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Overview Article

The comparative biodiversity of seven globally important wetlands: a synthesis

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Abstract. The species diversity data of seven globally important wetlands (Canadian peatlands, Florida Everglades, Pantanal, Okavango Delta, Sundarban, Tonle Sap, and Kakadu National Park) were compared. The available data for most groups of lower plants and animals are insufficient for a comparative analysis. Data on vertebrates and higher plants are more complete and show high species diversity. The large habitat diversity allows the coexistence of amphibious species with many immigrants from connected deepwater and terrestrial habitats. Several of these immigrant species find an important permanent refuge in the wetlands; some use the wetlands as periodic habitats. All wetlands are important habitats for long-distance migratory bird species. The species composition reflects the biogeography of the respective regions, e.g. the high diversity of large ungulates characteristic for Africa is also found in the Okavango Delta in Botswana, and the high fish species diversity typical for South America is also reflected in the Pantanal in Brazil.

The number of endemic species in most wetlands is low, except in the Everglades. The low numbers are explained to some extent by the dramatically changing paleo-climatic conditions that increased extinction rates, but also by the connection with large river systems that act as migratory and transport routes for species from large catchment areas and hinder the genetic isolation of wetland populations. The high number of endemic species in the Everglades is explained in part by its isolation on a peninsula. The relatively low nutrient status of most wetlands does not negatively affect species diversity and often leads to high animal densities. Large populations of endangered or rare species in all wetlands contribute to the great value of these areas for biodiversity protection.

All wetlands are subjected to an increasing degree to human pressure through, e.g. water abstraction, changes in the natural flood regime, land reclamation, pollution, over-utilization of natural resources, and poaching. High habitat diversity and a pronounced natural disturbance regime make some of the wetlands vulnerable to invasion by exotic species, as shown for the Everglades. All studied wetlands are at least in part protected by national and international conventions. This provides perspectives for long-term protection only to a limited extent because of major environmental changes in their surroundings. Further strong efforts are required to match protection and sustainable use of the wetlands proper with management activities in their catchments.

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Introduction

Biodiversity has been addressed by scientists for more than a century. Interest in the subject increased in the early 1980s, when accelerated habitat destruction and species loss raised international concern and resulted in 1992 in the adoption of the Convention on Biodiversity. However, for many years, studies and conferences concentrated on terrestrial and marine environments. With a few exceptions (e.g. Finlayson and Moser, 1992; Whigham et al., 1993) freshwater lake, river and wetland environments were overlooked despite the rapid rate of species decline and loss and degradation of wetland habitats (Finlayson et al., 2005). Therefore, one of the special symposia of the 5th International Wetlands Conference of INTECOL, held in 1996 in Perth, Australia, was devoted specifically to an analysis of the biodiversity of wetlands. The outcome of this symposium was the publication of two volumes (Gopal et al., 2000; 2001), which were the first major global overviews on wetland biodiversity. It showed that biodiversity was treated differently by individual authors, making inter-wetland comparisons difficult unless a very broad approach to biodiversity was taken.

Large wetlands represent a complex of permanent aquatic, palustrine and terrestrial habitats, and in the case of river floodplains and tidal zones, of large aquatic/terrestrial transition zones that periodically dry out. This complexity further supports the case for using a broad approach to biodiversity when making comparisons. The approach adopted here uses the definition of biodiversity provided by Gopal and Junk (2001), who defined wetland species as "all those plants, animals and microorganisms that live in a wetland permanently or periodically, (including migrants from adjacent or distant habitats), or depend directly or indirectly on the wetland habitat or on another organism living in the wetland". A broad definition is important for wetland management and conservation as many species depend on wetlands to varying extents, though obligate species may be the first priority of much wetland management. Furthermore, a strict separation between organisms living in rivers, lakes, wetlands and adjacent uplands is impossible, because many organisms share these habitats during different parts of their life cycles. A classification of wetland species is given in Table 1.

Seven overviews in this issue attempt to summarize the available knowledge to provide comparative data for large wetlands from different parts of the world. Unless indicated specifically, this summary derives data from the individual reviews (Warner and Asada, Gopal and Chauhan, Brown et al., Junk et al., Ramberg et al., Campbell et al., Finlayson et al., all this issue). The authors use different approaches according to the state of knowledge for their respective case studies. Brown et al. study of the Everglades is probably the most detailed overview because of the greater amount of knowledge on ecosystem properties. We discuss here major results of the individual articles in a synopsis and attempt to draw general conclusions about biodiversity in large wetlands and their threats and conservation. We also point to gaps in our knowledge and the needs for future work.

Characteristics of the study sites

Geography, geomorphology and geology

The seven wetland study sites are distributed in different parts of the globe. All of them are continuous and large, except the Canadian peatlands that cover large parts of Canada in patches of different sizes (Fig. 1). Most are situated at low altitude, a few tens of meters asl. The Okavango delta is situated about 1000 m asl, the Canadian Peatlands occur in altitudes up to 2000 m or more. All include terrestrial, aquatic and palustrine habitats to varying degrees (Table 2). Four of them are associated with major river systems; Pantanal with the Paraguay River, Okavango Delta with the Okavango River, Tonle Sap with the Mekong River, and Sundarban with the Ganges/Brahmaputra Rivers. The others (Kakadu National Park, Everglades, and Canadian peatlands) are connected to smaller rivers. Tonle Sap Great Lake and its floodplain are connected by the Tonle Sap River to the Mekong River. Flooding of the floodplain occurs when water levels rise in the Mekong.

All of these wetland systems have been impacted by humans; Everglades and Canadian peatlands by conventional agriculture and human settlements after drainage, Tonle Sap and Sundarban by timber extraction, fishing,

Table 1. Classification of wetland species according to their occurrence and behavior.

1. Residents of the wetland proper
   - 1.1. Obligate residents of wetlands
     - 1.1.1 Endemic species
     - 1.1.2 Non-endemic species
   - 1.2. Non-obligate residents of wetlands
2. Migrants
   - 2.1. Regular migrants from deep-water habitats
     - 2.1.1. Regular freshwater migrants
     - 2.1.2. Regular marine migrants
   - 2.2. Regular migrants from terrestrial uplands
   - 2.3. Regular migrants from other wetlands
   - 2.4. Occasional visitors
3. Parasites, pathogens and other dependents

Figure 1. Position of the study sites.

and paddy rice cultivation, the Pantanal by extensive cattle ranching, fisheries, increasing sediment load, and mercury release from gold mining within the catchment, the Okavango Delta by subsistence agriculture and fisheries, and the wetlands in Kakadu National Park by cattle grazing, tourism and mining. Ecotourism is becoming of increasing importance in most large wetlands (see paragraph below).

Past and present climate and hydrology

Six of the study sites lie in the tropical and subtropical belt of the globe, the seventh includes peatlands of North America in northern boreal and subarctic belts. All have been subjected to various changes in climate during their history. The region with the Canadian peatlands was covered by ice during the last glaciation which attained its maximum extent about 15,000 years ago and which ended about 7,000 years ago. The peatlands in Canada are of Holocene age which is less than 10,000 years, but most are of mid-Holocene age or younger.

The Florida peninsula has experienced several alternating episodes of submergence and emergence in response to the rise and fall of sea level over the past 40 million years. The Everglades at the southern tip of the Florida peninsula may have only recently emerged (in the last 5000 years) as judged by the age of the underlying peaty soils.

The age of the Okavango Delta is about 2.5 million years, during which time the climate fluctuated dramatically. A system resembling the present Okavango delta probably developed over the last 40,000 years. The last major wet period occurred during the Late Glacial Maximum (18,000–20,000 y BP). Significant drying took place about 7,000 years ago during the Holocene Altithermal (Patridge et al., 1999). Multi-annual dry and wet periods with about 8 and 18 years interval (Tyson et al., 2002) affect the delta.

The Pantanal is an old depression that underwent several changes between wet and dry episodes during the late Pleistocene and Holocene that are not completely understood yet (Assine and Soares, 2004) but are summarized as follows: 40,000 – 8,000 BP cold and dry, 8,000

Table 2. Major habitats and vegetation types.

N. Peatlands	Shallow lakes, streams, marshes, bogs, fens, swamps, boreal forest
Everglades	Sloughs, wet prairies, cypress swamps, mangrove swamps, periodically flooded and non-flooded tree islands, non-flooded pinelands, canals
Pantanal	Shallow lakes, rivers, channels, different types of flooded savannas, different types of flooded and non-flooded forests
Okavango	Shallow lakes, rivers, channels, permanent swamps, different types of seasonally flooded and non flooded savannas
Sundarban	Shallow water bodies, estuaries, creeks, channels, mangrove forest, flooded and non-flooded grass lands
Tonle Sap	A single large lake of 2,500 km^2 and a few small lakes, rivers, periodically flooded shrubland, floodplain forest, paddy rice fields
Kakadu NP	Shallow lakes, rivers, channels, permanent freshwater swamps, different types of seasonally flooded savannas, mangroves, salt flats

– 3,500 BP warm and wet, 3,500 – 1,500 warm and dry and 1,500 – Present warm and wet (Iriondo and Garcia, 1993; Stevaux, 2000). At present, multi-annual dry and wet periods occur.

Tonle Sap formed about 7,500 years BP and was first connected to the Mekong River about 5,000 to 6,000 years ago.

The Sundarban is of relatively recent origin and has undergone large scale changes in area and location as the River Ganga and Brahmaputra brought huge quantities of sediments from the Himalaya. The tectonic activity that tilts the delta towards the east has also resulted in the geomorphology and biota of the Sundarban.

Kakadu National Park's wetlands are about 1,500–4,000 years old with the present freshwater vegetation having been preceded by more widespread mangrove wetlands that developed after sea levels rises and the accumulation of estuarine mud some 8,000 years ago. The grasses and sedges characteristic of present conditions replaced the mangrove vegetation as distinct river channels re-established and cut through the estuarine planes and created freshwater floodplains and wetlands. A small fringe of mangroves remains, but the wetlands are now characterised by seasonally inundated freshwater vegetation.

General information on the present climate and hydrologic characteristics of the study sites is given in Table 3.

The hydrochemical and physical parameters of water in these large wetlands vary considerably over a wide range. Ground water, rain water, water from the parent rivers, the tides, evapo-transpiration, sediment-water interaction, and uptake and release of substances by plants and animals affect different wetland areas to different degrees. For instance, the electrical conductivity of the tributaries of the Pantanal varies from 40 to 80 µS cm^{-1}, but floodplain lakes can show lower conductivity values because of dilution by rain water during the rainy season, higher conductivity at low water level because of decomposing organic material and liberation of ions from the sediment, and very high conductivity (>5,000 µs cm^{-1}) in lakes, isolated for many years because of ion concentration by evaporation (*salinas*). In the Okavango Delta, gradients from low to high salinity of soil and groundwater are observed from the edges to the centre of islands because of evapotranspiration. These habitats are colonized by species-poor halophytic communities. At low water periods, animals concentrate in and around water bodies and increase ion concentration by bioturbation and defecation.

The freshwater streams and permanent lagoons in Kakadu National Park have electrical conductivity values in the range 20–100 µS cm^{-1} during the wet season flows increasing to more than 1,000 µS cm^{-1} during the dry season when the inflowing freshwater ceases and water evaporates and concentrates the ions, and in some localities the groundwater contributes more and more to the ionic concentrations. The freshwater wetlands abut hyper-saline flats that in turn are connected to the tidally inundated mangroves. General information on hydrochemistry parameters and the general trophic status of the different wetlands are given in Table 4.

Comparative species numbers

Total species numbers

Species lists of higher plants and vertebrates are rather complete for the Everglades, and cover with some exceptions about 80 to 90 % of the total numbers in Pantanal, Okavango, Sundarban and Kakadu National Park. Major

Table 3. Climatic and hydrologic characteristics of the wetland sites. (* = mean amplitude of the flood pulse refers to the parent rivers, in the case of Tonle Sap to Tonle Sap Great Lake).

	Geogr. Pos.	Climate	Tot. Precip. (mm)	Hydrol. Regime	Size (km^2)
C. peatlands	North of ca. 42°N; between ca. 52–123°W	Boreal & Subarctic	ca 300–3,050	Stable waterlevel Frozen in winter 35 % permafrost	1,100,000
Pantanal	16°–20°S, 55°–58°W	Tropics Wet/dry	1,200–1,400	Monomodal pulse Predictable 3.5 m mean ampl.*	160,000
Everglades	26°N, 81°W	Subtrop. Humid	1,000–1,650	Monomodal pulse Predictable 0.5–1.0 m mean ampl.	10,100
Okavango	18°30′–20°S, 22°–24°E	Tropics Wet/dry	460–490	Monomodal pulse Predictable 1.85 m mean ampl. 0.61 min. 2.71 max.	28,000
Sundarban	21°30′–22°40′N 88°–90°E	Subtrop. humid	1,600–2,800	Polymodal pulse Predictable 2–5 m tidal ampl.	10,000
Tonle Sap	13°N, 104°E	Tropics Wet/dry	~1,600	Monomodal pulse Predictable 8,2 m mean ampl.	15,000
Kakadu NP	13°2′S, 133°31′E	Tropics Wet/dry	1,300–1,450	Monomodal pulse Predictable 2–5 m mean ampl.	2,886

Table 4. pH and electrical conductivity values and the general trophic status of the different wetlands. [1)] = entire system, [2)] = salinity is highly variable and has changed in recent decades due to changes in freshwater regimes, [3)] = these data are for the more saline southern Everglades (top range), and the northern Everglades (bottom range).

	pH *Main tributary **Floodplain	**Electr. cond. µS cm^{-1}** *Main tributary **Floodplain	**Trophic status[1)]**
C. peatlands	3.5–4.3 (bogs) 4.0–7.5 (fens) 5.9–6.1 (swamps)	16–50 40–375 230–330	Dystrophic Mesotrophic oligo-mesotrophic
Pantanal	*6.5–7.4 **5.5–7.5 up to 9.8	*43–52 **10–240 >5000 in salinas	mesotrophic
Everglades	6.8 – 8.5 6.5 – 7.7	550–1,000[3)] 70– 900	oligotrophic, P-limited
Okavango	*6.3–7.4 **6.4–8.4	*40–50 **>5–10 times	mesotrophic
Sundarban	*7.5–85 **7.5–9.3	<5–33 ppt salinity[2)] (3–7 µS EC)	mesotrophic
Tonle Sap	median 6.95	3.5–18	meso- to eutrophic
Kakadu NP	3.5–6.5	20–100 wet season **~1,000 dry season	oligo-mesotrophic

gaps exist in Canadian peatlands and Tonle Sap. The estimates for the Indian and Bangladesh parts of Sundarban also differ considerably. The numbers of most aquatic and all terrestrial invertebrate groups are not known for any wetlands. A summary of the available numbers of species is given in Table 5. The data for the Everglades refer to the National Park only (6,000 km^2) and while only a subset of the larger Everglades proper is representative of the larger system. Species number of the entire area is considerably larger.

Algae

The status of knowledge on algae varies considerably between the wetland study sites and has to be considered insufficient to make statements about their diversity. There exist no data about species assemblages in the Okavango Delta and a compilation of algae from Canadian peatlands is missing. 123 species are reported from Tonle Sap lake, 337 species from the Pantanal and more than 700 with at least some 530 diatom taxa in Kakadu National Park.

Bryophytes and lichens

Low temperature and high air humidity in the swamps and bogs favor the occurrence of lichens and mosses in Canadian peatlands where they contribute considerably to species diversity. There are also reports on lichens in Sundarban but there are no references about lichens in the other wetlands.

Herbaceous plants

The number of herbaceous plants varies greatly between wetlands. Species diversity is relatively low in Tonle Sap (148), and in Kakadu National Park (n = 201) with its smaller area of wetland and less diverse habitats. Considering the large areas, covered by Canadian peatlands, species diversity (n = ca. 710 vascular and non-vascular plants) is also relatively low. Larger numbers are reported from Pantanal (n = 1,148) and Okavango Delta (n = 1,150) because of large habitat diversity. In Tonle Sap, coarse sediments are deposited at the entrance of the lake. Fine sediments are distributed over the entire floodplain and result in a very flat surface, and higher lying, shortly flooded habitats, such as levees inside the floodplain are rare. Under natural conditions, the entire floodplain is covered by a very dense scrub layer with individual trees or a floodplain forest that constrain the occurrence of herbaceous plants. Natural disturbance factors favoring co-occurrence of different successional stages, such as erosion and sedimentation are weak. Terrestrial habitats are found only at the edges of the floodplain and their species are not included in the inventories. In the Sundarban, the large gradient in salinity creates habitat diversity but their dynamism under the influence of polymodal tidal flooding appears to be a major constraint for herbaceous species.

Terrestrial species make up the majority of herbaceous plants in all large wetlands e.g., 72 % in the Pantanal, 70 % in the Okavango Delta, and 63 % in Kakadu National Park. Species diversity of aquatic macrophytes depends on flood amplitude, water transparency, shading by trees and salinity. In the Pantanal, shallow flooding with transparent water, little shading by trees and low salinity allow the growth of an extremely diverse (n = 248) and luxuriant aquatic and palustrine vegetation. Similar conditions occur in the Okavango Delta (n = ~350). In

Table 5. Estimates of species of different plant and animal taxonomic categories, confirmed for the different wetlands. For data sources see the individual papers. [1] = number unknown but few, [2] = strongly underestimated, [3] the number is not definitive, [4] including marine species, [5] = total plant species, [6] = terrestrial and aquatic invertebrates.

	C. Peatlands	Everglades	Pantanal	Okavango	Sundarban	Tonle Sap	Kakadu
	Total number reported						
Taxonomic category							
Algae			337	>50[2]	150	123	700[2]
Lichens	68		Few[1]		32		
Bryophytes	249						
Ferns and allies	14						
Herb. wetland plants	16		248	~350	80	34	75
Herb. terr. Plants	264	1,033[5]	900	~800	160[3]	114	126
Woody plants	100		756	~180	59	70	21
Tot. aquatic invert	48	590[6]			886	167[2]	900
Bivalves			23	6			2
Snails			5	16			12
Tot. terr. Invertebrates	264						
Fishes		432[4]	263	71	154	149	62
Amphibians		38	96	33	8	2[2]	26
Reptiles		60	40	64	58	24	30
Birds	>40	349	390	444	163	220	107
Mammals		76	130	122	40	11*	7

Tonle Sap, high water level fluctuations, the growth of a dense scrub vegetation in the floodplain, and at low water high turbidity in the lake create unsuitable light conditions for aquatic macrophytes. The annual drying, grazing and burning in Kakadu National Park has resulted in a lower diversity, but similar proportion of terrestrial species.

Bryophytes reach greatest diversity in Canadian peatlands where they contribute substantially to biomass production and peat formation because of permanent water logging and anoxia of the soils. In all other wetlands bryophytes are represented by few species only which contribute very little to organic matter production. The pulsing water level leads to periodic oxygenation of the sediments that favors decomposition of organic soil carbon. Organic matter accumulation occurs only in patches under multiannual water logging, such as in the *Cyperus papyrus* swamps in the Okavango Delta and in the dense floating plant islands (*batumes*) of the Pantanal. Similar, but small islands occur in Kakadu National Park, especially where alien species have formed dense mats.

Woody plants

Terrestrial ecosystems show a clear increase in woody plant species diversity from high latitudes to the equator with a decline in arid areas. This trend can also be observed in large wetlands that harbor terrestrial and flood tolerant species. In Canadian peatlands total number is low with about 10 species. Low species numbers are also reported from the mangrove forests of the Sundarban, because of salinity stress. High numbers are reported from the Pantanal because inventories cover many rarely and shallowly flooded habitats where rainfall is sufficiently high to allow tree growth. In the Okavango delta, low precipitation probably limits species numbers also in terrestrial habitats. The ranking of wetlands with respect to flood tolerant species is given in Table 6. The numbers include a certain level of uncertainty, because there is no uniform definition of flood tolerance nor complete lists of flood tolerant species e.g. in the Pantanal, however, except for Kakadu National Park the trend is clear. By far the highest number of flood tolerant species is found near the Equator in the Amazon River floodplain under tropical humid conditions.

Trees that maintain their leaves alive under water have been first reported from floodplains of Amazonian

Table 6. Total number of flood tolerant tree species in the different wetlands according to latitude, * Schnitzler et al., 2005.

		Latitude North/South	Flood-tolerant
1	C. Peatlands	>43	10
2	Rhine River*	50	53
3	Lower Mississippi*	35	150
4	Everglades	26	30
5	Sundarban	22	62
6	Okavango Delta	19	10
7	Pantanal	18	355
8	Tonle Sap	13	15
9	Kakadu NP	12	5
10	Amazonia	0	>1,000

Table 7. Species numbers of copepods, cladocerans, rotifers and mollusks reported from the different wetlands.

	Microcrustaceans			Mollusca	
	Copepoda	Cladocera	Rotifera	Gastropoda	Bivalvae
C. Peatlands			1		
Everglades	>10	37		21	
Pantanal	33	117	285	5	23
Okavango Delta	16	21		16	6
Sundarban	total 240			total 143	
Tonle Sap	7	16	23		
Kakadu NP	14	48	227	12	2

rivers (Junk, 1989). This remarkable adaptation has been developed also in other floodplains e.g., in the Pantanal (Nunes da Cunha and Junk, 2004) and Tonle Sap.

Aquatic invertebrates

For several wetlands, there is some information about microcrustaceans, rotifers and mollusks (Table 7) but these numbers will certainly change when a systematic sampling program has been started. Some groups are well described in some wetlands and allow a glimpse of the order of magnitude of species diversity that may be expected. For Canadian peatlands 70 species of biting flies, 35 water mite species and 196 Odonata species are recorded. For the Okavango Delta 94 Odonata species (33 Zygoptera and 61 Anisoptera) are described. The Everglades seem to be depauperate in aquatic invertebrates, because of limits of aquatic habitats and possibly the fluctuating climate. For all wetlands, there is certainly more information available in specialized literature, however, large effort is required to synthesize these data. Furthermore, there are taxonomic deficits in many groups that will seriously hamper inventories. For many aquatic insects, larval stages have to be described and related to the respective adults. Groups like Oligochaeta, Nematoda, Ostracoda and Hydracarina are little studied in most wetlands.

An aspect neglected so far in the discussion about wetland biodiversity are parasites. More than 200 species of fish parasites are described from the Okavango Delta. Parasite number is about 3 times larger than the number of fish species, because nearly every fish species has its own parasites. This points to highly complex co-evolution pattern between hosts and parasites and certainly holds true also for fish communities in other wetlands, as shown for the Amazon River floodplain (Thatcher, 2006). Parasite diversity in birds and mammals is even larger than in fishes (Poulin and Morand, 2000).

Terrestrial invertebrates

Terrestrial invertebrates represent the big open question in any biodiversity assessment of most terrestrial ecosystems worldwide, and certainly also in the wetlands. Very high species numbers, many undescribed species, and problems with keys and synonyms make studies very difficult. Some information exist about the soil and canopy fauna of the Pantanal, but only at the family-level. 124 species of butterflies have been recorded from the Okavango Delta. When flooding is periodic and shallow, soil living termites can play an important role as bioengineers in South American, African, Asian and Australian floodplains, because their mounds reach above the high water level and offer permanent habitat or temporary refuge to terrestrial plants and animals during the floods, increasing considerably number and diversity of terrestrial species. In the Pantanal they create a specific vegetation type, the termite savanna (*campo dos murunduns*), a grass land with many termite mounds up to 1.5 m height and up to 10 m^2 in size that are covered by trees of the non-flooded *Cerrado* savanna. Termite mounds in the Okavango delta are much larger and are the origin of most of the 150,000 islands in the delta.

Fishes

All wetlands, except Canadian peatlands are very rich in fish species. Number of species is related more to the number of species in the parent river than to the size of the wetland (Table 8). Parent rivers are hydrologically more stable than the wetlands and served as refuges for species during extreme hydrological and climatic events in the past and the present. Canadian peatlands are poor in fish species, because of species extinction during the last ice age and because there are only few species in connected rivers that are able to colonize the water bodies of the peatlands. The comparatively small Tonle Sap harbors twice as many species as the much larger Okavango Delta despite its young age. Most species migrated to Tonle Sap when it became connected to the Mekong River about 5,000 years ago. There are 86 fish species in the Okavango River and 83 % of them occur in the Delta. 62 species are reported from Kakadu National Park with 44 entirely freshwater, 4 catadromous, and 14 marine or estuarine species that commonly enter non-tidal freshwater.

Species composition reflects continental-wide pattern of dominance of a few families. In Africa cichlids and

Table 8. Number of fish families and species and the most diverse families in the different wetlands. In comparison: Number of fish species in parent rivers: Canadian peatlands: various, Everglades: Kissimmee River and sea, Pantanal: Paraguai River, Okavango Delta: Okavango River, Sundarban: Ganges*/Brahmaputra** River and sea, Tonle Sap: Mekong River (*in the Cambodian Mekong River 439 species). [1)] = in Sundarban, no family seems to have more than a few, max 12 species and in Kakadu National Park no more than 8 species. In this and subsequent tables, blanks indicate no data available.

	C. Peatlands	Everglades	Pantanal	Okavango	Sundarban[1)]	Tonle Sap	Kakadu
	Total number reported						
Parent river							
Total n of species		30	355	86	76*, 87**	923*	
Wetlands							
Total n of families		91	36	15		35	27
Total n of species		432	263	71		149	62
Most abund. fam.							
Cichlidae				25 %			
Cyprinidae		32		24 %		40 %	
Characidae			29 %				
Loricariidae			14 %				
Pimelodidae			9 %				
Bagridae						8 %	
Plotosidae							8 %
Melanotaeniidae							8 %
Terapontidae							10 %
Eleotrididae							13 %

cyprinids dominate, in South America characids and catfishes, in Asia cyprinids and catfishes, and in North America cyprinids and percids. About half the fish species encountered in Kakadu National Park are small to medium in size, being usually less than 30 cm in length. The small-bodied fish fauna of the region is dominated in overall abundance by centropomids (perchlets), melanotaeniids (rainbow fish) and atherinids (hardyheads); the larger bodied fish fauna is dominated by ariids and plotosids (fork and eel tailed catfish), clupeids (boney bream and tarpon) and to a lesser extent, terapontids (grunters).

Despite adverse salinity conditions, the Sundarban show a high number of fish species because they combine euryhaline freshwater species, characteristic mangrove species and a large number of marine immigrants. High fish species diversity is shown also by other mangrove systems, such as the mangroves of Vietnam from where 260 fish species have been reported (Sarker, 1989).

The classification of fish species in to more lenitic floodplain species (black fish), lotic river channel species that perform large spawning and feeding migrations (white fish) and species with an intermediate migration pattern (gray fish) (Welcomme and Halls, 2001) can be applied to certain extent to all wetlands connected to large rivers. In all floodplains we also find similar adaptations to low oxygen concentrations, periodically varying environmental conditions, and a highly variable food offer. Habitat selection is exemplified for the Okavango Delta and can be considered characteristic for all large wetlands.

High fish production leads in the Pantanal, the Okavango Delta, the Sundarban and the Tonle Sap to economically important fisheries. With 177,000–252,000 t yr^{-1} Tonle Sap fishery is probably the most intensive fishery world-wide (Lamberts, 2001).

Amphibians and reptiles

Low species numbers are reported from Canadian peatlands, because of cold climate. The low species numbers reported for Tonle Sap are certainly the result of insufficient inventories. However, Tonle Sap is the only wetland that lists 7 watersnakes. 5 species are so abundant that they are harvested for human consumption and as food for crocodile farms (8,500 specimens per day during the wet season 1999/2000). 40 amphibians and 96 reptile species are reported for the Pantanal, however, it is noteworthy that most reptile species benefit from terrestrial habitats inside the Pantanal. The same holds true for the Okavango Delta that harbors 33 amphibian and 64 reptile species, 12 reptile species are considered aquatic. Both areas have 10 Families in common, 5 of them belonging to the Serpentes. Most wetlands are refuges for endangered species, such as the turtles *Batagur basca, Cuora amboinensis* and *Hieremys annandalii* and the Siamese Crocodile (*Crocodylus siamensis*) in Tonle Sap, (Table 9). In Sundarban, the amphibian diversity is low whereas the reptiles are quite numerous. In Kakadu National Park there are 26 anurans from a variety of habitats with one introduced toad species, *Bufo marinus*. There are 127

Table 9. Orders and number of species of Amphibians and reptiles reported for the different wetlands. (Sauria and Serpentes are sub-orders).

	C. Peatlands	Everglades	Pantanal	Okavango	Sundarban	Tonle Sap	Kakadu
Order							
Anura			40	33		2	26
Chelonia		1	3	7	13	5	4
Chelidae		1					5
Squamata					45		
Sauria			26	31		?	5
+ Amphisbaenidae		2	2	5			
Serpentes			63	43	31	17	10
Crocodilia		1	2	1	1	1	2

reptile species with some 30 inhabiting the wetlands, including the file snakes *Acrochordus arafurae* and *A. granulatus*, and the crocodilians *Crocodylus porosus* and *C. johnstoni*.

Birds

All wetlands are rich in bird species and there are many observations on their occurrence and behavior, however these data are adequately elaborated for comparison only for the Pantanal and the Okavango Delta. In the Pantanal, 27 % of the species are restricted to wetland habitats (17 % aquatic and 10 % terrestrial) and 73 % are not restricted to wetlands. In the Okavango Delta the respective numbers are 38 % (25 % aquatic and 13 % terrestrial) and 62 % respectively. Waterbirds only are listed for Kakadu National Park with 50 % being migratory shorebirds. The over-regional importance is shown by the high number of migrating species (Table 10). All wetlands also serve as permanent or temporary habitat for species threatened by extinction (Table 11).

Table 10. Total number of birds and number of migrating species in the different wetlands. * nomadic, ** intra-african migrants, *** waterbirds only.

	Total Number	Palaearctic migrants	Austral migrants	Others
C. Peatlands	>40			
Everglades	349	294		
Pantanal	390	20	55	13*
Okavango Delta	444	58	–	42**
Sundarban	315	84		
Tonle Sap				
Kakadu NP***	107	54		

Table 11. Threatened species in the different wetlands according to BirdLife International (2004). CE = critically endangered, E = endangered, V = vulnerable, NT = near threatened. * in the Everglades E = endangered, V = Threatened , Nt = C2 candidate for listing according to USFWS status.

State	CE	E	V	NT
C. Peatlands	0	0	0	0
Everglades*		6	7	3
Pantanal	1	3	4	5
Okavango Delta		2	6	
Sundarban	3	26		
Tonle Sap	1	3	11	8
Kakadu NP		–	1	2

Mammals

Impressive differences exist between the studied wetlands with respect to species number, families and abundance of mammals. Largest numbers are reported from Okavango Delta followed by the Pantanal. In both wetlands, there are 10 orders, however, major differences exist in the respective species numbers. In the Pantanal, bats (39 %) are considerably more diverse than in the Okavango Delta (21 %) whereas the latter has more rodents (25 % versus 18 %). Also carnivores (18 %) and ungulates contribute significantly to the total mammalian fauna in the Okavango Delta (Table 12).

But it is not the number of species but also the number of individuals and their size that make the difference. In contrast to Africa, there are only relatively few large mammal species in South America and they occur only in small numbers. This situation is reflected in the Pantanal, where most mammals are of small size and have a cryptic behavior, such as bats. Certainly, the stocks of the few large species such as capybara, deer, tapir, peccaries, otters, and jaguar have been strongly reduced by man, but they certainly newer reached the biomass of the large mammals in the Okavango Delta. There 35,000 elephants, 60,000 buffaloes, 140,000 impalas, 60,000 Red Lechwe and 35,300 other ungulate specimen were calculated based on aerial counts for an area of 20,000 km^2, corresponding to a biomass of 12 t km^{-2}.

Furthermore, prior to fencing parts of the Delta by men, large herds of ungulates migrated between the surrounding savannas and deserts and the delta according to

Table 12. Orders and number of species of mammals reported from the different wetlands.

	C. Peatlands	Everglades	Pantanal	Okavango	Sundarban	Tonle Sap	Kakadu
	Total number reported						
Order							
Insectivora		3		5	1		
Macroscelidea				1			
Chiroptera		5	36	26	15	2	2
Primates			4	3	1	3	
Pholidota				1			
Lagomorpha		2		1	1		
Rodentia		7	16	31	7		2
Carnivora		13	17	28	13	6	
Tubulidentata				1			
Proboscidea				1			
Perissodactyla			1	2			
Artiodactyla		1	6	22			2
Didelphimorpha		1	7		3		
Xenarthra		2	6				
Cetacea		1			8		
Sirenia		1					1
Total		36	93	122	49	11	7

dry and rainy season. These migrations increased considerably animal density in the Delta during the dry season but also increased the survival rate of the populations in the adjacent areas, such as the Kalahari desert. The astonishingly high number of mammals in a nutrient-poor environment is explained by the extended feeding period and water availability in the delta and the predictability of the floods. Similar migrations between wetlands and uplands are also performed in South America by some species such as peccaries in Amazonia, however over much smaller distances and they include much smaller numbers of individuals.

There are only few mammal species in Tonle Sap, and they play a minor role in the ecosystem because the area is densely colonized by humans. Total species number is certainly underestimated because species-rich groups such as rodents and bats have not been adequately assessed. Kakadu National Park's wetlands similarly hold few mammal species. Sundarban is relatively rich in mammals of which tiger (*Panthera tigris*) is a major keystone species that thrives on a significant large population of herbivores.

Endemic species

Despite a large number of species the number of endemic species is low, with the exception of the Everglades. One endemic copepod (*Argyrodiaptomus nhumirim*) and a few endemic herbaceous plants have been described from the Pantanal (Reid, 1997). With 85 % of the global population occurring in the Okavango Delta, the Slaty Egret (*Egretta vinaceigula*) is a near-endemic bird species. The low number of endemic species can in part be explained by the fact, that most wetlands are connected with large rivers that serve as migratory routes or for passive transport of aquatic and in part also terrestrial organisms between the entire catchment area and the wetlands. Water level fluctuations and habitat dynamics favour mobility of the species inside the wetlands and hinder speciation by permanent gene flow between subpopulations. For instance, Cichlids have undergone impressive radiation in the large African lakes where intra-lacustrine speciation is favoured by stable hydrological conditions and isolation of specific habitats and their Cichlid-sub-populations. In the Okavango Delta, as in other African rivers, Cichlids did not radiate because of flood-pulse induced mixing of and current induced exchange between sub-populations.

Furthermore, most large wetlands are of relatively young age that did not allow speciation. Some groups, such as Cichlids are able to radiate in a few thousand years, but the large majority of species seem to require much larger time spans. The number of endemic species in the Amazon River floodplain is relatively large (Junk, 2000), because extinction rates during the ice ages were low in comparison with, for instance, the Pantanal, Tonle Sap, or Canadian peatlands. The high number of endemic species in the Everglades (65 taxa of higher plants, mostly concentrated in the rocky pinelands on the eastern Everglades and of tropical affinity) is due to the isolation of the area on a peninsular that hinders gene exchange with the Caribbean tropics.

Invasion of exotic species

The wetlands show different levels of invasion by exotic species. Most affected are the Everglades, followed by Kakadu National Park. In the other areas, the number of exotic species is low but the impact on native species can be high, as shown for the Pantanal, where diseases introduced with domestic animals strongly affect populations of deer and capybara. This raises the general question about the vulnerability of wetlands to the invasion by exotic species. At the first glance, dramatically changing environmental conditions in wetlands of the floodplain type seem to make invasion of exotics difficult. However, large habitat diversity and frequent disturbance by floods, droughts and fire provide also opportunities for exotics.

The sub-tropical Everglades are exposed to high pressure of exotic species, because subtropical climate favours the establishment of species from the subtropics, tropics and from temperate regions. The natural isolation on the Florida peninsula is overcome by the position near trade routes for ornamental plants and pet animals that escape or are released into the environment as shown by the large number of ornamental plants and aquarium fishes that lead the list of exotics (221 introduced plant species, 32 fish species, about 30 amphibian and reptile species, and ten mammal species).

Similar climatic conditions occur in Kakadu National Park where the wetlands have been disturbed by changes in fire regimes and grazing as well as invasion by alien plants. The competitive weakness of many Australian species resulting from prolonged isolation may favour invasion. But what about the other wetlands? Permanent water logging, high acidity, and low electrolyte and nutrient content make peat swamps habitats that can only be colonized by highly adapted plant species. These conditions in combination with harsh climate, may provide some protection for Canadian peatlands. However, as soon as the nutrient status rises and /or the water level drops because of drainage, species from the surroundings start to invade the area. The Tonle Sap seems to be protected by the dense shrub communities that hinder invasion of herbaceous species. Intense fishery with fine mesh sizes would keep even small sized exotic fish species under control. But in Asian wetlands, the South American Golden Apple Snail (*Pomacea* sp.) is creating many problems and will certainly extend to Tonle Sap if it is not there already. In the mangroves of the Sundarban, polymodal flooding and varying salinity may hinder the invasion of exotics. The Pantanal, however, seems to be vulnerable because of large habitat diversity and frequent disturbance by floods, droughts and fire. Intensified cattle ranching already leads locally to the establishment of exotic flood adapted grasses. The *tucunaré* (*Cichla ocellaris*), a predatory Amazonian fish species was introduced about 10 years ago and has now successfully established in some parts of the Pantanal with negative impact on the native fish fauna. Diseases of domestic animals have spread into populations of deer and capybara. African bees that escaped in 1956 in São Paulo State, have established all over the Pantanal, and the Asian golden mussel (*Limnoperna fortunei)*, introduced in 1993 to the La Plata system established in the Pantanal in 2001.

Threats and protection of biodiversity

Humans have colonized wetlands for millennia and have mostly treated them wisely because they depended on their sustainable management (Gopal et al., in press). Furthermore, technical capacity to modify the environment greatly was limited until the beginning of the 19th century, when new, non-sustainable management approaches of Europeans and North Americans started to

Table 13. Direct and indirect threats to species diversity in different wetlands.

Wetland	Major threats
C. Peatlands	Land reclamation for urbanization and agriculture, deforestation, hydroelectric reservoirs.
Everglades	Water exploitation, change of the flood pulse, dike and channel construction, land reclamation for civil construction and agriculture (now stopped), eutrophication, mercury-intoxication.
Pantanal	Increase of sediment load by erosion in the catchment, release of mercury from gold mining, poaching, intensification of cattle ranching, deforestation. In the future: Hydrological changes by reservoir construction, canalisation (hidrovia), dike and road construction, and pollution by industry (locally).
Okavango Delta	Water abstraction, channelling of water inside the delta, aerial spraying of insecticides against tsetse flies. In the future: Hydrological changes by reservoir construction. Increased and intensified agriculture in the basin.
Sundarban	Alterations in freshwater flow regimes causing salinity changes, growth of human population, land reclamation for civil construction and agriculture, over-harvesting of natural resources.
Tonle Sap	Growth of human population, over-harvesting of natural resources, governance deficiencies. In the future: hydrological changes through reservoir construction along the Mekong River
Kakadu NP	Invasion by alien plants and animals, changed fire regime, water pollution from urban, tourism and mining activity, and salinisation and future climate change and sea level rise.

modify wetlands in larger scale. These techniques were later transferred to the tropics. Today, wetlands are worldwide subject to human activities that threaten species diversity, directly or indirectly, however, to different degree (Finlayson et al., 2005; Table 12).

The fact that most of them are connected with large rivers makes them very vulnerable to changes in the catchment area. For instance, the construction of reservoirs will in future be a major threat to the integrity of the Pantanal, Okavango Delta and Tonle Sap mainly by changes in the hydrograph, but also by changes in dissolved and particulate load. In the case of Okavango Delta and Tonle Sap, many dams are planned outside of the respective countries, which makes negotiations of protection measures very difficult. Increased sediment transport and mercury release into the Pantanal is the result of inefficient erosion control respectively the gold mining in the catchment area. Efficient control of poaching requires collaboration between Brasil, Bolivia and Paraguay which own parts of the Pantanal. Kakadu National Park is in a much better management situation with its main catchments being contained either in the national park or the adjacent Aboriginal-owned land and hence not subject to the same development pressures as other wetlands being considered here.

The most modified wetland is the Everglades that passed during the last century through heavy human intervention. 39 % of the area was transferred into agricultural land and 8 % into urban areas. Large scale flood protection measures including 16 powerful pump stations, 200 gates, 1,000 miles of man-made canals and 720 miles of dikes modify the hydrological regime. The release of urban stormwater and nutrient laden run-off from agricultural areas increased the nutrient status. These changes affected dramatically flora and fauna of the area. 90–95 % of the wading bird population has been lost since the 1930's, thirty-five plant species and 68 animal species are listed as threatened or endangered. Therefore integrated resource management plans for the wetlands and the catchment areas are crucial for the protection of biodiversity. The estimated cost of the Comprehensive Everglades Restoration Plan (CERP) is $ 7.8 billion with annual operation and maintenance costs of about $ 182 million.

National protection efforts in collaboration with international and local Non Governmental Organizations (NGO's) and the establishment of protected areas under public or private ownership makes a strong contribution to the maintenance of habitat and species diversity. In some wetlands governance deficiencies diminish the efficiency of protection measures as shown for Tonle Sap and the Pantanal. Environmental education is urgently needed in most wetlands to increase the acceptance of protection measures by the local population. In all wetlands, ecotourism is considered an economically important alternative to counteract destructive management methods, however the share of the benefits by the local population has to be guaranteed, to assure acceptance as shown for the Okavango Delta and the Pantanal.

The Everglades National Park is recognized as a Natural World Heritage site and a Ramsar Convention site. 6,100 km^2 (including land and water) of the Everglades and connected wetlands are under protection. The Brazilian Constitution declared the Pantanal as National Heritage. It is since 1993 a Ramsar Convention site, was declared by UNESCO in 2000 as a World Biosphere Reserve and was granted in the same year by UNESCO the Natural World Heritage Certificate. The Okavango Delta was in 1997 denominated a "wetland of international importance" under the Ramsar Convention. Parts of the Tonle Sap are declared as a UNESCO Biosphere Reserve. Similarly, a part of the Sundarban is also designated as a Biosphere Reserve whereas several other smaller areas are protected as sanctuaries. Kakadu National Park is also listed as a World Heritage and Ramsar site covering the vast majority of the wetlands of the catchments that comprise the park.

Species diversity and level of protection is correlated with the size of wetlands, because with increasing size habitat diversity and buffer capacity against natural and man-made stressors increases. This gives large wetlands an over-regional importance for the long-term protection of species diversity. For instance, only large wetlands can support viable populations of top predators and large herbivores by providing prey and undisturbed habitats for their survival. Therefore any discussion to determine minimum sizes for wetland protection is questionable. Maximum size should be the goal under long-term economic, social, and ecologic perspective.

Conclusions and recommendations

Large wetlands harbour wetland-specific species, but are also periodically or permanently used by terrestrial and aquatic species from the surrounding uplands and deepwater habitats, in mangroves also from marine environments (Table 1). This complex mixture of species has not been addressed adequately in studies on biodiversity. Therefore, the species numbers given for specific plant and animal groups in different wetlands are often incomplete and make comparative studies very difficult.

The status of the knowledge on the various plant and animal groups varies in the seven globally important wetlands discussed here. Most is known about higher plants and vertebrates. In contrast, the information on phytoplankton and zooplankton is inadequate. Many planktonic species have large, often worldwide distributions, but some species have a restricted range, and are of specific interest for biodiversity studies. Periphytic algae have not been assessed at all. The information on decapod crustaceans and molluscs is reasonable or can be gathered rather quickly because of the relatively low number of species. A greater effort will be needed to gather information on other aquatic invertebrates, such as insects, oligochaetes, ostracodes, hydracarines, and nematodes, because of high species numbers and high numbers of undescribed species. Many insects would have to be grown in laboratory to relate the larvae with the respective adults; an exception might be the dragonflies, which have been better studied, e.g. in the Okavango Delta. Parasite diversity has been given little attention, but it might contribute considerably to overall biodiversity, as shown by studies in the Okavango Delta, where the number of fish parasites is about three-fold higher than the number of fish species. Studies on terrestrial invertebrates are just beginning. Some data, especially on attractive groups of terrestrial invertebrates, has been collected from a few wetlands, e.g., butterflies in the Okavango Delta and butterflies, moths, and tiger beetles in the Everglades, but the bulk of the species has not been assessed at species level, as shown for the Pantanal. The total number of species present in the wetlands probably approaches tens of thousands, and many of these have not yet been discovered or described. Studies on bacteria, fungi, and viruses are also lacking.

A first important step toward improving the situation is a better cooperation between scientists working in different wetlands. Information should be exchanged, sampling methods adjusted, results compared, and joint research projects planned. For some groups of species, such as aquatic and terrestrial invertebrates, large multinational sampling programs in different large wetlands with standardised methods during different periods of the year are required to build a sound basis for classification. The Global Wetland Consortium (GWC) could serve as a basis for planning and realisation of such efforts.

The species composition in the studied wetlands to certain extent represents flora and fauna of the specific biogeographic region. For instance, the biodiversity and species numbers of large ungulates is higher in Africa than in South America and Australia, and this is also reflected in their wetlands. South America is famous for its species-rich fish fauna, which is also mirrored in the larger number of fish species of the Pantanal than in wetlands of other continents, e.g. species-poor Australia. Overall species diversity in wetlands is high and increases from high latitudes to the equator. This trend, however, does not hold true for all groups and all sites. Mosses and lichens are more diverse in high latitudes. The smaller wetlands of Kakadu National Park and Tonle Sap support large populations of many species without being as species rich as some of the other wetlands considered.

The number of endemic species in the studied wetlands is relatively low because wetlands are very sensitive to climatic changes and suffered strong alterations in hydrology during the Pleistocene and Holocene epochs. These alterations resulted in high extinction rates and hindered speciation. Frequent and severe changes in habitat conditions select for plants and animals that are mobile or readily dispersed. Furthermore, connection to large rivers or the ocean and mobility of floodplain organisms induced by flood pulses favour gene flow and counteract speciation. However, many terrestrial organisms develop wetland-adapted subpopulations (ecotypes) that increase genetic variability and may on the long run favour speciation after isolation. The number of endemic species increases when the wetlands include ancient, rather stable habitats. For example, Kakadu National Park harbours a relatively high number of endemic amphibians and reptiles that live in the ancient, permanent, terrestrial sandstone formations and their small water bodies bordering the lowland wetlands. A large number of endemic species are also found in the Florida Everglades because these wetlands lie at the end of a long peninsula relatively isolated from the main North American landmass and because the Everglades is the only subtropical area of the continent and is cut off from direct land contact with other tropical and subtropical areas. The low number of endemic species in the other wetlands is, however, not an argument for reduction of protection efforts because they harbour large populations of rare or threatened species. Furthermore, they are of utmost importance for migrating animals, such as long-distance migrating birds.

Most of the studied wetlands are of low to intermediate nutrient status, but this does not seem to affect species diversity, except probably in the Canadian peatlands. The articles in the present issue have not concentrated on productivity, but the species lists and information given in the individual articles indicate that the wetlands differ considerably in productivity and food-web structures. Canadian peatlands are dystrophic, and the Everglades are oligotrophic. All other wetlands are mesotrophic and sustain large populations of higher animals. Because of the flood pulse large parts of the studied wetlands oscillate every year between a terrestrial and an aquatic phases that mobilizes nutrients and stimulates productivity (Junk et al., 1989). The Okavango Delta is highly efficient in transforming plant carbon to higher food-web levels through terrestrial mammals. In the Tonle Sap, this transformation is most efficient through fishes. Low food supply is certainly not the reason for the today's low native mammal density in the Pantanal, because the Brazilian part alone supports 4.5 million introduced cattle, 49,000 horses, and about 50,000 feral pigs. The Everglades are a phosphorous-limited system but man-made disturbance and not the lack of food has caused the 95 % reduction in the wading bird population. Animals of high food-web levels usually have key functions in the ecosystem. Therefore, more emphasis has to be given to studies that consider the role of biodiversity with respect to carbon-use efficiency, food-web structure, and ecosystem complexity (see Brown et al., in this issue).

The overall species diversity depends on the habitat diversity because it increases the number of habitat specialists, but also allows colonisation by species that require more than one habitat for their development or daily activities. Canadian peatlands are characterised by a rather stable water level. The other wetlands have a pulsing water level with site-specific amplitude, duration, timing, predictability, and shape. A fluctuating water level increases habitat diversity because of intermediate disturbance by annual and multiannual flood events, erosion and sediment deposition, fire, hurricanes, and the activity of bio-engineers such as termites, elephants, hippopotamus, and beavers, which modify the environment and lead to small-scale habitat patches and the coexistence of different successional stages of plant communities. Pulsing systems provide a larger variety of food items to food webs than systems with a stable water level. They also serve as periodic refuges for upland and deep-water species, providing food and water during adverse periods, and thereby increasing the carrying capacity of the adjacent ecosystems. On the other hand, the shift between aquatic and terrestrial phases results in dramatic annual and multi-annual fluctuations in population size of plants and animals because of changing habitat conditions and/or the lack of refuge areas for aquatic and terrestrial species. Mass mortality of organisms is a common phenomenon, as shown for the fish fauna in many river floodplains. Floodplain organisms counteract these adverse conditions with different survival strategies, including quick growth, early maturity, and high reproductive rates.

The natural disturbance regime and high habitat diversity make many wetlands vulnerable to the immigration of exotic species. The wetlands of Kakadu National Park suffered dramatic environmental damage by feral water buffaloes (*Bubalo bubalis*) until their removal from the park. Also the careless release of exotic species in the Everglades is creating serious problems for the entire system. Great care should be taken when introducing exotic species with the aim of improving agricultural and fishery productivity. In the Pantanal for instance, the peacock bass (*Cichla ocellaris*), introduced from Amazonia is spreading and heavily feeding on native species.

Most of the wetlands are home for human populations which sustainably used their resources during centuries. However, all studied wetlands are subject to increasing human pressure, such as water abstraction, changes in the hydrological cycle, land reclamation, pollution, over-harvesting of natural resources, and poaching. The wetlands are especially sensitive to changes in hydrology because it is the major driving force. Any major change in the natural hydrological pattern will profoundly affect the ecological conditions in the affected parts and will modify species number, distribution and abundance, community structures and productivity, and the overall biodiversity, as shown for the Everglades. The construction of large reservoirs in the up-river catchments of all studied wetlands has already commenced or is planned. Wetlands are also sinks in the landscape that accumulate dissolved and solid substances transported by the water. Therefore, they are very sensitive to major modifications of the natural vegetation in their catchments and pollution of their tributaries, as shown for the Everglades and the Pantanal. On the long run, regional development planning in the catchment areas that considers the quantity and quality of inflowing water and sediment load, and the natural discharge pattern of major tributaries of all wetlands is the basis of sustainable management of the wetlands proper.

All studied wetlands are at least in part under the protection of national laws and international agreements, but administrative weakness and lack of funding threaten these areas in most tropical countries. Strong financial and moral support of large international environmental organisations will be required to endorse national activities in efficient wetland protection.

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