DIVERSITY IN SOME TROPICAL WETLAND SYSTEMS OF SOUTH AMERICA

Juan José Neiff
Centro de Ecología Aplicada del Litoral (CECOAL), Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Casilla de Correo 222 (3400) Corrientes, Argentina.

Abstract

Large wetlands in South America constitute complex systems that generally include various ecosystems. For this reason, it is necessary to consider them as macrosystems composed of permanent and seasonal wetlands, and also sections of upland habitat. Two well-defined families of large freshwater wetlands: *Water-logged or "pantanales"* and *River floodplains (alluvial wetlands)* are classified into nine types of wetlands for comparing their functioning and diversity patterns. Hydrologic and fire pulses are recognised as dominant factors regulating the biotic complexity. Species richness is discussed in relation to the longitudinal and transversal gradients in river floodplains. The species richness or diversity should be used as a synthetic attribute of the complexity of wetlands when it refers to temporal and spatial scales. The number of species present at a particular place and moment in time is always much lower than the number of expected species, especially in the floodplains due to the fluctuations in the hydrological regime of the wetlands themselves. The species richness is reflected partly by the elasticity quotient, which is a measure of the seasonal change in the water spread (area at maximum flooding: area at maximum drought). The highest species richness is registered in wetlands with an elasticity quotient lower than 4 and higher than 1. It is also necessary to consider the turnover of species in the system, because many wetlands have a relatively constant value of complexity (expressed as number of species or any of the indices of species diversity), although there is a high qualitative renewal of the system elements. Wetlands have a variability regime very different from the aquatic systems and from those of the upland, such that the biodiversity could have a different significance. Systems with a low number of species could be very stable and vice-versa. Hence, diversity as an expression of functional complexity could be studied advantageously with indices that reflect the fluxes (information in a broader sense) through the system.

Introduction

One of the main ecological characteristics of South America is the existence of large wetlands, individually and globally the most extensive in the biosphere, considering the development of the continental masses (Table 1). The largest area occupied by the wetlands in South America lies in the drainage basin of the large rivers, and more than 80% of the total area lies within the tropical and subtropical belt.

The area and persistence of the wetlands depend on the availability of surface water covering the soils. In large flatlands of humid South America, the water covers the soil for 30-80% of the time within a century. These areas are called *"humedales"* or *"pantanales"* (wetlands) that, in general, are not "ecotones" between land and water systems, because of their particular structural and functional patterns (Neiff et

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Table 1. Large wetlands in tropical South America.

Order No. in Figure 1	System	Area (*)	Area (+)	Source	Waterlogging/ Inundation frequency)
1	Pantanal of Mato Grosso (Brazil)	138	?	Adámoli (1995)	A+I = annual
2	Mar de arena pampeano (Argentina)	100	2	Iriondo (1990)	A = secular
3	Plains of the Orinoco (Venezuela)	90	?	Welcomme (1985)	A+I = annual
4	Pantanal of Rio Branco-Negro (Brazil)	80	?	Iriondo (1992)	I = annual
5	Central Amazonia (Brazil)	75	?	Sioli (1975)	A+I = annual-seasonal
6	Lowlands of Juruá/Solimoes	58.3	?	Diegues (1990)	I = seasonal-annual
7	Bananal Island (Brazil)	50	?	Iriondo (1990)	A = annual
8	Chaco Oriental (Argentina)	42	3.4	Neiff et al.	A+I = annual (1994)
9	Paraná river floodplain (Argentina)	38	5	Neiff et al. (1994)	I = seasonal-annual
10	Roraima and Rupupuni Lowlands (Brazil)	33	?	Klinge et al. (1990)	I = annual
11	Ucamara (Ecuador)	30	?	Iriondo (1992)	I = annual
12	Lowlands of Napo (Ecuador)	30	?	Iriondo (1992)	I = annual
13	Lowlands of south Brazil (Lagoas costeiras)	30	?	Klampt (1982)	A+I+F = annual
14	Floodplain of Purus river (Brazil)	26.7	?	Diegues (1990)	I+A = annual
15	Lowlands of Guaporé river (Brazil)	26.2	7	Diegues (1990)	I+A = annual
16	Floodplain of Magdalena river (Colombia)	20	?	García Lozano and Dister (1990)	A+I = annual
17	Plains of the Mamore (Colombia)	15	2.5	Iriondo (1992)	A+I = annual
18	Iberá (Argentina)	12	7.8	Neiff et al. (1994)	A = annual
19	Lowlands of Western Region (Paraguay)	10	1	Mereles et al. (1992)	A = annual
20	Lowlands of Beni (Bolivia)	10	1.5	This study	A = annual
21	Lowlands of Isozog (Bolivia)	9	1	This study	A = annual
22	Ñeembucú swamps (Paraguay)	8	4	Mereles et al. (1992), This study	A = annual
23	Low Guayas valley (Ecuador)	7.5	?	Iriondo (1992)	A+I = quinquennial
24	Lowlands of the Poopó Region (Bolivia)	6	?	Iriondo (1992)	A+I = annual
25	Lowlands of Mar Chiquita (Argentina)	6	2	Iriondo (1992)	A+F = decennial
26	Lowlands of Uruguay/Ibicuí (Brazil/Uruguay/Argentina)	5.5	1.3	This study	A+I = annual
27	Atrato valley (Colombia)	5	?	Welcomme (1985)	A+I = annual
28	Catumbo	5	?	Welcomme (1985)	?
29	Humid Chaco (Paraguay)	4.5	?	Mereles et al. (1992)	A = annual

(*) = Maximum area $\times 10^3$ km^2; (+) = Minimum area $\times 10^3$ km^2; A = rainfall accumulation; I = inundation; F = ground water discharge; (?) = not known.

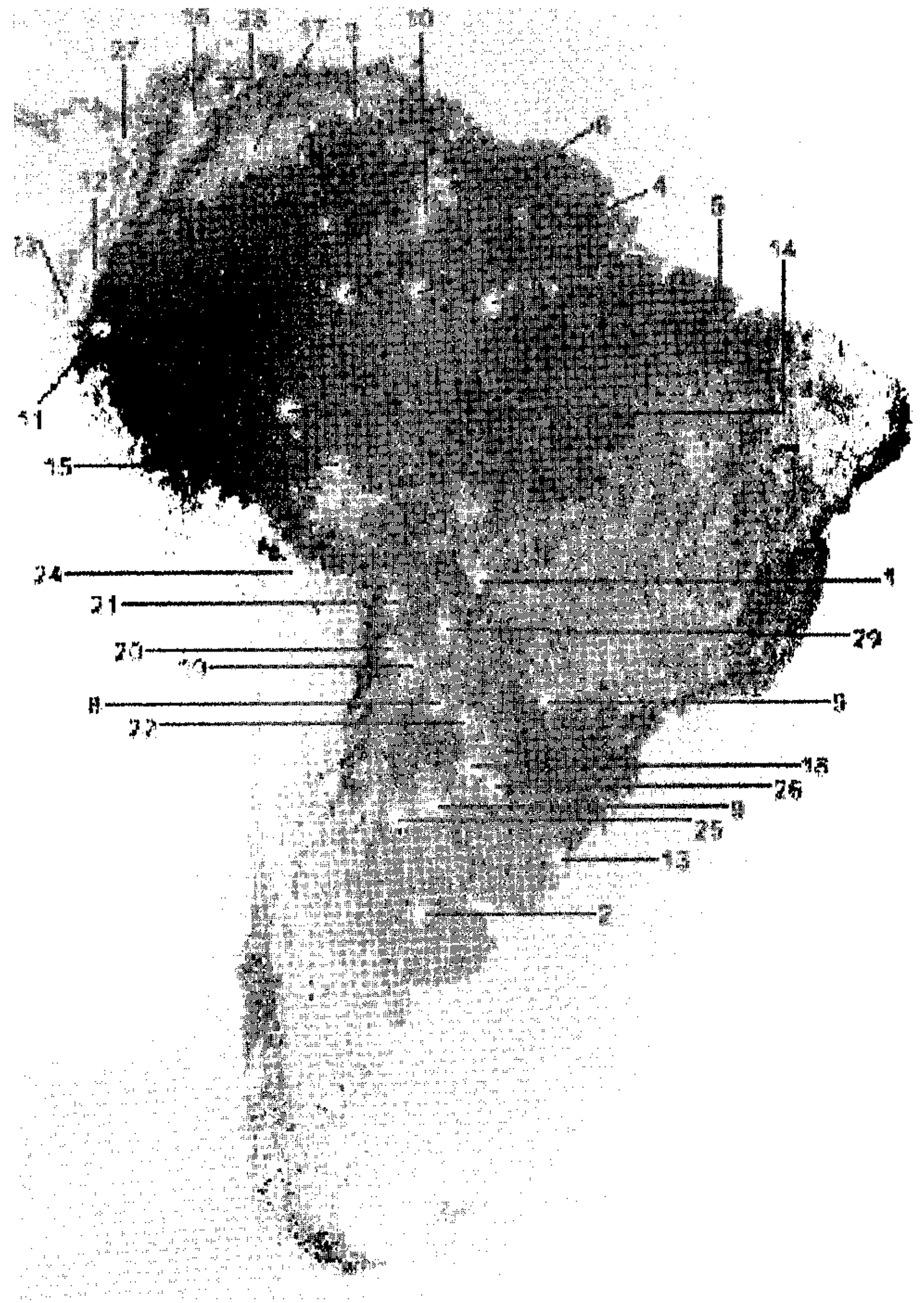

Fig. 1. Scheme showing location of the maintropical and subtropical wetlands mentioned in table 1.

al. 1994). The availability of surface water depends on the positive water balance between rainfall and evaporation, and the landscape physiography to retain it, accumulate it, or allow its runoff towards the sea. Due to its triangular shape with its vortice looking south, the climate of South America has a great oceanic influence, and consequently, it is warmer than at the same latitude in the northern hemisphere. In relation to orography, the wetlands of South America are influenced by a continuous mountain chain (the Andes), and two shields: the Guayana Shield and the Brazilian Shield. The remaining surface corresponds to large masses of flatland with little depressions, except in the southern Andes region and in a part of the Patagonia where many lakes occur under a temperate climate. A minor amount of running water has a predominant North-South direction (Paraguay, Paraná and Uruguay rivers) with neutral to slightly acid waters and assorted sediments (clay to coarse sand) coming from the geological erosion of the Brazilian shield. According to the orographic origin, and the biotic transformations that occur in extensive wetlands, waters collected by the rivers may be (a) "white waters" with a great amount of fine silt-sand and loam from the Andes mountains, (b) "black waters" with few suspended sediments and a high content of dissolved and particulate organic matter, or (c) "clear waters" with intermediate characteristics (Sioli 1975).

During the past few years, studies on various aspects of wetlands in different parts of the world have appeared in numerous publications, including proceedings of conferences and workshops. However, neither a theoretical framework on the functioning of wetlands has yet been developed nor the causes and consequences of biodiversity of these systems are properly understood.

Interestingly, there is no agreement on the definition of wetland yet and many researchers include lakes, ponds, rivers, streams, marshes and other marine littoral ecosystems in this definition. In many international programs, wetlands were defined as *ecotones* from the definition of Cowardin et al. (1979), which has been accepted by many researchers (Naiman and Décamps 1990, Lachavanne and Juge 1997). There are structural and functional characteristics to define wetlands as entities very different from ecosystems of the upland and permanent waters (Gopal et al. 1982, 1993, Mitsch et al. 1988, Tiner 1993, Neiff et al. 1994). Mitsch and Gosselink (1993) reviewed the existing definitions of wetlands, explained their own characteristics and emphasized the difficulties in obtaining an unique definition. The IUCN and the Ramsar Convention have proposed very broad definitions which include a large variety of systems such as rivers and lakes. In South America, the IUCN definition for the inventory of wetlands in Brazil, which would cover 1,082,466 km^2 only in that country, has been used (Diegues 1990, 1994). In Argentina, the definition proposed by Ramsar has been used, so that the area covered by wetlands would be approximately 180,000 km^2 (Canevari et al. 1998). If this definition was applied to the whole of South America, the area would be approximately 2.4 million km^2, which would be an overestimate of the real extent of these systems.

The extent of wetlands, the comprehension of the functions and their future management will depend on the definition used. Obviously, biodiversity values are related to the extent and quality of the ecosystems according to the adopted definition. In this study, we consider that, "the large wetlands of South America are systems of sub-regional extent in which the spatial and temporal variations in flooding cause characteristic biogeochemical fluxes, soils of accentuated hydromorphism, and a biota whose structure and dynamics are well adapted to a wide range of water availability. They can be considered as macrosystems whose complexity grows with hydrosedimentological variability and geographic extent" (Neiff et al. 1994). Wetlands depend on the source of water feeding them (local rains, river flooding or lateral fluxes of marine water). Accordingly, the large freshwater wetlands would occupy an area somewhat larger than a million km^2 in South America.

The objectives of this paper are: (a) to describe the continental wetlands of tropical South America, with the exception of the Amazonia, and to present an operative classification of wetlands, (b) to review the usefulness of some terms commonly used to characterize the complexity of these systems and to explain some patterns of variability in these environments, and (c) to discuss some values of diversity and species richness based on the published literature and our own study.

Definitions

It will be useful to define a few terms that we use in this paper to describe the characteristics of their complexity and biodiversity.

- *Elasticity* (Neiff et al. 1994). It is defined as the quotient between the area occupied during the period of greatest flooding and/or inundation, and that occupied at the period of maximum drought.
- *Large wetland.* It is a macrosystem where the principal factor is rainfall accumulation and, secondarily, flooding.
- *"Pantanal"*. It is a large sandy depression periodically inundated predominantly by local rainwater, and with poorly organized surface drainage. Water exchanges with the atmosphere are largely vertical.
- *Floodplain wetland.* It is a large wetland presenting fluvial forms fashioned by alluvial fine-grained deposits with organized (directional) fluxes of allochthonous water.
- *Marginal wetland.* It is an area periodically covered by water adjacent to and directly influenced by a large body of water (e.g., lake, river, sea). Water exchanges are largely horizontal.
- *Marginal fluvial wetland.* It is a periodically flooded area adjacent to a river whose biotic structure is the cause and consequence of bi-directional interactions with the river.
- *Marginal lacustrine wetland.* It is a flooded area adjacent to a lake. Such wetlands generally correspond to ecotones between terrestrial and lacustrine systems.
- *Marginal littoral wetland.* It is a periodically flooded coastal area with biological characteristics influenced by recurring daily and seasonal cycles.
- *Ecodiversity.* It is a variety of patches (size, shape and contrast) which characterize a landscape pattern. It is based on the characteristics of vegetation, soils, drainage, urban areas, etc. It is a measure of the landscape complexity, of the distribution of its elements and it also allows to study, quantitatively, the degree of fragmentation of the landscape (Naveh 1994, Hoover and Parker 1991, MacGarigal 1995).
- α *(species) diversity.* It is the diversity within a specific habitat (Whittaker 1965).

- β *(habitat) diversity.* It is the diversity between different habitats or cross-habitat diversity, measured as a gradient of changes in diversity along different landscape patches (Whittaker 1965).
- χ *(landscape) diversity.* It is the total diversity of a whole geographically or ecologically defined region or landscape type (Whittaker 1965).
- *Current specific richness.* It is a qualitative attribute which expresses the potential of finding species (taxonomic entities, in a broader sense) in a particular wetland. In practice, it is a list of species present in a sample. The use of this complexity indicator has the problem that many species have low density populations, so that the chance of registering them in the sample is very low. Another problem is that some South American wetlands have a marked seasonality. In consequence, species which usually would be in that place and are not registered at that moment could be excluded. However, the reiteration of samples (in space and time) allows to decrease the error and gives a measure of the carrying capacity of the system.
- *Potential specific richness* (Neiff 1997). It is the total number of species registered historically by different biologists in a particular type of landscape. It expresses the number of species expected in that environment. When these collections are precisely localized in time and space, and at the same time it is possible to know the climatic and hydrological conditions of the wetlands for the moment in which the collections were made, it is possible to infer the relationships between the occurrence of taxa and the spatio-temporal variability of the system. The potential specific richness does not allow to know the number of coexistent species nor the carrying capacity of the ecosystem. It is an indicator of the *potential biotic complexity* of the wetlands which allows, for example, to know the number of species which could be affected by anthropic alterations.
- *Species turnover.* Θ It is the fraction of the total number of species which enters (or leaves) in a specific period of time; it is the reciprocal of the turnover rate and designates the length of time needed for the complete exchange of a current existing number of species. For example: if 200 species are present at one time and 10 species leave or enter each month, the turnover rate is 10/200 i.e., 0.05 or 5% month^{-1}.
- *Biological spectrum.* It is the variety of biological forms (animals or plants), structurally and functionally different, within the ecosystem. This concept, developed by Raunkiaer (1934) for plant bioforms, has been applied in an analogous way to classify the communities of invertebrates by their trophic habit (Merritt and Cummins 1978, Poi de Neiff and Carignan 1997), of birds into different guilds in floodplains of the Paraná (Beltzer and Neiff 1992), and of fish and other communities.
- *Periodicity.* It defines the temporal variability of diversity or species richness of a landscape. It is diagnosed based on the records of the presence of a species or a group of species through time in one or more landscapes. Basically, there are wetlands with *high seasonality* (due to temperatures or, frequently, to the fluctuation of the water level) and others defined as *isodynamic* due to the low amplitude of fluctuation. There are many myths in relation to the high specific diversity of South American tropical wetlands. Postcards which show a rich and varied fauna concentrated in small space are often sold. The pictures correspond to the period of droughts in wetlands as the Pantanal, the east Chaco, the Llanos de Apuré, and other systems. Unfortunately, there are no pictures of the same

Table 2. Elasticity of some large wetlands.

System	Area (*)	Area (+)	Elasticity quotient	Source
Chaco Oriental	42	3.4	12.35	Neiff et al. (1994)
Paraná	38	5	7.6	Neiff et al. (1994)
Lowlands of Guaporé	26.2	5(?)	5.24(?)	Diegues (1990)
Iberá swamps	12	7.8	1.54	Neiff et al. (1994)
Lowlands of Western Paraguay	10	1	10	Mereles et al. (1992) This study
Mar Chiquita	6	2	3	Neiff et al. (1994)
Ñeembucú	8	4	2	Mereles et al. (1992) This study
Beni (Bolivia)	10	1.5	6.66	This study
Uruguay/Ibicui floodplains	5.5	1.3	4.23	This study

(*) – Maximum area, ×10^3 km^2, (+) = Minimum area, ×10^3 km^2, (?) = estimated by the author

sites taken during the inundation phase, when the number of species and individuals in low. It is also not mentioned that the high concentration of animals in a small space could correspond to a situation of stress in which the carrying capacity of the environment was exceeded.

Main Types of Wetlands

In South America, there are at least two well-defined families of large freshwater wetlands:

Water-logged wetlands or "pantanales"

They are large areas with sandy soils, with expanses of fossil and aeolian dunes, poorly-organized surface drainage and numerous water bodies that become separated at medium or low water. The impermeable layer can occur close to the surface, or can be found up to tens of meters below the surface. Depending on the position of this layer, two phases can be distinguished: (a) the accumulation (or saturation) phase and (b) the waterlogged phase, when the rainfall exceeds the soil's storage capacity. At high waters, the soil can be covered with up to two meters of water. The excess of water on the landscape is from local rainfall. Water percolates through the sand on the highest portions of the landscape (the fossilized sand dunes) and slowly infiltrates and fills the depressions over several weeks.

The scarcity of nutrients is due to the lack of clays in the system and to the origin (direct rainfall) of the water. Many of these wetlands exhibit oligotrophic characteristics during the dry phase, and become eutrophic during the rainy season, owing to the transport and circulation of minerals in surface-flowing water.

River floodplains (alluvial wetlands)

In the river floodplain wetlands, the waterlogging of the soil (and flooding with 2 4 m deep water) is largely a consequence of river overflow, with the water originating from distant sources. Consequently, the change of seasons in the system may be out of phase by some months with rainfall and water levels (for example, the Lower Paraguay floodplains).

These wetlands are characterized by a predominance of both modern and ancient fluvial features: alluvial levees, ancient oxbows of meanders, etc. The drainage of the inundated areas is more or less "organized", though very slow; water tends to form networks of anastomosing channels, tending to reunite watercourses below. Sediments are predominantly fine (very fine sands, loams, and clays) which results in an adequate capacity for the storage of nutrients and major ions. Furthermore, inundation and water movements generate an important influx and/or translocation of mineral materials (solutes, suspended sediments), organic matter (as colloidal or particulate) and biotic information (seeds, eggs, organisms).

In alluvial wetlands or floodplains, large morphological and biotic spatial gradients are observed in relation to the distance from the main river channel (Neiff 1990b, 1996, Marchese and Ezcurra de Drago 1992). The species diversity increases toward the border of the floodplain (Marchese and Ezcurra de Drago 1992).

Pattern of Landscape Patches as Support for Diversity (Ecodiversity)

Both categories of large wetlands have a characteristic landscape pattern which combines patches of different sizes and shapes. This pattern of ecodiversity depends mainly on the geomorphology and distribution of the periods of excess and deficiency of water in a time series smaller than a century. The physico-chemical conditions of the soils and the frequency and intensity of the fire are also important but are factors subordinated to a great extent to the hydrological dynamics in the landscape.

Wetlands of similar physiognomic characteristics constitute a *functional type*, since the species richness, the biomass production and, to a great extent, the characteristics of the ecological niches result in ecological equivalents although separated by thousands of km. For example, the *"mallines"* (Iriondo et al. 1972), also called *"vegas"* (water meadows) in the southern end of South America (Collantes and Faggi 1999), have a great physiognomic and ecological similarity with the *"esteros"* (swamps) and *"cañadas"* (streams) of the humid subtropical Chaco (Neiff 1986) and with some *"bañados rasos"* (flat marshlands) of the Pantanal of Mato Grosso in the humid tropics:

They have a sandy to muddy-sandy soil seated in an impermeable horizon at 1-1.5 m depth.

They are fed by waters with low content of salts, and which are neutral to slightly acid.

The species richness and the biological spectrum are strongly conditioned by the temporal presence of the shallow flooding of the soil.

They have a strong hydric and biotic seasonality.

They are very productive areas compared with other landscapes at the same latitude.

They cannot accumulate a peat horizon, or if it exists it is only a few cm thick.

They have a high bird richness, with many migratory species.

The combination of these landscape patches (number, size, proximity, contrast, borders) could explain the patterns of and diversity, when the information of the field inventories (diversity) is compared with the fractal analysis of the landscape (MacGarigal 1995).

Schematically, these patches of landscape could be grouped into at least nine structurally and functionally different landscape types (Figure 2 and Table 3).

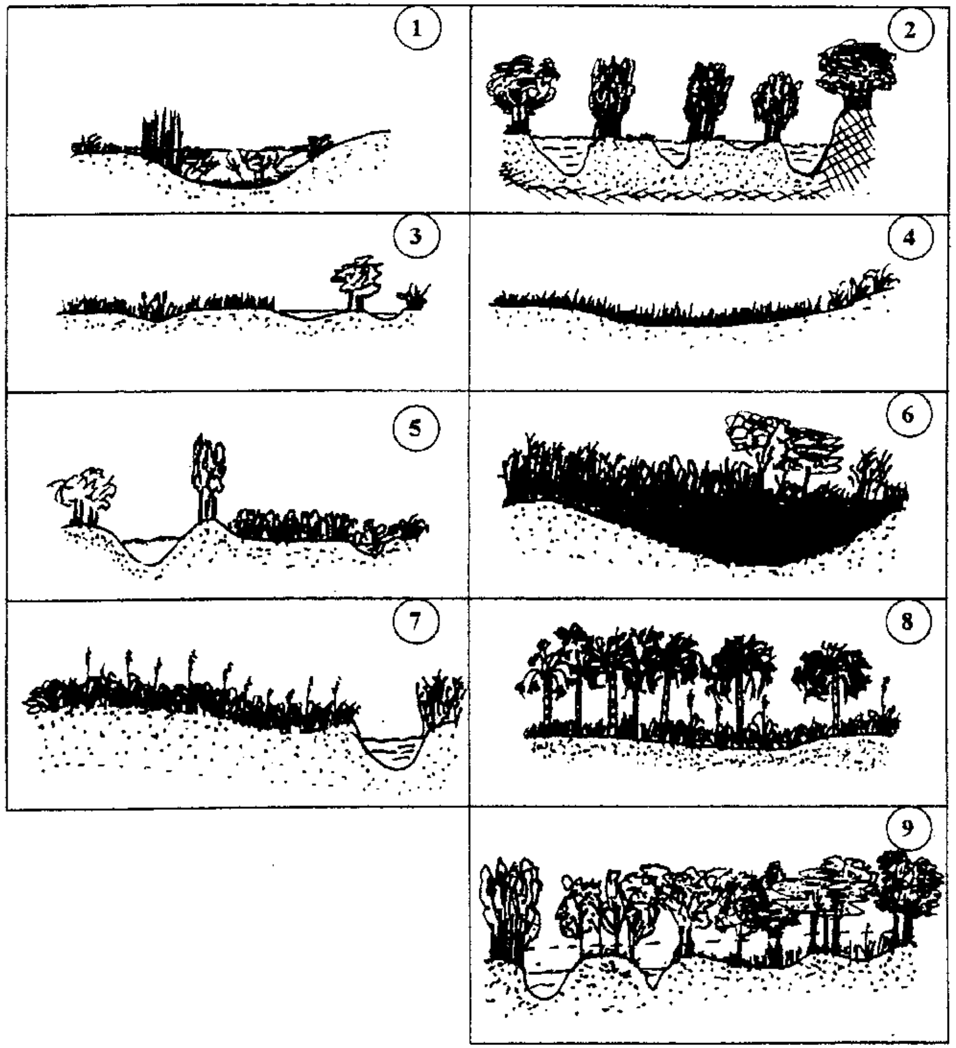

Fig. 2. Main types of continental wetlands of tropical South America. 1. Shallow lakes and ponds, 2. Sand bars in river channels, 3. Pools, 4. Waterlogged short grasslands, 5. Rooted emerged meadows (reed and broad leaved meadows), 6. Tropical peatland swamps, 7. Hard tall grasses wetlands, 8. Palm wetlands (like savannas), 9. Flooded gallery forests. (see Table 3 for details).

Table 3. Main types of South American continental wetlands (see Figure 2).

	Subsystem				
Wetland type	**Geoform and slope**	**Soil**	**Hydroperiod**	**Vegetation**	**Fauna**
1. Shallow lakes and ponds	Permanent water-bodies 1-4 m depth. Soft slope. Eq≅<1.5	Fine sands. Loam/clay. Silts. Organic matter 5-20% in surface.	Annual water level variation 1-3 m. 4 m within a century.	Free floating. Rooted leaved, submerged and littoral. Coverage up to 90%.	Abundant, specially fishes, amphibians and reptiles.
2. Sand bars in rivers	Temporal bars and islands in early stage. Eq≅>10	Middle to gross sand sediments emergent only for a few months.	Wide fluctuation. Flood phase predominant.	Pioneer forest of *Tessaria, Salix, Phyllantus* or others.	Very poor, except a very specialized guild of birds.
3. Pools	Temporal water bodies 1-2 m depth. Eq≅10-15	Loam/clay. Silts. Organic matter <3%.	Wide fluctuation. Drought period predominant.	Scarce, free floating (terrestrial) pterido-phytes, some Geophytes.	Temporal assemblages. Abudnant invertebrates, fishes and amphibians.
4. Waterlogged short grasslands	Lowlands with soft and concave slope. Eq≅6-15	Loam/clay or sandy/loam silts. 2-6% organic matter content.	Fast seasonality. Drought phase every year.	Short grassland dominated by Grami-neae up to 0. m tall.	Abundant. Amphibians. Reptiles, Birds. Mammals. Several species of small fishes.
5. Rooted emerged meadows (reed and broad leaved medaows)	Oxbow lakes, meander scrolls or back swamps adjacent to the river course or within the riverine islands. Eq≅5	Fine or medim sand layer alternating with others of loamy silts. The vertical pattern of the sol evolution is not present.	Wide fluctuation of water elevation during the year, several phases of flood and drought. It's? are very irregular between years.	Continuous reed meadow (*Panicum grumossm* or other Gramineae), broader or leaved plants (*Polygonum* spp., *Ludwigia* spp.).	Rich fauna of fishes, amphibians and mammals. Apparently, it is corridor for birds.
6. Tropical peatland areas	Shallow lakes <2 m depth. Eq≅1.5	Loam/sandy silts with a gross layer of organic debris on the bottom, as joint peat.	Waterlogged areas. Always soaked. Acid waters (pH 4-5.5), very poor in nutrients.	100% covered by a canopy of Geophytes that grow on organic soil (Histosols).	Low diversity and abundance of fishes, birds and mammals.
7. Hard tall grasslands	Flood plain areas receiving the over-flow in annual floods. Poor drainage.	Clay sandy or loam sandy, with high content of iron and manganese. 5-10% of organic matter.	During 3-7 months per year the soil remains covered by water. During the drought phase hydric stress is frequent.	Matrix of tall grasses dominated by one species. Plants in cushions separated by 1-3 meters.	Depend on the phase of the hydroperiod. Amphibians, reptiles and ants are always present. Birds and fish are seasonal.

Table 3. (Continued).

	Subsystem				
Wetland type	**Geoform and slope**	**Soil**	**Hydroperiod**	**Vegetation**	**Fauna**
8. Palm (Savanna) wetlands	Lowlands. Slope <0.01%. Eq≅10-12	Hydromorphic clay-loamy predominant. pH 7-8.5.	Seasonal waterlogged or flooded up to 2 m over the sol. Strong deficiency of water in the phase of drought.	Matrix of short or tall grasses with evenly distributed palms.	Strong seasonal changes as a consequence of hydro-logical pulses and of the fire events.
9. Forested wetlands	Levees, bars on floodplains	Sand and loam with abundant litter on A_0 horizons. pH 6.0-7.5.	Wide fluctuation. Drought period predominant in long time series.	1-3 layers with trees. Short grasses could be present depending on the hydroperiod.	High diversity of birds. Monkies and some others mammals are also presents.

Diversity Patterns and Scales

Diversity: Advantages and Disadvantages in Wetlands

The notion of diversity is not always clear. In the scientific literature, it is common to misunderstand the term species diversity, which is the quantitative relationship between the number of species and the population abundance of the species (expressed as number of individuals, biomass, volume or coverage), i.e., a synthetic attribute which expresses the quantity of taxonomic entities (coexisting in a territory at a given moment), among which the individuals existing in that place and at that moment are distributed. This parameter is very useful because it indicates the possible connectivity of the elements of the system, the trophic complexity, the carrying capacity of the environment, and mainly the restrictions or conditions the physico-chemical medium imposes on the development of the wetland biota.

Diversity is a useful parameter if the numbers or the index could explain the causes of origin of this value, and if it is possible to know how the indices correspond to a "normal" situation or state of the system, or if, on the contrary, the obtained values correspond to a particular state of environmental stress.

An original and potentially useful descriptive parameter is the elasticity of the wetland macrosystem (Neiff et al. 1994), defined as the quotient between the area occupied during the period of greatest flooding and/or inundation, and that occupied at the time of maximum drought.

Diversity of South American Wetlands on a Continental Scale

It seems obvious that diversity in natural systems is a parameter positively related to the area under consideration. In spite of this, many studies do not state the area of which the measurements were taken, and very few show the area relationship between the maximum and minimum landscape flooding (elasticity index). Consequently, many studies have overestimated diversity, since samples were taken in the small ponds in which the fauna concentrates in the critical phase of low waters.

Within the large South American wetlands, the highlands, non-flooded forests, cultivated forests, etc., are also included, although they should have been treated separately to avoid including in the wetlands upland populations that have other environmental determinants.

Also in these wetlands, diversity is strongly related with temperature, so that the highest diversity in South American wetlands is found in waters with annual mean temperature of 18 to 30°C, and values always higher than 10°C. However, it is probable that the higher diversity of bioforms found in these environments will not only be directly related to benign temperatures but also to the higher ecodiversity found in the subtropical and tropical environments which allows a higher availability of resources for feeding, refuge and for rearing the juveniles.

Using the published information on biodiversity for comparing different communities and types of wetlands, various problems and limitations arise. Only a few published contributions specify how the information had been collected and processed. The same value, taken with the same diversity index and applied to sys-

Table 4. Hydrological regime of the main types of fresh water wetlands (numbers correspond to Figure 2).

	Hydrologic features						
Wetland type	**Water source**	**Water surplus frequency (excess??)**	**Magnitude of inundation**	**Water flow Intensity and duration**	**Seasonality of low water phase**	**Low water phase duration**	**Fire events**
1. Shallow lakes and ponds	Mainly local rains.	Permanent water bodies.	Fluctuation ≅1-2 meters in a year.	Uncommon.	Regular, spring to summer time.	4-6 months.	No.
2. Sand bars in rivers	River overflow.	Seasonal or monthly.	Up to five meters over the soil.	Velocity of up to 0.5 m/s-several weeks.	Short and irregular.	Weeks to 4 months.	Uncommon.
3. Pools	Mainly local rains.	Irregular, several times in the year.	<1 meter.	Uncommon.	Irregular, spring to summer time.	6 months to several years.	Sporadically.
4. Waterlogged short grasslands	Mainly local rains.	Regular. Seasonal.	<1 meter.	Uncommon. Slow some times.	Very regular. Spring to summer.	5-8 months.	Very frequent, at the beginning of spring.
5. Rooted emerged (reed and broad leaved meadows)	River overflow.	Seasonal or monthly.	3-5 meters over the soil.	Velocity of up to 1 m/s-several weeks.	Short and irregular.	1-5 months per year.	Sporadically, at the end of the longest drought phase.
6. Tropical peatland areas	Mainly local rains.	Permanent waterlogged.	Fluctuation ≅1 meter per year.	Uncommon.	At the end of winter or spring.	1-2 months per year.	Frequent, during the storms or by an anthropic cause.
7. Hard tall grasslands	River overflow.	Seasonal or annual.	1-3 meters over the soil.	<0.3 m/s, short time.	Winter to summer 2-8 months per year.	2-8 months per year.	Very frequent, at the beginning of spring.
8. Palm (Savanna) wetlands	Local rains and or river overflow.	Seasonal or annual.	1-3 meters over the soil.	Uncommon.	Variable, depending on the origin of the water.	2-12 months.	Very frequent, at the spring and summer time.
9. Forested wetlands	River overflow.	Seasonal or annual.	1-2 meters over the soil.	Velocity of up to 0.3 m/s. Several weeks.	Annual or seasonal, irregular.	5-7 months per year.	Uncommon.

tems of different turnover, could have a very different ecological significance. Similarly, the number of species of a particular wetland could give little information if it is not complemented with that on the ecodiversity of the landscape and the habitat resources offered by the patches which are part of the analyzed landscape pattern. Some authors carry out difficult calculations referred to a system diversity, of which only small sectors are known. In some cases, estimations of the species which have become extinct, have also been made. The geographic extension and ecodiversity of the large South American wetlands (Tables 1-3) lead us to think that there is not enough scientific information to support these hypotheses.

Evaluations of specific diversity and/or species richness frequently end up with the presentation of numbers which try to explain the complexity of the system under study. Only rarely, we advance on the causes which determine the high or low diversity. For example, the fish fauna of South America known today is estimated at about 3,000 species, that is about 24% of all known fish species (Vari and Malabarba 1998). But very little is known about the past and present ecological conditions that could explain this complexity? Have the groups of species found today originated by current processes and interactions? Or when and as a consequence of which phenomena was the biotic complexity produced? In case of the freshwater fish, it has been demonstrated that the greatest part of the present day species were already found in the Middle Miocene, and that the geological and ecological events occurring from the end of the Miocene to the Holocene have had little importance in the increase of the number of families and genera of fish (Lundberg et al. 1998).

The treatment of the floral and faunal diversity at a continental and phylogenetic scale has recently started (Malabarba et al. 1998, Machado-Allison et al. 1999). Conceptual models, which allow to analyze biodiversity values in wetlands and reservoirs in a theoretical context explaining the dynamics of the aquatic systems, have also been formulated (Tundisi et al. 1999a,b).

Hydrologic Pulses and Diversity

Wetlands of South America are controlled by the pulse regime. The biotic complexity and specially the faunal diversity vary greatly in time and space depending on the hydrological period in which the diversity data are collected.

The ecological processes in wetlands (variability of the water sheet, nutrient fluxes) follow a sinusoidal pattern caused by temporal differences in the water availability and transported materials (organisms, dissolved and suspended solids). Each one of the waves is composed of positive and negative values in relation to the ordinate. The variability pattern of these waves in a temporal sequence – at some point of the waterlogged plain- or river section – constitutes the pulse regime (Neiff 1990, 1996, Neiff et al. 1994, Schnack et al. 1995, Tundisi et al. 1999a). The properties of the pulse regime were first defined for rivers. Today, the analysis of pulses in freshwater wetlands could explain to a great extent the complexity and variability of the biotic groups. The presence or absence of organisms (or size classes), their abundance, the duration and intensity of the reproductive period, the migratory movements and the proportions between herbaceous and woody plants are only some of the characteristics conditioned by pulses.

The *frequency of phases* of inundation or drought in a temporal series of various decades could select plant and animal bioforms in wetlands.

The *intensity* (or magnitude reached by a drought or inundation) could temporally exclude certain populations or sizes of plants or animals that inhabit the wetlands.

The *tension* or value of the standard deviation from the maximum or minimum means in a curve of pluriannual hydrometric fluctuation allows to establish the variability of the events of drought and inundation.

The *recurrence* is the statistical probability that an event of inundation or drought of a certain magnitude occurs within a century or millennium.

The *amplitude* of the phase is the duration of drought and inundation of a particular magnitude.

The *seasonality* is the seasonal frequency with which the droughts and inundations occur. The organisms that live in wetlands (except for the humans) have their reproductive rhythms adjusted to the season in which the inundation and drought occur. If only the pulse seasonality would be modified, impacts on biodiversity could be produced. In fact, all plants known for the South American wetlands cannot germinate with the soil inundated with only 5 cm deep water.

Variability has a sinusoidal pattern originating in the difference between the excess and deficiency of water in and on the soil at a regional level. This determines sinusoidal hydrometric curves in the hydrometers placed in the river course. Such value of the hydrometric rule in which the flooding is produced at a particular point of the river plain is considered as value 0. Those waves (or portion of them) which are found above this value are considered positive and define the period of inundation or *potamophase*. The hydrometer values which are found below, negative, correspond to a situation of isolation of the inundation valley in relation to the main course, also called dry phase or *limnophase*.

In the potamophsae, horizontal fluxes are produced (water, sediments, minerals, organisms, "information") from the river course to the floodplain. In the limnophase, the flux (not always transversal to the river course) carries information from the plain to the river course.

Requirements of predictability of the organisms are related to life time (decades for trees, lustrums for fish, days for plankton). Consequently, it is usual to find groups of organisms which have individual adaptations and population patterns better adjusted to the hydrometric variability in different sectors of the waterlogged plain. Almost all processes which occur in large wetlands have a positive or negative relationship with frequency, duration, magnitude and other characteristics of the sequence of the potamophase or the limnophase (Table 5). Transport and deposition of sediments (Drago 1994, Orfeo 1996); colonization, production and decomposition of the herbaceous and woody vegetation, consumption and mineralization of the organic matter, migratory activity of the organisms (Neiff 1990 and Neiff et al. 1994), fishing (Quirós 1990), activities of river settlers, tourism and other fluxes are adjusted to the river pulse regime.

Some structure are predominantly conditioned by the potamophase, others by the limnophase (called *phase strategists*), and still others are favoured by their ability to adapt to a wide range of hydrological conditions and are known as *eurytypical*. Some communities of organisms are more conditioned by the duration of a

Table 5. Processes associated with the pulse regime.

	Associated FITRAS Attribute		Author
Limnophase			
Increase of particulate organic carbon concentrations in the river	Intensity	+	4
Increase of nutrient concentration in floodplain lagoons	amplitude	+	3
Sediment exposition in the alluvial floodplain	amplitude	+	1,3
	intensity	+	
Increase of primary productivity in floodplain lagoons	amplitude	+	3
Increase of alpha diversity in lakes and lagoons and great decrease in herbaceous swamps	amplitude	+	3
	intensity	+	
Concentration of organisms in lakes and ponds (ecosystem stress caused by overloading)	intensity	+	3
	amplitude	+	
Bird reproduction and nestling	seasonality	+	3
	amplitude	+	
Colonization of exposed sediments by woody vegetation	amplitude	+	3
	tension	+	
Risk of natural and anthropic predation	amplitude	+	3
	intensity	+	
Beginning of fish migration from floodplain lagoons to the river	intensity	+	2
	seasonality	+	
Size and density of amphibian populations	amplitude	–	3
	seasonality	+	
Fire occurrence	intensity	+	3
	amplitude	+	
Fragmentation of floodplain aquatic habitats, replacement of lotic communities by lentic communities, particularly aquatic invertebrates and their predators (other invertebrates, amphibians)	amplitude	+	3
	intensity	+	
	tension	–	
Potamophase			
Transport and deposit of sediments in the floodplain	intensity	+	1
	amplitude	+	
Decomposition of terrestrial organic matter, detrital accumulation and increase of bacterial activity in sediments	intensity	+	2,4
	amplitude	+	
Reactivation of paleobeds	intensity	+	1
Integration of floodplain aquatic habitats, predominance of theophile communities	amplitude	+	3
	intensity	+	
	tension	+	
Increase of dissolved organic carbon in the river	amplitude	+	4
	intensity	–	
	frequency	+	
Fish mortality in lowlands, floodplains and tropical rivers	amplitude	+	6
	intensity	+	
	seasonality	–	
Germination of plants from seeds	amplitude	–	This study
	intensity	–	
	seasonality	+	
Abundance of phytophile invertebrates	intensity	–	5
Fish migration back to floodplain lakes	intensity	+	2
	seasonality	+	
Fish fecundity (gonad maturation and number of viable eggs)	intensity	–	This study
	amplitude	–	
	seasonality	+	
Habitat availability for large mammals	intensity	–	This study
	amplitude	–	
Habitat availability for amphibians	intensity	+	This study
	amplitude	+	

The sign + or – refers to that of the estimated or inferred correlation between the event and the attribute. 1. Drago (1994), 2. Quirós (1990), 3. Neiff (1990b, 1996); Neiff et al. (1994); 4. Paolini (1990); 5. Poi de Neiff and Bruquetas de Zozaya (1989), 6. Hamilton et al. (1997).

phase (e.g., inundations) than the magnitude of the phenomenon (Poi de Neiff and Bruquetas 1989).

The adaptation of organisms to drought and inundation varies with species and age of the population. In general, plants are adapted to persist in the inundated soil; many have growth rates even higher in this phase (Neiff 1990b, Joly and Crawford 1982, 1996). The production of fruits is reduced of fails completely during prolonged inundation. Many plants such as palms which grow in the extensive wetlands of the Orinoco, Paraguay or Paraná, could stay completely covered by water for a month. When inundation ends, they continue growing normally. When inundation of exceptionally high magnitude and duration occurs after a prolonged phase of dryness, a sharp decline in the dissolved oxygen together with a high CO_2 concentration in water often results in massive mortality of thousands of fish in the tropical floodplains (Hamilton et al. 1997). Many bird populations migrate during the inundation phase or do not complete their reproductive functions. Similarly, egg maturation is not completed in many fish when inundations of great amplitude and magnitude occur.

The extraordinary droughts produce drastic effects in fluvial forests because of the mortality of the herbaceous vegetation, the massive leaf fall from trees and shrubs, and the inhibition of flowering and fruiting. The occurrence of fire during extraordinary droughts is an associated factor which affects the vegetation and also the fauna.

Drought/Fire Events and Biotic Complexity

Fire and drought could occur by natural causes or provoked by humans to obtain different effects (e.g., to favour crops, cattle breeding, hunting of wild animals, etc.).

It is difficult to dissociate fire and droughts as ecological factors conditioning the biotic complexity of wetlands, especially because both occur together. Both depend on the seasonality of rains and also on a surplus of organic production of the vegetation that functions as fuel. Therefore, the effects of fire on the wetland biota is related to a great extent to the frequency, intensity and the season (seasonality). They are phenomena with a pulse dynamics. An important difference between the two processes as modifiers of biodiversity is that droughts have generally more gradual effects in time and more localized impacts. Fire is less predictable than droughts and also affects some organisms more than others.

On a landscape scale, all wetlands are influenced by droughts (dry phase of pulse). Fire has a great effect on some wetlands than on others. Among the nine types of continental wetlands of South America recognized in this study (Figure 2), types 3, 4, 7 and 8 are influenced most by fire. Wetland types 1, 2 and 5, when found in the same landscape, function as refuges or reservoirs for plants and animals during fires or after them. Wetlands of types 4, 7 and 8 are very frequent in the Savanna ecosystems, where fire has occurred for millennia. In these wetlands, there has been a favourable selection of plants with roots and rhizomes at a depth greater than 5 cm and especially of the Monocotyledoneae. Palms *(Copernicia alba)* colonize sites (wetlands type 4) subjected to periodic fires because the vascular bundles of the stems are not damaged by fire and the pericarp of their fruits is partially burned facilitating germination.

In these environments, birds are not much affected by fires, except when fire occurs in the reproductive season. Mammals in general are able to escape from fire by migrating or burying themselves (as burrowing animals and many amphibians do). Fish that live in wetlands of types 4, 7 and 8 are smaller than 20 cm, so that many find refuge in small ponds. Invertebrates, if there are small water ponds, are able to survive the fire and replace their populations in the rainy season. Some species of ants and termites build cupola-like nests ("tacurúes") of up to 1.5 m height, in which the population is protected from fire. Some species of *Atta* and *Acromirmex* are favoured by the frequency of fires.

Many fish of Savannah wetlands (types 3 and 4) are well adapted to anoxia produced by drought. *Oplosternon litorale* has the stomach with a profuse blood supply and incorporates oxygen from the air through osmosis after capturing it with the mouth. The dipnoan *Lepidosiren paradoxa* ("lola" or "lungfish"), an endemic species in South American wetlands, builds a cave in the bottom mud, blocking with mucus and sediment the cave entrance, and thus regulating the humidity and the entrance of gases during its long summer resting period.

Fire that frequently occurs when swamps get dry does not affect it because it raises the temperature by 3-4°C only in the first 5 cm of the soil and only for a few hours.

Fire as a Disturbance

In evaluating the effects of fire on biodiversity of wetlands, some distinctions should be made between the fire as a perturbation (fires occuring naturally without human intervention) and fire as a disturbance (fires caused deliberately by humans). The characteristics of natural fire (perturbation) and human-induced fire (disturbance) are compared on the basis of our experience (Table 6), though this synopsis has to be improved by future studies.

Experiments with controlled fire were made on a 5 ha area in the "Sábalo cattail swamp" (Chaco, Argentina). In the peripheral area of this wetland (of type 6), covered by *Cyperus giganteus* which was completely dry at the end of the winter, with a dead biomass accumulated on the ground of 18 Mg ha^{-1}, fire produced 2 m-high flames which lasted for 40 minutes. Although the temperature at 1 m above the ground reached 580°C (reducing all organic matter to ash) and temperature at the ground level reached 210°C for a few minutes, only a few degrees increase was produced at 3 cm depth (Figure 3). In some remaining ponds, water temperature increased by only 5°C during the experiment (reaching 24°C), and no dead animals were found after the experiment. Roots, rizhomes and rosette leaves of plants were not affected.

However, several questions still have to be answered. For examnple, could the results be extrapolated to wider areas with a combination of different types of wetlands? What happens when fire compromises an area of hundreds of km? What happens when the frequency of fires increases? How do high frequency climatic changes affect the frequency of fires and biodiversity?

Table 6. Possible impacts of fire on biodiversity of wetlands.

Characteristics	Natural fire	Fire disturbance	Comments
Frequency	Low: decades	High: 1-3 years	
Intensity	Very high	Medium-high	Depends on accumulated fuel
Tension	High	Low	
Regularity	Low	Medium-high	
Amplitude	High	Low	Duration of fire is inversely proportional to frequency and intensity
Seasonality	High: summer-fall	Medium: late winter-early summer	
Most affected wetlands (see Figure 2)	Types 3 to 9	Types 3, 4, 6, 7 and 8	Occasionally types 1 and 2
Vegetation	Selects adapted bioforms	Selects adapted bio-forms and modifies the proportion (biological spectrum)	Depends mainly on frequency
Predominance of Monocotyledons?	Variable, depends on frequency	Yes	
Exclusion of trees?			
Area of palm trees increases?	No	Yes	
Dominant bioforms	Yes Pterophytes/ Geophytes	Yes Geophytes/ Pterophytes	In wetlands, type 8
Fauna			
Reduces the number of species?	Moderately	Strong reduction	
Reduces number of niches?	Yes	Yes	Consequence of the reduction in available habitats
Interfered functions	Not known	Reproduction, feeding refuge	Very little information

Which Wetlands have Greater Species Richness?

It is very difficult to assess the species richness of wetlands because they are very elastic systems (Eq: 1.5 to 15; Table 3) with drastic changes in the available habitats. During the high water period many animals migrate and many plants (except trees) die and are substituted by others. Aquatic vertebrates and amphibians are able to explore several times greater area, resulting in a large dispersion of the organisms. In the dry phase, the density of aquatic and amphibian species which inhabit a water body is very high. For example, in the Pantanal of Mato Grosso, up to 150 alligators could be found in a 5 ha lagoon (Mourao and Campos 1995).

The literature available for the South American wetlands does not allow to relate quantitatively the species richness with the hydrological state of the system. Some studies have been made at the hydrographic basin level while others have covered a very small area (Table 7). Some of these studies have also considered the uplands within the wetland resulting in an overestimation of the number of species.

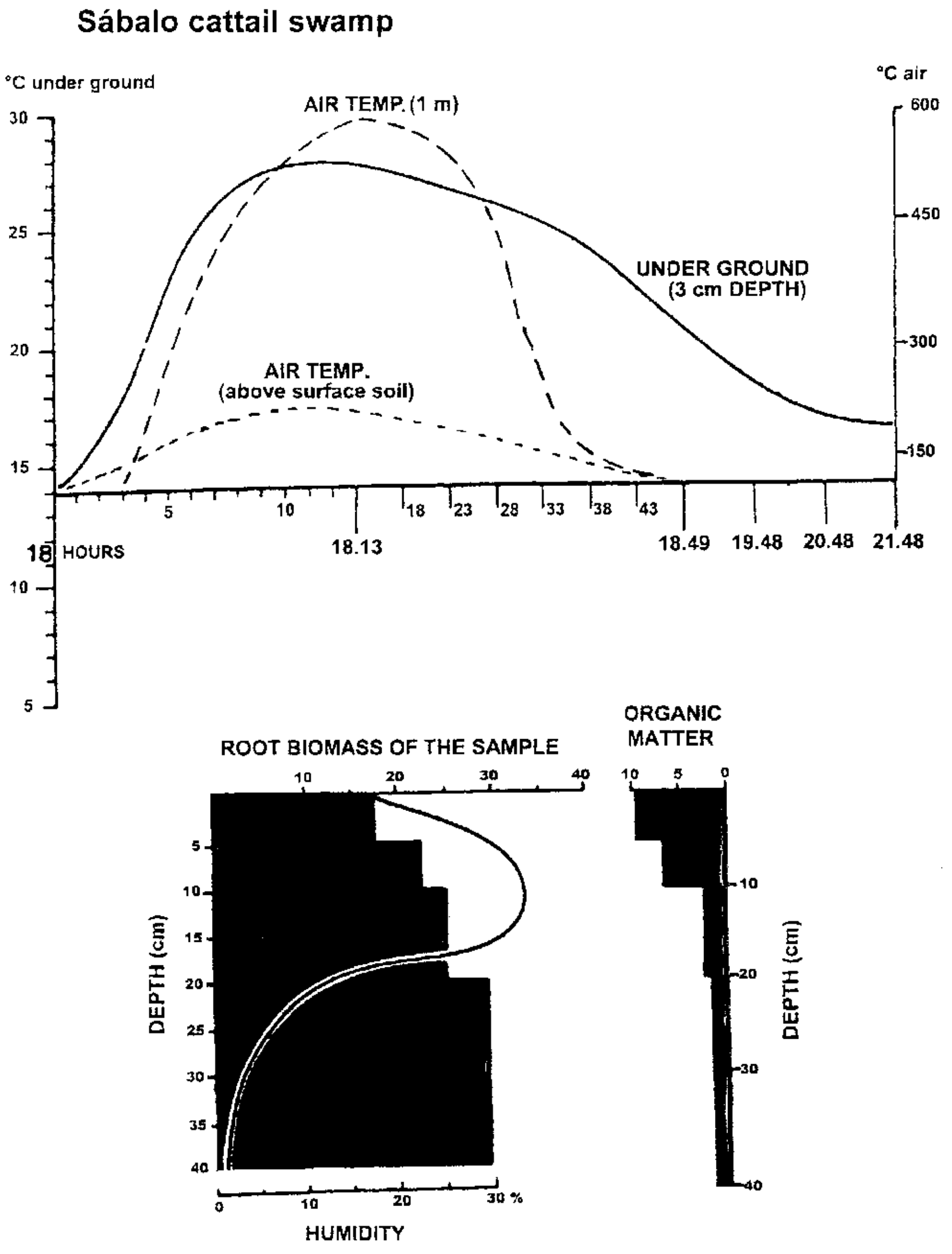

Fig. 3. Effect of fire in the Sábalo cattail swamp (Chaco, Argentina).

Table 7. Species richness in some tropical wetlands of South America.

Wetland system	Community landscape	Species number	Authority
Paraná River Delta Types: 1,2,3,5,7,9 Predominant: 1,2,7,9	The vegetation	632 Gra=47; Com=89; Leg=44; others=452	Malvarez (1997)
Paraná River Delta Types: 1,2,3,4,5,6,8,9			
Orinoco River Delta Types: 1,3,4,8,9	Ichtthyofauna	97 Sil; Cha; Perciformes	Ponte Johansons and Lasso (1995)
Claro River (Orinoco basin) Types: 1,2,3	Ichthyofauna	81 (D=0.73)	Taphorn and Garcia Tenía (1991)
Orinoco River Basin 1 to 9	Ichthyofauna	800 to 1000	Taphorn and Garcia Tenía (1991)
Orinoco floodplain system Types: 1,2,8,4,3,5,9	Ichthyofauna of the basin	494	Lowe-McConnell (1987)
Apure River Basin 1 to 9	Ichthyofauna	354 Cha=138	Taphorn (1992)
Lowlands of Cuyuní River (Orinoco basin) Types: 3,4,5,8,9,2	Ichthyofauna of the basin	136 Cha=32; Lor=19; Cich=16; Pim=15	Machado-Allison et al. (1999)
Lowlands of Orinoco (Western *Llanos*) Types: 9,3,4,1	Ichthyofauna	360	Taphorn and Garcia Tenía (1991)
Caris and Pao Basins (Orinoco region) Types: 2,1,4,5,8	Ichthyofauna	100	Machado Allison (1987)
Maporal stream (Orinoco basin)	Ichthyofauna	115	Machado Allison (1987)
Floodplain lakes of the Orinoco River Types: 1,3,9	Ichthyofauna	170 Cha; Sil; Cich	Rodriguez and Lewis (1990)
Lower Orinoco Floodplain lakes Type 1	Ichthyofauna	93 Cha=55; Sil=22; Per=8	
Low Paraná floodplain lakes Types: 1,3,4	Ichthyofauna	93 Cha=49; Sil=27; Cha=49; Gym=6	Cordiviola de Yuan and Pignalberi (1981)
Lowlands of Mogí Guaçu River (Paraná basin) Types: 1,5,9,2	Ichthyofauna of the lakes and surrounding wetlands, connected to the river	35 Cha=72.2%, Sil=11.1%; Per=8.3; Gym=5.6	Galetti Jr. et al. (1990)
High Paraná Riverine System Types: 1,2,3,4,5,9	Ichthyofauna	221	Agostinho et al. (1995); Araujo Lima et al. (1995)

Table 7. (Continued).

Wetland system	Community landscape	Species number	Authority
High Paraná River floodplain Types: 3,4,1,2,5	Phytoplankton	300	Agostinho et al. (1999)
	Phytoplankton (river channel, only)	113	Oliveira et al. (1994) Oliveira et al. (1994)
	Macrophytes	48	Souza et al. (1997)
	Periphyton (on *Eichhornia azurea*)	228	Rodrigues, L. (cited by in: Agostinho (1999)
	Zoobenthos	80	Takeda et al. (1997)
	Zooplankton	329	Agostinho et al. (1999)
	Ichthyofauna	170	Landsac-Toha et al. (1997) Agostinho et al. (1999)
Low Paraná River	Zooplankton	76-109 (only river course) 62-86 (river course + flood-plain wetlands)	José de Paggi (1980, 1984) José de Paggi (1983); Paggi (1980)
Iberá 1,3,4,5,6,7,9 Predominant: 6	The vegetation	1290 (Dicot. 896; Monocot. 362. Pter. 31) Gra=170; Leg=128; Com=117; Cyp=74	Arbo and Tressens (1997)
Wetlands of Pilcoma-yo floodplain River Types: 1,3,4,8,9	Ichthyofauna in the low basin	136 (Cypr=71; Sil=47; Perc=8; Others)	Menni et al. (1992)
Forested islands of the Pantanal of Mato Grosso Type: 9	The vegetation only sporadically flooded in a transection	108 Leg=13; Bign=8 Other 20 families with 1 sp.	Damasceno Jr. et al. (1996)
Savanna wetlands of Panatal (Brazil) Types: 1,3,4,8,2,7,9	Ichthyofauna of the lakes and surrounding wetlands	Fi=262; An=45; Re=162; Bi=700	Kawakami de Resende (1998)
Forested Peatlands of Taim (Brasil) Type: 6	Trees of Peat forest	12-D=1,88 Leg. Dominants	Waechter and Jarenkow (1998)

References: Monocot = Monocotyledons; Dicot = Dicotyledons; My = Macrophytes; Tr = Trees; Pter = Pteridophyta; Gra = Gramineae; Leg = Leguminosae; Com = Compositae; Bign = Bignoneaceae; Fi = Fishes; Re = Reptiles; An = amphibians; Bi = Birds; Ma = Mammals; In = Invertebrates.

Apparently, the species richness varies with the area of the wetland system and hydrophase during sampling.

The wetland systems with highest ecodiversity (Tables 4 and 7) have higher species and bioform richness at a potential specific richness level, i.e., of expected species. This is due, to a great extent, to the fact that each patch of the environment has its own species complex. The presence/absence data for some 1,600 species inhabiting the six main types of wetlands in the Paraná-Paraguay river basin (about two million square kilometers) show poor affinity between the wetlands, i.e., each landscape unit has a characteristic complex of species, and less than one-third part of them occur in some other patches of the landscape types in a river basin.

Most of South American freshwater wetlands are included in the basins of the large rivers. Wetlands related with the pulse regime have higher species richness. However, there are wetlands which are currently isolated from the fluvial dynamics (e.g., Iberá, Figure 1) but have a very high species richness due to the high ecodiversity and the connectivity of landscape patches of Paraná, Paraguay and Uruguay river basins.

Many studies on wetland biodiversity include all plant and animal species which occur in the geographical area occupied by the particular wetland system (including species which grow in mountains or on the upland). Although the wetlands and uplands exhibit connectivity that is most evident for the birds, I consider here only those species which depend on the fluctuation of the water level.

Biota of Different Wetland Types in the Paraguay-Paraná Riverine System

The Paraná-Paraguay system is a mega-laboratory for the study of wetland biodiversity, not only because 40% of the South American continental wetlands and a huge ecodiversity exist here, but also because this fluvial system, with its axis oriented in a N-S direction from 20°S to 35°S Latitude, passes through different climates and receives water and sediments from two main geographic centers of distribution of the continent: the Brazilian Shield and the Andes mountains.

During the 20th century, more than 2,500 species of plants were recorded in the wetlands of the Paraguay-Paraná system (TGCC 1997). Of these, some 1,600 plant species occur in wetlands influenced by river pulses. According to this study, the forested wetlands were the most species-rich environments whereas the cattail swamps and the tall grass wetlands had least diversity – only about half of that in the forested wetlands (Table 9). Another outstanding feature is that the probability of occurrence of trees in wetlands decreases with increasing duration of flooding with stagnant water. However, some species are adapted to organic soils that are permanently flooded in the Iberá cattail swamps and in some islands of the Paraná river. Shrubs are also influenced by this characteristic, although they could survive at sites somewhat less flooded. Herbaceous plants and soft grasses have a large

Table 8. Similarities (Jaccard Index) of vascular vegetation in different wetland types of the Paraguay-Paraná riverine system.

Wetlands types	Flooded gallery forest	Palm wetlands (Savanna)	Hard tall grasses wetlands	Short and soft grasses wetlands	Cattail/ bulrushes swamps	Lakes/ ponds littoral
Flooded gallery forest	1					
Palm wetlands (Savanna)	0.19	1				
Hard tall grass wetlands	0.14	0.47	1			
Short and soft grass wetlands	0.15	0.24	0.43	1		
Cattail/bulrush swamps	0.06	0.11	0.27	0.28	1	
Lakes/ponds littoral	0.04	0.09	0.17	0.24	0.18	1

Table 9. Potential species richness of vascular plants in wetlands of the Paraguay-Paraná riverine system. The number of species in each column was compiled from different publications during the past thirty years. Each species can be included in one or more columns.

	Wetland type					
Biotic Group	**Forested wetlands**	**Palm water-logged Savannas**	**Hard tall grasses wetlands**	**Water-logged short and soft grasses**	**Cattail and bulrushes swamps**	**Littoral zone of the lakes**
Total number of vascular plant species	450	314	206	405	216	282
Trees	61	17	11	5	7	0
Herbs	312	186	149	307	19	219
Shrubs	72	88	19	12	6	11
Geophytes	5	23	27	69	84	52

number of species in all environments (Table 9) because they have a short life cycle and are adapted to varying periods of inundation. Most of these plants are adapted to fire pulses and are vegetatively or sexually regenerated.

The TGCC study (1997) also compiled data on the fauna of the Paraguay-Paraná system on the basis of published studies and field surveys (Table 10). These data represent only preliminary results, and are valid only for analysis at 1:500,000 to 1:1,000,000 scale. It seems that the highest species richness of vertebrates is found in wetlands with short and soft grasses where 14% more species occur than in the forested wetlands. The lowest diversity occurs in the cattail and bulrush swamps, which support only about 100 vertebrate species (Table 10). Interestingly, about 20 fish species depend on the forested wetlands and more than one-third of the fishes of the fluvial system visit the forested wetlands during flooding.

These results are similar to those reported for the Orinoco river basin and other large South American rivers which are better investigated for their fish communities (Table 7). Roughly, less than 100 fish species could be found in wetland systems associated with the first- and second-order rivers, and between 300 and 1,000 species in the fifth- or higher order rivers. An exception is the Amazon basin where more than 2,500 fish species have been recorded (Lowe-McConnel 1987, Junk 1993, Lundberg et al. 1998).

Rivers as Corridors between Wetlands

Undoubtedly, rivers favour the dispersal of animal and plant organisms as adults, seeds or eggs. But, do all basin wetlands have a similar diversity? Are there more species in wetlands next to a river course or in the floodplain which is more distant from the course? As the rivers are vectorial systems, is the number of species higher near the mouth? There is surely not a unique answer, because of geographical and hydrological differences, or because there is not enough information, especially for large rivers. The answer will also be different depending on the group of animal or plant organisms analyzed.

Table 10. Potential species richness of fauna in wetlands of the Paraguay-Paraná riverine system. The number of species was compiled from different publications. Each species can be included in one or more columns (Taylor et al. 1996).

	Wetland type					
Biotic Group	**Forested wetlands**	**Palm water-logged Savannas**	**Hard tall grasses wetlands**	**Water-logged short and soft grasses**	**Cattail and bulrushes swamps**	**Littoral zone of the lakes**
Expected number of vertebrates	307	235	219	355	101	201
Birds	218	107	61	207	32	58
Mammals	28	39	51	42	15	22
Reptiles	31	55	64	25	13	19
Amphibians	9	7	13	39	18	43
Fish	21	27	30	42	23	59

In the Paraguay-Paraná system, the greatest algal species richness occurs in the high basin, in the Pantanal of Mato Grosso, where Zalocar (1999) found almost 600 species. Differing from other rivers, the algal species richness falls markedly when the Paraguay River leaves the Pantanal (175,000 km^2) system, and exceeds 200 species in the lower section of the river (Zalocar 1999). A similar trend is noted for the number of fish species: almost 400 species recorded in the upper basin of the Paraguay (Pantanal) and only about 230 species in the lower section next to the Paraná delta. Both communities greatly depend on the assembly and area covered by different types of wetlands (ecodiversity) of the fluvial system.

However, the vascular plants behave differently. In the delta there are about 800 species which depend on the pulse dynamics in the wetlands linked to the river, and this number is equal to or somewhat higher than that in the higher basin (TGCC 1997, Malvárez 1997, see also Table 7).

Equally interesting is the variation in the biotic complexity (number of species) in the fluvial wetlands from the river course to the outer, distal part of the flood plain. Marchese and Ezcurra de Drago (1992) reported an increase in the number of species of benthos from the river course of Low Paraná to its floodplain boundary. Zalocar (1999) observed a similar phenomenon for the phytoplankton in the wetlands of this river. It is also known for the River Paraná that the number of species and bioform spectrum of the vegetation increases in the long term (over millennia) when the connectivity is totally interrupted – an event that occurred in Iberá (Neiff 1997). Iberá, with 1,359 plant species (Arbo and Tressens 1997), corresponds to the old floodplain of the Paraná from which it became isolated during the Pleistocene.

Disturbance and Wetland Diversity

Pollution

South American wetlands are less affected by pollution than those in other continents. This is not due to a greater ecological awareness, or because the law is more efficient, but because the conditions in Nature are different. In South America, wetlands are generally larger in size, a greater part of the water comes from local rains. The population density is relatively low and so is also the industrial development. The agriculture has lesser technological inputs together with a lower use of agrochemicals. Therefore, the load of toxic substances and their residence in the environment is spatially and temporally lower than in other continents. Yet, in the 1990s were recorded massive fish mortalities; for example, the one in the Paraná delta in 1993 when 8,000 Mg of fish died due to the biocides used in agriculture. Pollution, acute or chronic, does not allow populations to develop adaptive responses, and always results in a sharp fall in biodiversity selecting only the resistant and tolerant organisms.

Anthropic Alterations of the Hydroperiod

The wetland landscape could be drastically altered by the anthropic modification of the inundation and drought phases. Table 5 shows how some processes and functions depend on the pulse attributes.

Civil engineering works for diversion of water courses, channelization for improvement of navigation and also the reservoirs built on the rivers could have important effects on the functioning of wetlands and their biodiversity. The impacts on the biodiversity of these systems depends upon the quality, magnitude and frequency of the alterations. It is not possible to generalize the impacts produced by civil constructions on biodiversity of South American wetlands, especially because there are few quantitative studies published. Some studies have reported drastic alterations in the landscape dynamics and in their biotic components (Colonnello 1995). In southern Brazil and Uruguay, large areas of wetlands has been altered for rice cultivation which also requires modification of the duration of flooding and removal of all existent biodiversity to avoid competition with the rice. After 3-5 years of rice cultivation, these fields are abandoned, and there proceeds a secondary succession characterized by a biological spectrum which is very different from the one found before the rice cultivation (Neiff 1997).

Is Diversity a Sensitive Indicator in Large Wetlands of South America?

In conclusion, biodiversity should not only be considered a synthetic attribute of the complexity of wetlands, but also a consequence of the landscape ecodiversity, of its extension, of the source of water, the nutrient provision, the climatic/hydrological variability, the fire regime and the quality and magnitude of the anthropic interventions. In this context, the species richness could be an indicator of the life conditions existing in the wetlands. But to be used as a good indicator, the studies should specify the spatial and temporal scale. It is necessary to consider the turnover of species in the system, because many wetlands have a relatively constant value of complexity (expressed as number of species or any of the indices of specific diversity), although there is a high qualitative renewal of the system elements. Also, wetlands have a variability regime very different from the aquatic systems and from that of the upland, so that the values of biodiversity could have a different significance. Systems with a low number of species could be very stable and vice-versa. Hence, diversity as an expression of functional complexity could be studied advantageously with indices which allow to reflect the fluxes (information in the wide sense) through the system (Neiff 1996, 1999).

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