castro, J.C., Mata del Valle, M. and Robinson, D.C. 1991. Management of olive ridley sea turtles (*Lepidochelys olivacea*) nesting at Playas Nancite and Ostional, Costa Rica. *In*: Robinson, J.G. and Redford, K.H. (eds), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, Illinois, USA, pp. 111–135.

Corves, C., Gray, D. and Zisman, S. 1989. The use of LANDSAT TM imagery for vegetation mapping in Belize. *In*: Furley, P. (ed.), Advances in Environmental and Biogeographical Research in Belize (Biogeographical Monographs No. 3). Department of Geography, University of Edinburgh, Edinburgh, Scotland, pp. 131–136.

Costa, C.S.B. and Davy, A.J. 1992. Coastal saltmarsh communities of Latin America. *In*: Seeliger, U. (ed.), Coastal Plant Communities of Latin America. Academic Press, San Diego, California, USA, pp. 179–199.

Cowardin, L.M., Carter, V., Golet, F.C. and LaRoe, E.T. 1979. Classification of Wetlands and Deepwater Habitats of the United States. U.S. Fish and Wildlife Service, FWS/OBS-79/31, Washington, DC, USA, 103 pp.

Cubit, J.D., Thompson, R.C., Caffey, H.M. and Windsor, D.M. 1988. Hydrographic and meteorological studies of a Caribbean fringing reef at Punta Galeta, Panamá: hourly and daily variations for 1977–1985. Smithsonian Contributions to Marine Science 32: 1–220.

D'Croz, L. and Kwiecinski, B. 1980. Contribución de los manglares a las pesquerías de la Bahía de Panamá. Revista de Biología Tropical 28: 13–29.

Davidson, I. and Gauthier, M. 1993. Wetland Conservation in Central America. Report 93-3 of the North American Wetlands Conservation Council (Canada), Ottawa, Ontario, Canada.

Davy, A.J. and Costa, C.S.B. 1992. Development and organization of saltmarsh communities. *In*: Seeliger, U. (ed.), Coastal Plant Communities of Latin America. Academic Press, San Diego, CA, pp. 157–178.

Dawes, C., McCoy, E. and Heck, K. 1991. The tropical Western Atlantic including the Caribbean Sea. *In*: Mathieson, A. and Nienhuis, P. (eds), Ecosystems of the World 24: Intertidal and Littoral Ecosystems. Elsevier, Amsterdam, London, pp. 215–233.

de Weerdt, W.H., Rützler, K. and Smith, K.P. 1991. The Chalinidae (Porifera) of Twin Cays, Belize, and adjacent waters. Proceedings of the Biological Society of Washington 104: 189–205.

Denslow, J.S. 1987. Tropical rainforest gaps and tree species diversity. Annual Review of Ecology and Systematics 18: 431–452.

DeWitt, C.B. 1995. Ecology and ethics: relation of religious belief to ecological practice in the biblical tradition. Biodiversity and Conservation 4: 838–848.

Dickerman, R.W. 1975. Nine new specimen records for Guatemala. The Wilson Bulletin 87: 412–413.

Dickerman, R.W. 1977. Three more new specimen records for Guatemala. The Wilson Bulletin 89: 612–613.

Dittle, A., Epifanio, C. and Lizano, O. 1991. Flux of crab larvae in a mangrove creek in the Gulf of Nicoya, Costa Rica. Estuarine, Coastal and Shelf Science 32: 129–140.

Dixon, M.G. 1994. The Ramsar convention and conservation of non-waterfowl species. Ramsar Newsletter 19: 3.

Donnelly, M.A. 1994. Amphibian diversity and natural history. *In*: McDade, L.A., Bawa, K.S., Hespenheide, H.A. and Hartshorn, G.S. (eds), La Selva: Ecology and Natural History of a Neotropical Rainforest. University of Chicago Press, Chicago, Illinois, USA, pp. 199–209.

Duellman, W.E. 1966. The Central American herpetofauna: an ecological perspective. Copeia 1966: 701–719.

Duellman, W.E. 1970. The hylid frogs of Middle America. Monographs of the Museum of Natural History of the University of Kansas 1: 1–753.

Duellman, W.E. 1988. Patterns of species diversity in anuran amphibians in the American tropics. Annals of the Missouri Botanical Garden 75: 79–104.

Duellman, W.E. 1990. Herpetofaunas in neotropical rainforests: comparative composition, history, and resource use. *In*: Gentry, A.H. (ed.), Four Neotropical Rainforests. Yale University Press, New Haven, Connecticut, USA, pp. 455–505.

Dugan, P. (ed.). 1993. Wetlands in Danger. Mitchell Beazley, London, UK, 187 pp.

Duke, N.C. and Pinzón, M.Z.S. 1992. Aging *Rhizophora* seedlings from leaf scar nodes: a technique for studying recruitment and growth in mangrove forests. Biotropica 24: 173–186.

Durán, L.C. 1977. Situacion actual de los bosques salados en El Salvador. Agricultura en El Salvador 16: 44–53.

Dyrcz, A. 1984. Breeding biology of the mangrove swallow *Tachycineta albilinea* and the grey-breasted martin *Progne chalybea* at Barro Colorado Island, Panama. Ibis 126: 59–66.

Earle, S.A. 1972. A review of the marine plants of Panamá. Bulletin of the Biological Society of Washington 2: 69–88.

Eisenberg, J.F. 1989. Mammals of the Neotropics, Vol. 1: Panamá, Colombia, Venezuela, Guyana, Suriname, French Guiana. University of Chicago Press, Chicago, IL, USA, 449 pp.

Ellison, A.M. and Farnsworth, E.J. 1990. The ecology of Belizean mangrove-root fouling communities. I. Epibenthic fauna are barriers to isopod attack of red mangrove roots. Journal of Experimental Marine Biology and Ecology 142: 91–104.

Ellison, A.M. and Farnsworth, E.J. 1992. The ecology of Belizean mangrove-root fouling communities: patterns of distribution and abundance and effects on root growth. Hydrobiologia 247: 87–98.

Ellison, A.M. and Farnsworth, E.J. 1993. Seedling survivorship, growth, and response to disturbance in Belizean mangal. American Journal of Botany 80: 1137–1145.

Ellison, A.M. and Farnsworth, E.J. 1996. Anthropogenic disturbance to Caribbean mangrove ecosystems: past impacts, present trends, and future predictions. Biotropica 28: 549–565.

Ellison, A.M. and Farnsworth, E.J. 2001. Mangrove communities. *In*: Bertness, M.D., Gaines, S.D. and Hay, M.E. (eds), Marine Community Ecology. Sinauer Associates, Sunderland, MA, USA, pp. 423–442.

Ellison, A.M., Farnsworth, E.J. and Twilley, R.R. 1996. Facultative mutualism between red mangroves and root-fouling sponges in Belizean mangal. Ecology 77: 2431–2444.

Emmons, L.H. 1990. Neotropical Rainforest Mammals: A Field Guide. University of Chicago Press, Chicago, IL, USA, 281 pp.

Farnsworth, E.J. and Ellison, A.M. 1991. Patterns of herbivory in Belizean mangrove swamps. Biotropica 23: 555–567.

Farnsworth, E.J. and Ellison, A.M. 1993. Dynamics of herbivory in Belizean mangal. Journal of Tropical Ecology 9: 435–453.

Farnsworth, E.J. and Ellison, A.M. 1996. Scale-dependent spatial and temporal variability in biogeography of mangrove-root epibiont communities. Ecological Monographs 66: 45–66.

Farnsworth, E.J. and Ellison, A.M. 1997. Global conservation ecology of mangrove ecosystems. Ambio 26: 328–334.

Feller, I.C. 1995. Effects of nutrient enrichment on growth and herbivory of dwarf red mangrove (*Rhizophora mangle*). Ecological Monographs 65: 477–506.

Feller, I.C. and Mathis, W.N. 1997. Primary herbivory by wood-boring insects along an architectural gradient of *Rhizophora mangle*. Biotropica 29: 440–451.

Feller, I.C. and McKee, K.L. 1999. Small gap creation in Belizean mangrove forests by a wood-boring insect. Biotropica 31: 607–616.

Feller, I.C., McKee, K.L., Whigham, D.F. and O'Neill, J.P. 2003. Nitrogen vs. phosphorus limitation across an ecotonal gradient in a mangrove forest. Biogeochemistry 62: 145–175.

Finlayson, C.M. and van der Valk, A.G. 1995. Wetland classification and inventory: a summary. Vegetatio 118: 185–192.

Finlayson, C.M., Davidson, N.C., Spiers, A.G. and Stevenson, N.J. 1999. Global wetland inventory – current status and future priorities. Marine and Freshwater Research 50: 717–727.

Fosberg, F.R., Stoddart, D.R., Sachet, M.-H. and Spellman, D.L. 1982. Plants of the Belize cays. Atoll Research Bulletin 258: 1–77.

Frederick, P.C., Sandoval, J.C., Luthin, C. and Spalding, M. 1997. The importance of the Caribbean coastal wetlands of Nicaragua and Honduras to Central American populations of waterbirds and Jabiru storks (*Jabiru mycteria*). Journal of Field Ornithology 68: 287–295.

Fuchs, H.P. 1970. Ecological and palynological notes on *Pelliciera rhizophorae*. Acta Botanica Neerlandica 19: 884–894.

Garcia, M.L.E. 1983. Hydrology of Central America. Beiträge zur Hydrologie 9: 24–40.

Garrity, S.D. and Levings, S.C. 1990. Effects of an oil spill on the gastropods of a tropical intertidal reef flat. Marine Environmental Research 30: 119–153.

Garrity, S.D., Levings, S.C. and Burns, K.A. 1994. The Galeta oil spill. 1. Long-term effects on the physical structure of the mangrove fringe. Estuarine, Coastal and Shelf Science 38: 327–348.

Gentry, A.H. 1982. Phytogeographic patterns as evidence for a Choco refuge. *In*: Prance, G.T. (ed.), Biological Diversification in the Tropics. Columbia University Press, New York, pp. 112–136.

Gentry, A.H. (ed.). 1990. Four Neotropical Rainforests. Yale University Press, New Haven, Connecticut, USA.

Glooschenko, W.A., Tarnocai, C., Zoltai, S. and Glooschenko, V. 1993. Wetlands of Canada and Greenland. *In*: Whigham, D.F., Dykyjová, D. and Hejný, S. (eds), Wetlands of the World: Inventory, Ecology and Management, Volume I. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 415–514.

Glynn, P.W. 1972. Observations on the ecology of the Caribbean and Pacific coasts of Panamá. Bulletin of the Biological Society of Washington 2: 13–30.

Golley, F.B., McGinniw, J.T., Clements, R.G., Child, G.I. and Duever, M.J. 1975. Mineral Cycling in a Tropical Moist Forest Ecosystem. University of Georgia Press, Athens, GA, USA, 248 pp.

Gomez, M. and Winkler, S. 1991. Bromelias en manglares del Pacifico de Guatemala. Revista de Biología Tropical 39: 207–214.

Gómez, L.D. 1984. Las Plantas Acuáticas y Anfibias de Costa Rica y Centroamérica: 1. Liliopsida. Editorial Universidad Estatal a Distancia, San José, Costa Rica.

Gómez, L.D. 1985. Vegetación de Costa Rica: Apuntes para una Biogeografía Costarricense. 1. Vegetación y Clima de Costa Rica. Editorial Universidad Estatal a Distancia, San José, Costa Rica.

Government of Honduras. 1993. Ley General del Ambiente. Decreto Ejecutivo No. 104-93, 82 pp.

Graham, A. 1977. New records of *Pelliciera* (Theaceae/Pelliceriaceae) in the Tertiary of the Caribbean. Biotropica 9: 48–52.

Graham, A. 1987. Tropical American tertiary floras and paleoenvironments: Mexico, Costa Rica, and Panamá. American Journal of Botany 74: 1519–1531.

Graham, A. 1995. Diversification of Gulf/Caribbean mangrove communities through Cenozoic time. Biotropica 27: 20–27.

Granger, O. 1991. Climate change interactions in the greater Caribbean. The Environmental Professional 13: 43–58.

Greenfield, D.W. and Johnson, R.K. 1981. The blennioid fishes from Belize and Honduras, Central America, with comments on their systematics, ecology, and distribution (Blenniidae, Chaenopsidae, Labrisomidae, Tripterygiidae). Fieldiana Zoology (new series) 8: 1–106.

Griesinger, B. and Gladwell, J.S. 1993. Hydrology and water resources of tropical Latin America and the Caribbean. *In*: Bonell, M., Hufschmidt, M.M. and Gladwell, J.S. (eds), Hydrology and Water Management in the Humid Tropics. Cambridge University Press, Cambridge, UK, pp. 84–98.

Groombridge, B. (ed.). 1992. Global Biodiversity: Status of the Earth's Living Resources. Chapman and Hall, London, UK, 585 pp.

Guzmán, H.M., Jackson, J.B.C. and Weil, E. 1991. Short-term ecological consequences of a major oil spill on Panamanian subtidal reef corals. Coral Reefs 10: 1–12.

Guzmán, H.M. and Jiménez, C.E. 1992. Contamination of coral reefs by heavy metals along the caribbean coast of Central America (Costa Rica and Panama). Marine Pollution Bulletin 24: 554–561.

Hagberg, H.A. 1970. Un estudio ecológico de la Bahía de Bluefield, Nicaragua con especial referencia a las poblaciones de ostras, *Crassostrea rhizophorae* Guilding. Boletín Técnico, Proyecto Regional de Desarrollo Pesquero en Centroamérica 3: 1–19.

Hall, P., Chase, M.R. and Bawa, K.S. 1994a. Low genetic variation but high population differentiation in a common tropical forest species. Conservation Biology 8: 471–481.

Hall, P., Orrell, L.C. and Bawa, K.S. 1994b. Genetic diversity and mating system in a tropical tree, *Carapa guianensis* (Meliaceae). American Journal of Botany 81: 1104–1111.

Hartshorn, G.S. 1983. Plants. Introduction. *In*: Janzen, D.H. (ed.), Costa Rican Natural History. University of Chicago Press, Chicago, IL, pp. 118–183.

Hartshorn, G.S. 1988. Tropical and subtropical vegetation of meso-America. *In*: Barbour, M.G. and Billings, W.D. (eds), North American Terrestrial Vegetation. Cambridge University Press, Cambridge, UK, pp. 365–390.

Hartshorn, G.S., Nicolait, L., Hartshorn, L., Bevier, G., Brightman, R., Cal, J., Cawich, A., Davidson, W., DuBois, R., Dyer, C., Gibson, J., Hawley, W., Leonard, J., Nicolait, R., Weyer, D., White, H. and Wright, C. 1984. Belize Country Environmental Profile. Trejos. Hermanos Sucs. S.A. San José, Costa Rica, 151 pp.

Hartshorn, G.S. and Hammel, B.E. 1994. Vegetation types and floristic patterns. *In*: McDade, L.A., Bawa, K.S., Hespenheide, H.A. and Hartshorn, G.S. (eds), La Selva: Ecology and Natural History of a Neotropical Rainforest. University of Chicago Press, Chicago, Illinois, USA, pp. 73–89.

Hartup, B.K. 1994. Community conservation in Belize: demography, resource use, and attitudes of participating landowners. Biological Conservation 69: 235–241.

Hay, M.E. 1984. Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? Ecology 65: 446–454.

Hay, M.E. 1991. Marine-terrestrial contrasts in the ecology of plant chemical defenses against herbivores. Trends in Ecology and Evolution 6: 362–366.

Hay, M.E., Fenical, W. and Gustafson, K. 1987. Chemical defense against diverse coral-reef herbivores. Ecology 68: 1581–1591.

Herbst, H.V. 1960. Copepoden (Crustacea, Entomostraca) aus Nicaragua und Südperu. Gewässer und Abwässer 27: 27–54.

Holdridge, L.R. 1967. Life Zone Ecology. Tropical Science Center, San José, Costa Rica, 206 pp.

Holdridge, L.R. and Budowski, G. 1956. Report of an ecological survey of the Republic of Panama. Caribbean Forester 17: 92–110.

Holdridge, L.R., Grenke, W.C., Hathaway, W.H., Liang, T. and Tosi, J.A., Jr. 1971. Forest Environments in Tropical Life Zones: A Pilot Study. Pergamon Press, Oxford, UK, 747 pp.

Horwich, R.H. and Lyon, J. 1990. A Belizean Rain Forest. Orang-utan Press, Gays Mills, Wisconsin, USA, 420 pp.

Humann, P. 1989. Reef Fish Identification: Florida, Caribbean, Bahamas. New World Publications, Orlando, Florida, USA, 288 pp.

Humann, P. 1992. Reef Creature Identification: Florida, Caribbean, Bahamas. New World Publications, Orlando, Florida, USA, 344 pp.

Humann, P. 1993. Reef Coral Identification: Florida, Caribbean, Bahamas. New World Publications, Orlando, Florida, USA, 252 pp.

Hunter, L.A. 1988. Status of the endemic Atitlán grebe of Guatemala: is it extinct? Condor 90: 906–912.

Incer, J. 1976. Geography of Lake Nicaragua. *In*: Thorson, T.B. (ed.), Investigations of the Ichthyofauna of Nicaraguan Lakes. University of Nebraska–Lincoln, Lincoln, Nebraska, USA, pp. 2–15.

IUCN-ORCA. n. d. Wetlands Programme for Central America. World Conservation Union Regional Office for Central America, Turrialba, Costa Rica, 20 pp.

Jackson, J.B.C., Cubit, J.D., Keller, B.D., Batista, V., Burns, K., Caffey, H.M., Cladwell, R.L., Garrity, S.D., Getter, C.D., Gonzalez, C., Guzman, H.M., Kaufmann, K.W., Knap, A.H., Levings, S.C., Marshall, M.J., Steger, R., Thompson, R.C. and Weil, E. 1989. Ecological effects of a major oil spill on Panamanian coastal marine communities. Science 243: 37–44.

Jackson, J.B.C. and Kaufmann, K.W. 1987. *Diadema antillarum* was not a keystone predator in cryptic reef environments. Science 235: 687–689.

Janzen, D.H. 1976. The microclimate difference between a deciduous forest and adjacent riparian forest in Guanacaste Province, Costa Rica. Brenesia 8: 29–33.

Janzen, D.H. 1978. Description of a *Pterocarpus officinalis* (Leguminosae) monoculture in Corcovado National Park, Costa Rica. Brenesia 14/15: 305–309.

Janzen, D.H. 1985. Mangroves: where's the understory? Journal of Tropical Ecology 1: 89–92.

Janzen, D.H. and Schoener, T.W. 1968. Differences in insect abundance and diversity between wetter and dried sites during a tropical dry season. Ecology 49: 96–110.

Jiménez, J.A. 1984. A hypothesis to explain the reduced distribution of the mangrove *Pelliciera rhizophorae* Tr. & Pl. Biotropica 16: 304–308.

Jiménez, J.A. 1987. A clarification on the existence of *Rhizophora* species along the Pacific coast of Central America. Brenesia 28: 25–32.

Jiménez, J.A. 1988. The dynamics of *Rhizophora racemosa* Meyer, forests on the Pacific coast of Costa Rica. Brenesia 30: 1–12.

Jiménez, J.A. 1990. The structure and function of dry weather mangroves on the Pacific coast of Central America, with emphasis on *Avicennia bicolor* forests. Estuaries 13: 182–192.

Jiménez, J.A. 1992. Mangrove forests of the Pacific coast of Central America. *In*: Seeliger, U. (ed.), Coastal Plant Communities of Latin America. Academic Press, Incorporated, San Diego, California, USA, pp. 259–267.

Jiménez, J.A., Lugo, A.E. and Cintron, G. 1985. Tree mortality in mangrove forests. Biotropica 17: 177–185.

Jiménez, J.A. and Sauter, K. 1991. Structure and dynamics of a mangrove forests along a flood gradient. Estuaries 14: 49–56.

Jiménez, J.A. and Soto, R. 1985. Patrones regionales en la estructura y composición florística de los manglares de la Costa Pacífica de Costa Rica. Revista de Biología Tropical 33: 25–37.

Junk, W.J. 1993. Wetlands of tropical South America. *In*: Whigham, D.F., Dykyjová, D. and Hejný, S. (eds), Wetlands of the World: Inventory, Ecology and Management, Vol. 1. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 679–740.

Kathiresan, K. and Bingham, B.L. 2001. Biology of mangroves and mangrove ecosystems. Advances in Marine Biology 40: 84–251.

Keller, B.D. and Jackson, J.B.C. (eds). 1991. Long-term Assessment of the Oil Spill at Bahía Las Minas, Panamá, Interim Report. U.S. Department of the Interior Minerals Management Service Gulf of Mexico OCS Region, New Orleans, Louisiana, USA, 450 pp.

Kellman, M. 1979. Soil enrichment by neotropical savanna trees. Journal of Ecology 67: 565–577.

Kellman, M. 1984. Synergistic relationships between fire and low soil fertility in neotropical savannas: a hypothesis. Biotropica 16: 158–160.

Kellman, M. 1985a. Forest seedling establishment in neotropical savannas: transplant experiments with *Xylopia frutescens* and *Calophyllum brasiliense*. Journal of Biogeography 12: 373–379.

Kellman, M. 1985b. Nutrient retention by savanna ecosystems. III. Response to artificial loading. Journal of Ecology 73: 963–972.

Kellman, M., Hudson, J. and Sanmugadas, K. 1982. Temporal variability in atmospheric nutrient influx to a tropical ecosystem. Biotropica 14: 1–9.

Kellman, M. and Miyanishi, K. 1982. Forest seedling establishment in neotropical savannas: observations and experiments in the Mountain Pine Ridge savanna, Belize. Journal of Biogeography 9: 193–206.

Kellman, M., Miyanishi, K. and Hiebert, P. 1985. Nutrient retention by savanna ecosystems. II. Retention after fire. Journal of Ecology 73: 953–962.

Kellman, M. and Sanmugadas, K. 1985. Nutrient retention by savanna ecosystems. I. Retention in the absence of fire. Journal of Ecology 73: 935–951.

Kellman, M., Tackaberry, R., Brokaw, N. and Meave, J. 1994. Tropical gallery forests. National Geographic Research and Exploration 10: 92–103.

Kelly, M.G. 1991. Remote sensing of the near-shore benthic environment. *In*: Mathieson, A.C. and Nienhuis, P.H. (eds), Ecosystems of the World 24: Intertidal and Littoral Ecosystems. Elsevier Scientific Publishers, Amsterdam, The Netherlands, pp. 461–473.

Klekowski, E.J., Jr., Corredor, J.E., Lowenfeld, R., Klekowski, E.H. and Morell, J.M. 1994a. Using mangroves to screen for mutagens in tropical marine environments. Marine Pollution Bulletin 28: 346–350.

Klekowski, E.J., Jr., Corredor, J.E., Morrell, J.M. and Delcastillo, C.A. 1994b. Petroleum pollution and mutation in mangroves. Marine Pollution Bulletin 28: 166–169.

Knight, D.H. 1975. A phytosociological analysis of species-rich tropical forest on Barro Colorado Island, Panama. Ecological Monographs 45: 259–284.

Knowlton, N. and Jackson, J.B.C. 1994. New taxonomy and niche partitioning on coral reefs: jack of all trades or master of some? Trends in Ecology and Evolution 9: 7–9.

Knowlton, N., Weil, E., Weigt, L.A. and Guzman, H.M. 1992. Sibling species in *Montastraea annularis*, coral bleaching, and the coral climate record. Science 255: 330–333.

Lagueux, C.J. 1991. Economic analysis of sea turtle eggs in a coastal community on the Pacific coast of Honduras. *In*: Robinson, J.G. and Redford, K.H. (eds), Neotropical Wildlife Use and Conservation. University of Chicago Press, Chicago, Illinois, USA, pp. 136–144.

Lara, O.A.M. and Zamora, J.A.V. 1995. Poliquetos (Annelida: Polychaeta) del estero de Jaltepeque, El Salvador, una comparación 1959–1991. Revista de Biología Tropical 43: 195–205.

Lee, J.C. 1996. The Amphibians and Reptiles of the Yucatán Peninsula. Comstock Publishing Associates, Ithaca, New York, USA, 500 pp.

Lee, J.C. 2000. A Field Guide to the Amphibians and Reptiles of the Maya World. Comstock Publishing Associates, Ithaca, New York, USA, 402 pp.

Lee, S.Y. 1999. Tropical mangrove ecology: physical and biotic factors influencing ecosystem structure and function. Australian Journal of Ecology 24: 355–366.

Lefebvre, G. and Poulin, B. 1996. Seasonal abundance of migrant birds and food resources in Panamanian mangrove forests. Wilson Bulletin 108: 748–759.

Lefebvre, G. and Poulin, B. 1997. Bird communities in Panamanian black mangroves: potential effects of physical and biotic factors. Journal of Tropical Ecology 13: 97–113.

Leigh, E.G., Jr., Rand, A.S. and Windsor, D.M. (eds). 1982. The Ecology of a Tropical Forest: Seasonal Rhythms and Long-term Changes. Smithsonian Institution Press, Washington, D.C., USA, 468 pp.

Lessios, H.A. 1988. Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? Annual Review of Ecology and Systematics 19: 371–394.

Levings, S.C., Garrity, S.D. and Burns, K.A. 1994. The Galeta oil spill. 3. Chronic reoiling, long-term toxicity of hydrocarbon residues and effects on epibiota in the mangrove fringe. Estuarine, Coastal and Shelf Science 38: 365–395.

Leyden, B.W. 1984. Guatemalan forest synthesis after Pleistocene aridity. Proceedings of the National Academy of Sciences, USA 81: 4856–4859.

Lieberman, D., Lieberman, M., Peralta, R. and Hartshorn, G.S. 1985a. Mortality patterns and stand turnover rates in a wet tropical forest in Costa Rica. Journal of Ecology 73: 915–924.

Lieberman, M., Lieberman, D., Hartshorn, G.S. and Peralta, R. 1985b. Small-scale altitudinal variation in lowland wet tropical forest vegetation. Journal of Ecology 73: 505–516.

Linhart, Y.B. 1980. Local biogeography of plants on a Caribbean atoll. Journal of Biogeography 7: 159–171.

Littler, D.S., Littler, M.M., Bucher, K. and Norris, J. 1989. Marine Plants of the Caribbean. Smithsonian Institution Press, Washington, D.C., 263 pp.

Lötschert, W. 1955. La vegetación de El Salvador. Comunicaciones, Universidad de El Salvador, Instituto Tropical de Investigaciones Cientificas 4: 65–79.

Lowe-McConnell, R.H. 1987. Ecological Studies in Tropical Fish Communities. Cambridge University Press, Cambridge, UK, 382 pp.

Lugo, A.E. 1980. Mangrove ecosystems: successional or steady state? Biotropica 12(Suppl.): 65–72.

Lugo, A.E. 1986. Mangrove understory: an expensive luxury? Journal of Tropical Ecology 2: 287–288.

Lugo, A.E. and Snedaker, S.C. 1974. The ecology of mangroves. Annual Review of Ecology and Systematics 5: 39–64.

Lundell, C.L. 1937. The Vegetation of Petén. Carnegie Institution of Washington, Washington, D.C., USA, 224 pp.

Lyster, S. 1985. International Wildlife Law. Grotius Ltd., Llandysul, UK, 470 pp.

Mabberly, D.J. 1993. The Plant-Book. Cambridge University Press, Cambridge, UK, 707 pp.

MacDougall, A. and Kellman, M. 1993. The understorey light regime and patterns of tree seedlings in tropical riparian forest patches. Journal of Biogeography 19: 667–675.

Mathis, W.N. 1989. A review of the beach flies of the Caribbean and Gulf of Mexico. Proceedings of the Biological Society of Washington 102: 590–608.

Matthews, E. and Fung, I. 1987. Methane emission from natural wetlands: global distribution, area and environmental characteristics of sources. Global Biogeochemical Cycles 1: 61–86.

Mayo Meléndez, E. 1965. Algunas caracteristicas ecológicas de los bosques inundables de Darién, Panama, con miras a su posible utilización. Turrialba 15: 336–347.

McCarthy, R.M. 1994. Cambios ocurridos con la ley de conservación de la vida silvestre en la relación humedales de Costa Rica – humedales protegidos por la sistema de area protegidas de Costa Rica. 20 pp. Unpublished document obtained from R. McCarthy, Programa de Humedales para Mesoamérica, Costa Rica.

McCoy, M.B. and Rodríguez, J.M. 1994. Cattail (*Typha dominguensis*) eradication methods in the restoration of a tropical, seasonal, freshwater marsh. *In*: Mitsch, W.J. (ed.), Global Wetlands: Old World and New. Elsevier Science B.V., Amsterdam, The Netherlands, pp. 469–482.

McDade, L.A., Bawa, K.S., Hespenheide, H.A. and Hartshorn, G.S. (eds). 1994. La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago, Illinois, USA, 486 pp.

McHargue, L.A. and Hartshorn, G.S. 1983. *Carapa guianensis* (Cedro Maco, Caobilla). *In*: Janzen, D.H. (ed.), Costa Rican Natural History. University of Chicago Press, Chicago, Illinois, USA, pp. 206–207.

McKee, K., Mendelssohn, I. and Hester, M. 1988. Reexamination of pore water sulfide concentrations redox potentials near the aerial roots of *Rhizophora mangle* and *Avicennia germinans*. American Journal of Botany 79: 1352–1359.

McKee, K.L. 1993. Soil physicochemical patterns and mangrove species distribution – reciprocal effects? Journal of Ecology 81: 477–488.

McRoy, C.P. and Helfferich, C. 1980. Applied aspects of seagrasses. *In*: Phillips, R.C. and McRoy, C.P. (eds), Handbook of Seagrass Biology: An Ecosystem Perspective. Garland Press, New York, USA, pp. 297–344.

Meave, J. and Kellman, M. 1994. Maintenance of rain forest diversity in riparian forests of tropical savannas: implications for species conservation during Pleistocene drought. Journal of Biogeography 21: 121–135.

Meave, J., Kellman, M., MacDougall, A. and Rosales, J. 1991. Riparian habitats as tropical forest refugia. Global Ecology and Biogeography Letters 1: 69–76.

Miller, R.R. 1966. Geographical distribution of Central American freshwater fishes. Copeia 1966: 773–802.

Ministerio de Recursos Naturales, Energía y Minas/Dirección General de Vida Silvestre (MIRENEM/DGVS). 1994a. Memórias I Taller de Pariticipación y Consulta Estrategía Nacional de Conservación y Desarrollo Sostenible de Humedales. MIRENEM/DGVS, San José, Costa Rica, 23 pp.

Ministerio de Recursos Naturales, Energía y Minas/Dirección General de Vida Silvestre (MIRENEM/DGVS). 1994b. Memórias II Taller de Pariticipación y Consulta Estrategía Nacional de Conservación y Desarrollo Sostenible de Humedales. MIRENEM/DGVS, San José, Costa Rica, 27 pp.

Moll, D. 1986. The distribution, status, and level of exploitation of the freshwater turtle *Dermatemys mawei* in Belize, Central America. Biological Conservation 35: 87–96.

Moll, D. 1989. Food and feeding behavior of the turtle *Dermatemys mawei*, in Belize. Journal of Herpetology 23: 445–447.

Moll, E.O. and Legler, J.M. 1971. The life history of a neotropical slider turtle, *Pseudemys scripta* (Schoepff), in Panamá. Scientific Bulletin of the Los Angeles County Museum of Natural History 11: 1–102.

Montgomery, W.L. 1990. Zoogeography, behavior and ecology of coral-reef fishes. *In*: Dubinsky, Z. (ed.), Coral Reefs. Elsevier Scientific Publishers, Amsterdam, The Netherlands, pp. 329–364.

Morales-Vela, B., Olivera Gomez, D., Reynolds, J.E., III and Rathbun, G.B. 2000. Distribution and habitat use by manatees (*Trichechus manatus manatus*) in Belize and Chetumal Bay, Mexico. Biological Conservation 95: 67–75.

Mortimer, J.A. 1981. The feeding ecology of the West Caribbean green turtle (*Chelonia mydas*) in Nicaragua. Biotropica 13: 49–58.

Murren, C.J. and Ellison, A.M. 1996. Effects of habitat, plant size, and floral display on male and female reproductive success of the neotropical orchid *Brassavola nodosa*. Biotropica 28: 30–41.

Muzik, K. 1982. Octocorallia (Cnidaria) from Carrie Bow Cay, Belize. *In*: Rützler, K. and Macintyre, I.G. (eds), The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize. I. Structure and Communities. Smithsonian Institution Press, Washington, D.C., USA, pp. 303–310.

Myers, C.W. and Rand, A.S. 1969. Checklist of amphibians and reptiles of Barro Colorado Island, Panama, with comments on faunal change and sampling. Smithsonian Contributions to Zoology 10: 1–11.

Myers, R.L. 1984. Growth form, growth characteristics, and phenology of *Raphia taedigera* in Costa Rican palm swamps. Principes 28: 64–72.

Myers, R.L. 1990. Palm swamps. *In*: Lugo, A.E., Brinson, M. and Brown, S. (eds), Forested Wetlands. Elsevier Science Publishers, Amsterdam, The Netherlands, pp. 267–286.

National Oceanic and Atmospheric Administration (NOAA) 2002. Historical hurricane tracks database. http://hurricane.csc.noaa.gov/hurricanes/.

Neumann, C.J., Jarvinen, B.R. McAdie, C.J. and Elms J.D. 1992. Tropical Cyclones of the North Atlantic Ocean, 1871–1992. National Climatic Data Center, Asheville, North Carolina, USA, 193 pp.

Olmsted, I. 1993. Wetlands of Mexico. *In*: Whigham, D.F., Dykyjová, D. and Hejný, S. (eds), Wetlands of the World: Inventory, Ecology and Management, Volume I. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 637–678.

Patterson, S.G. 1986. Mangrove Community Boundary Interpretation and Detection of Areal Changes on Marco Island, Florida: Application of Digital Image Processing and Remote Sensing Techniques. United States Fish and Wildlife Service, Biological Report 86(10), 87 pp.

Perkins, J.S. and Carr, A., III. 1985. The Belize Barrier Reef: status prospects for conservation management. Biological Conservation 31: 291–301.

Perry, D.M. 1988. Effects of associated fauna on growth and productivity in the red mangrove. Ecology 69: 1064–1075.

Phillips, P.C. 1981. Diversity and fish community structure in a Central American mangrove embayment. Revista de Biología Tropical 29: 227–236.

Phillips, R.C. and McRoy, C.P. (eds). 1990. Seagrass Research Methods. UNESCO, Paris, France, 210 pp.

Phillips, R.C. and Meñez, E.G. 1988. Seagrasses. Smithsonian Contributions to the Marine Sciences 34: 1–104

Phillips, R.C., Vadas, R.L. and Ogden, N. 1982. The marine algae and seagrasses of the Miskito Bank, Nicaragua. Aquatic Botany 13: 187–915.

Platt, S.G. and Thorbjarnarson, J.B. 2000a. Population status and conservation of Morelet's crocodile (*Crocodylus moreletii*) in northern Belize. Biological Conservation 96: 21–29.

Platt, S.G. and Thorbjarnarson, J.B. 2000b. Status and conservation of the American crocodile. *Crodocylus acutus*, in Belize. Biological Conservation 96: 13–20.

Polisar, J. and Horwich, R.H. 1994. Conservation of the large, economically important river turtle *Dermatemys mawii* in Belize. Conservation Biology 8: 338–340.

Pool, D.J., Snedaker, S.C. and Lugo, A.E. 1977. Structure of the mangrove forests in Florida, Puerto Rico, Mexico, and Costa Rica. Biotropica 9: 195–212.

Pope, K.O., Rey-Benayas, J.M. and Paris, J.F. 1994. Radar remote sensing of forest and wetland ecosystems in the Central American tropics. Remote Sensing of Environment 48: 205–219.

Porter, J.W. 1972. Ecology and species diversity of coral reefs on opposite sides of the isthmus of Panamá. Bulletin of the Biological Society of Washington 2: 89–116.

Portig, W.H. 1976. The climate of Central America. *In*: Schwerdtfeger, W. (ed.), World Survey of Climatology, Vol. 12: Climates of Central and South America. Elsevier Scientific Publishing Co, New York, USA, pp. 405–478.

Pringle, C.M. and Triska, F.J. 1991. Effects of geothermal groundwater on nutrient dynamics of a lowland Costa Rican stream. Ecology 72: 951–965.

Quesada, Q.R., Madrigal, C.E., Alfaro, M.J., Pacheco, U.O. and Zamora, M.E. 1985. Crecimiento y supervivencia del ostión de manglar (*Crassostrea rhizophorae* Guilding, 1828), traslado de Estero Vizcaya, Costa del Caribe a estanques de cultivo de camarones en Chomes, Costa Pacífica de Costa Rica. Revista de Biología Tropical 33: 7–12.

Rabinowitz, D. 1978a. Dispersal properties of mangrove propagules. Biotropica 10: 47–57.

Rabinowitz, D. 1978b. Early growth of mangrove seedlings in Panama, and an hypothesis concerning the relationship of dispersal and zonation. Journal of Biogeography 5: 113–133.

Rabinowitz, D. 1978c. Mortality and initial propagule size in mangrove seedlings in Panama. Journal of Ecology 66: 45–51.

Rabinowitz, D. 1985. *Pelliciera rhizophorae* Triana & Planchon. Unpublished manuscript prepared for IUCN Plant Red Data Book, 2 pp.

Ramirez, C.A.R., Lopez, S.M.I. and Szelistowski, W.A. 1990. Composition and abundance of ichthyoplankton in a Gulf of Nicoya mangrove estuary. Revista de Biología Tropical 38: 463–466.

Ramsar Convention Bureau. 2002. The Annotated Ramsar List of Wetlands of International Importance. Ramsar Convention Bureau, Gland, Switzerland.

Raven, P.H. and Axelrod, D.I. 1975. History of the flora and fauna of Latin America. American Scientist 63: 420–429.

Reynolds, J.E., III, Szelistowski, W.A. and León, M.A. 1995. Status and conservation of manatees *Trichechus manatus manatus* in Costa Rica. Biological Conservation 71: 193–196.

Ridgely, R.S. and Gwynne, J.A. 1989. A Guide to the Birds of Panama: With Costa Rica, Nicaragua, and Honduras. Princeton University Press, Princeton, New Jersey, USA, 534 pp.

Robertson, A.I. and Duke, N.C. 1987. Mangroves as nursery sites: comparisons of the abundance and species composition of fish and crustaceans in mangroves and other nearshore habitats in tropical Australia. Marine Biology 96: 193–205.

Robertson, D.R., Petersen, C.W. and Brawn, J.D. 1990. Lunar reproductive cycles of benthic-brooding reef fishes: reflections of larval-biology or adult-biology? Ecological Monographs 60: 311–329.

Rojas, D.E., Lara, X. and López, M.I. 1991. Taxonomía del ictioplancton costero del Pacífico Norte de Costa Rica. Revista de Biología Tropical 39: 215–218.

Roth, L.C. 1992. Hurricanes and mangrove regeneration: effects of Hurricane Joan, October 1988, on the vegetation of Isla del Venado, Bluefields, Nicaragua. Biotropica 24: 275–284.

Roth, L.C. and Grijalva, A. 1991. New record of the mangrove *Pelliciera rhizophorae* (Theaceae) on the Caribbean coast of Nicaragua. Rhodora 93: 183–186.

Rützler, K. 1969. The mangrove community, aspects of its structure, faunistics and ecology. *In*: Lagunas Costeras, un Simposio. UNAM-UNESCO, Mexico, pp. 515–535.

Rützler, K. 1987. Recruitment of sponges and their space competitors to settling plates in Twin Cay mangrove habitats. *In*: Rützler, K. (ed.), Caribbean Coral Reef Ecosystems: Progress report 1987. National Museum of Natural History, Smithsonian Institution, Washington, D.C., pp. 23–24.

Rützler, K. (ed.). 1999. Smithsonian CCRE Reports 1996–1998. Smithsonian Institution, Washington, D.C., 36 pp.

Rützler, K. and Feller, C. 1987. Mangrove swamp communities. Oceanus 30: 16–25.

Rützler, K. and Macintyre, I.G. (eds). 1982a. The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize. I. Structure and Communities. Smithsonian Institution Press, Washington, D.C., USA, 539 pp.

Rützler, K. and Macintyre, I.G. 1982b. The habitat distribution and community structure of the barrier reef complex at Carrie Bow Cay, Belize. *In*: Rützler, K. and Macintyre, I.G. (eds), The Atlantic Barrier Reef Ecosystem at Carrie Bow Cay, Belize. I. Structure and Communities. Smithsonian Institution Press, Washington, D.C., USA, pp. 9–45.

Rützler, K. and Smith, K. 1992. Guide to Western Atlantic species of *Cinachyrella* (Porifera: Tetillidae). Proceedings of the Biological Society of Washington 105: 148–164.

Saenger, P., Hegerl, E. and Davie, J. (eds). 1983. Global Status of Mangrove Ecosystems. International Union for Conservation of Nature and Natural Resources,

Sale, P.F. 1994. Taxonomy and coral reef ecology. Trends in Ecology and Evolution 9: 398.

Sand, P.H. (ed.). 1992. The Effectiveness of International Environmental Agreements: A Survey of Existing Legal Instruments. Grotius Publications Limited, Cambridge, UK, 539 pp.

Sanford, R.L., Jr., Paaby, P., Luvall, J.C. and Phillips, E. 1994. Climate, geomorphology, and aquatic systems. *In*: McDade, L.A., Bawa, K.S., Hespenheide, H.A. and Hartshorn, G.S. (eds), La Selva: Ecology and Natural History of a Neotropical Rainforest. University of Chicago Press, Chicago, Illinois, USA, pp. 19–33.

Sarmiento, G. 1984. The Ecology of Neotropical Savannas. Harvard University Press, Cambridge, Massachusetts, USA, 235 pp.

Savage, J.M. 1966. The origins and history of the Central American herpetofauna. Copeia 1966: 719–766.

Savage, J.M. 1975. Systematics and distribution of the Mexican and Central American stream frogs related to *Eleutherodactylus rugulosus*. Copeia 1975: 254–306.

Savage, J.M. 1982. The enigma of the Central American herpetofauna: dispersals or vicariance. Annals of the Missouri Botanical Garden 69: 464–547.

Savage, J.M. 2002. The Amphibians and Reptiles of Costa Rica: A Herpetofauna between Two Continents, between Two Seas. University of Chicago Press, Chicago, IL, USA, 934 pp.

Schemske, D.W. 1980. Evolution of the floral display in the orchid *Brassavola nodosa*. Evolution 34: 489–493.

Scott, D.A. and Carbonell, M. (eds). 1986. A Directory of Neotropical Wetlands. International Union for Conservation of Nature and Natural Resources (IUCN), Cambridge, UK, 684 pp.

Scott, N.J. and Limerick, S. 1983. Reptiles and amphibians: introduction. *In*: Janzen, D.H. (ed.), Costa Rican Natural History. University of Chicago Press, Chicago, Illinois, USA, pp. 351–367.

Scott, N.J., Savage, J.M. and Robinson, D.C. 1983. Checklist of reptiles and amphibians. *In*: Janzen, D.H. (ed.), Costa Rican Natural History. University of Chicago Press, Chicago, Illinois, USA, pp. 367–374.

Slud, P. 1980. The birds of Hacienda Palo Verde, Guanacaste, Costa Rica. Smithsonian Contributions to Zoology 292: 1–92.

Smethurst, D. and Nietschmann, B. 1999. The distribution of manatees (*Trichechus manatus*) in the coastal waterways of Tortuguero, Costa Rica. Biological Conservation 89: 267–274.

Smith, D.L. 1985. Caribbean plate relative motions. *In*: Stehli, F.G. and Webb, S.D. (eds), The Great American Biotic Interchange. Plenum Press, New York, NY, USA, pp. 17–48.

Smith, T.J., III, Chan, H.T., McIvor, C.C. and Robblee, M.B. 1989. Comparisons of seed predation in tropical tidal forests from three continents. Ecology 70: 146–151.

Smith, T.J., III, Robblee, M.B., Wanless, H.R. and Doyle, T.W. 1994. Mangroves, hurricanes, and lightning strikes. BioScience 44: 256–262.

Snedaker, S.C. 1982. Mangrove species zonation: why? *In*: Sen, D.N. and Rajpurohit, K.S. (eds), Contributions to the Ecology of Halophytes. Dr. W. Junk, The Hague, The Netherlands, pp. 111–125.

Snedaker, S.C. and Snedaker, J.G. (eds). 1984. The Mangrove Ecosystem: Research Methods. UNESCO, Paris, France, 251 pp.

Sollins, P., Sancho, M.F., Mata, Ch.R. and Sanford, R.L., Jr. 1994. Soils and soil process research. *In*: McDade, L.A., Bawa, K.S., Hespenheide, H.A. and Hartshorn, G.S. (eds), La Selva: Ecology and Natural History of a Neotropical Rainforest. University of Chicago Press, Chicago, Illinois, USA, pp. 34–63.

Soto, R. and Jiménez, J.A. 1982. Análisis fisonómico estructural del manglar de Puerto Soley, La Cruz, Guanacaste, Costa Rica. Revista de Biología Tropical 30: 161–168.

Spalding, M.D., Blasco, F. and Field, C.D. 1997. World Mangrove Atlas. International Society for Mangrove Ecosystems, Okinawa, Japan, 178 pp.

Standley, P.C. 1931. Flora of the Lancetilla Valley, Honduras. Field Museum of Natural History, Series Botany 10, Publication 283.

Stehli, F.G. and Webb, S.D. 1985a. A kaleidoscope of plates, faunal and floral dispersals, and sea level changes. *In*: Stehli, F.G. and Webb, S.D. (eds), The Great American Biotic Interchange. Plenum Press, New York, NY, USA, pp. 3–16.

Stehli, F.G. and Webb, S.D. (eds). 1985b. The Great American Biotic Interchange. Plenum Press, New York, NY, USA, 532 pp.

Sterrer, W. 1986. The Marine Flora and Fauna of Bermuda. John Wiley and Sons, New York, NY, USA, 724 pp.

Stiles, F.G. and Skutch, A.F. 1989. A Guide to the Birds of Costa Rica. Cornell University Press, Ithaca, New York, USA, 511 pp.

Stiles, F.G. and Smith, S.M. 1977. New information on Costa Rican waterbirds. The Condor 79: 91–97.

Stiling, P.D. 1992. Introductory Ecology. Prentice Hall, Englewood Cliffs, New Jersey, USA, 597 pp.

Stoddart, D.R. 1962. Three Caribbean atolls: Turneffe islands, Lighthouse reef and Glover's reef, British Honduras. Atoll Research Bulletin 87: 1–151.

Stoddart, D.R. 1963. Effects of hurricane Hattie on the British Honduras reefs and cays, October 30–31, 1961. Atoll Research Bulletin 95: 1–142.

Stoddart, D.R. 1969. Post-hurricane changes on the British Honduras reefs and cays: resurvey of 1965. Atoll Research Bulletin 131: 1–36.

Stoddart, D.R. and Johannes, R.E. (eds). 1978. Coral Reefs: Research Methods. UNESCO, Paris, France, 581 pp.

Stoddart, D.R., Fosberg, F.R. and Spellman, D.L. 1982. Cays of the Belize barrier reef and lagoon. Atoll Research Bulletin 256: 1–76.

Stout, R.J. 1981. How abiotic factors affect the distribution of two species of tropical predaceous aquatic bugs (Family: Naucoridae). Ecology 62: 1170–1178.

Stout, R.J. 1982. Effects of a harsh environment on the life history patterns of two species of tropical aquatic Hemiptera (Family: Naucoridae). Ecology 63: 75–83.

Stout, R.J. and Vandermeer, J.H. 1975. Comparison of species richness for stream-inhabiting insects in tropical and mid-latitude streams. American Naturalist 109: 263–280.

Sylvander, R.P. 1978. Los bosques del país y su distribución por provincia. PNUD/FAO-COS/72/103, Documento de Trabajo No. 5, San José, Costa Rica.

Taylor, B.W. 1959. Estudios Ecologicos para el Aprovechamiento de la Tierra en Nicaragua. Ministerio de Economia, Instituto de Fomento Nacional, Nicaragua, 338 pp.

Thayer, G.W., Bjorndal, K.A., Ogden, J.C., Williams, S.L. and Zieman, J.C. 1984. Role of larger herbivores in seagrass communities. Estuaries 7: 351–376.

Thom, B.G. 1982. Mangrove ecology – a geomorphological perspective. *In*: Clough, B.F. (ed.), Mangrove Ecosystems in Australia. Australian National University Press, Canberra, Australia, pp. 3–17.

Thorson, T.B. 1971. Movement of bull sharks, *Carcharhinus leucas*, between Caribbean Sea and Lake Nicaragua demonstrated by tagging. Copeia 1977: 336–338.

Thorson, T.B. (ed.). 1976a. Investigations of the Ichthyofauna of Nicaraguan Lakes. University of Nebraska–Lincoln, Lincoln, Nebraska, USA, 663 pp.

Thorson, T.B. 1976b. Observations on the reproduction of the sawfish, *Pristis perotteti*, in Lake Nicaragua, with recommendations for its conservation. *In*: Thorson, T.B. (ed.), Investigations of the Ichthyofauna of Nicaraguan Lakes. University of Nebraska–Lincoln, Lincoln, Nebraska, USA, pp. 641–650.

Thorson, T.B., Cowan, C. M and Watson, D.E. 1966a. Sharks and sawfish in the Lake Izabal – Rio Dulce System, Guatemala. Copeia 1966: 620–622.

Thorson, T.B., Watson, D.E. and Cowan., C.M. 1966b. The status of the freshwater shark of Lake Nicaragua. Copeia 1966: 385–402.

Tomlinson, P.B. 1986. The Botany of Mangroves. Cambridge University Press, Cambridge, UK.

Tribble, G.W. 1981. Reef-based herbivores and the distribution of two seagrasses (*Syringodium filiforme* and *Thalassia testudinum*) in the San Blas Islands (Western Caribbean). Marine Biology 65: 277–281.

Twilley, R.R. 1995. Properties of mangrove ecosystems and their relation to the energy signature of coastal environments. *In*: Hall, C.A.S. (ed.), Maximum Power. University of Colorado Press, Boulder, Colorado, USA, pp. 43–62.

Twilley, R.R., Chen, R.H. and Hargis, T. 1992. Carbon sinks in mangroves and their implication to carbon budget of tropical ecosystems. Water, Air, and Soil Pollution 64: 265–288.

United Nations Educational, Scientific, and Cultural Organization (UNESCO). 1975. International Classification and Mapping of Vegetation. UNESCO, Paris, France, 93 pp.

United Nations Environment Program (UNEP). 1985. Ecological Interactions Between Tropical Coastal Ecosystems. United Nations Environment Program, Nairobi, Kenya, 71 pp.

United States Agency for International Development (USAID). 1989. Environment Profile of Honduras. United States Agency for International Development, Washington, D.C., USA.

United States Department of Agriculture (USDA), Soil Survey Staff. 1975. Soil Taxonomy. United States Government Printing Office, Washington, D.C., USA, 754 pp.

Urquhart, G.R. 1999. Long term persistence of *Raphia taedigera* Mart. swamps in Nicaragua. Biotropica 31: 565–569.

Virnstein, R.W., Nelson, W.G., Lewis, F.G., III and Howard, R.K. 1984. Latitudinal patterns in seagrass epifauna: do patterns exist, and can they be explained? Estuaries 7: 310–330.

Wake, D.B. 1991. Declining amphibian populations. Science 253: 860.

Walter, H., Harnickell, E. and Mueller-Dombois, D. 1975. Climate-Diagram Maps of the Individual Continents and the Ecological Climatic Regions of the Earth. Springer-Verlag, Berlin, Germany, 36 pp.

Warkentin, I.G. and Hernández, D. 1996. The conservation implications of site fidelity: a case study involving Nearctic-Neotropical migrant songbirds wintering in a Costa Rican mangrove. Biological Conservation 77: 143–150.

Weers, E.T. and Zaret, T.M. 1975. Grazing effects on nanoplankton in Gatún Lake, Panamá. Verhandlungen Internationale Vereingigung für Theoretische und Angewandte Limnologie 19: 1480–1483.

Weinstein, M.P. and Heck, K.L., Jr. 1979. Ichthyofauna of seagrass meadows along the Caribbean coast of Panamá and in the Gulf of Mexico: composition, structure and community ecology. Marine Biology 50: 97–107.

Wellington, G.M. 1974. An Ecological Description of the Marine and Associated Environments at Monumento Nacional Cahuita. Subdirección de Parques Nacionales, San José, Costa Rica, 81 pp.

Wells, S.M. (ed.). 1988. Coral Reefs of the World: Vol. 1: Atlantic and Eastern Pacific. IUCN, Gland, Switzerland, 373 pp.

West, R.C. 1977. Tidal salt-marsh and mangal formations of Middle and South America. *In*: Chapman, V.J. (ed.), Wet Coastal Ecosystems. Elsevier Scientific Publishing Company, Amsterdam, The Netherlands, pp. 193–213.

Wilen, B.O. and Tiner, R.W. 1993. Wetlands of the United States. *In*: Whigham, D.F., Dykyjová, D. and Hejný, S. (eds), Wetlands of the World: Inventory, Ecology, and Management, Vol. 1. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp. 515–636.

Wilbur, R.L. and Collaborators. 1994. Vascular plants: an interim checklist. *In*: McDade, L.A., Bawa, K.S., Hespenheide, H.A. and Hartshorn, G.S. (eds), La Selva: Ecology and Natural History of a Neotropical Rain Forest. University of Chicago Press, Chicago, Illinois, USA, pp. 350–378.

Windevoxhel, L.N.J. 1992. Valoración Económica Parcial de los Manglares de la Región de Nicaragua. M.S. Thesis, Centro Agronómico Tropical de Investigación y Enseñaza, Turrialba, Costa Rica, 107 pp.

Wood, D.S., Leberman, R.C. and Weyer, D. 1986. Checklist of the Birds of Belize. Carnegie Museum of Natural History, Special Publication number 12, Pittsburgh, Pennsylvania, USA, 24 pp.

World Resources Institute (WRI) 2001. EarthTrends. http://earthtrends.wri.org/.

Wright, A.C.S., Romney, D.H., Arbuckle, R.H. and Vial, V.E. 1959. Land in British Honduras. Her Majesty's Stationary Office, London, England, 326 pp.

Zieman, J.C. and Wetzel, R.G. 1980. Productivity in seagrasses: methods and rates. *In*: Phillips, R.C. and McRoy, C.P. (eds), Handbook of Seagrass Biology: An Ecosystem Perspective. Garland Press, New York, NY, USA, pp. 87–116.