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Overview Article

Biodiversity and its conservation in the Pantanal of Mato Grosso, Brazil†

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Abstract. The Pantanal of Mato Grosso, Brazil, is famous for its luxurious plant and animal life. We combine a literature review with recent work and show that species diversity is large but that most major plant and animal groups contain a large number of not wetland-specific species that depend on permanently terrestrial habitats within the Pantanal, or are restricted to dry areas during the low water period. These species occur also in the neighbouring biomes of Cerrado, Amazon Forest or Chaco. Until now, very few endemic species have been described, however, there are large populations of species in the Pantanal that are considered rare or endangered in South America. The number of trees adapted to long term flooding is low in comparison with the Amazon River floodplain. We hypothesize that the reason for the lack of local endemisms and the occurrence of a large number of species with a large ecological amplitude is the climatic instability of the region of the Pantanal, which suffered severe drought during glacial periods. The instability of the actual climate, which is characterized by multi-annual wet and dry periods, has a strong impact on distribution, community structure and population size of many plant and animal species and hinders spatial segregation of populations. The dependence of the system on the flood pulse makes the Pantanal very vulnerable to human induced changes in hydrology and the predicted changes in global climate.

Key words. Pantanal; seasonal wetland; floodplain; neotropics; Paraguay River.

Introduction

Wetlands are among the most fragile and threatened ecosystems on earth as they are subject to the impact of human activities – both on land and in water (Gopal and Junk, 2000). They accumulate substances from the catchment area that can be detrimental to environmental conditions and wetland organisms. Changes in hydrology, as for instance water deviation for agriculture, channelization to improve ship traffic or the construction of dams for hydroelectric power generation, may seriously affect fundamental wetland structures and functions. Natural

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† Dedicated to our collegue Dr. Vangil Pinto da Silva, who was killed in March 2004 by African bees during an excursion in the Pantanal.

multi-annual dry and wet episodes affect wetlands much more than most other ecosystems because a change in the annual amount of precipitation of a few decimeters often changes considerably the area covered by water, the water depth and the water balance with dramatic consequences for the organisms living there.

Despite a heavy and still increasing human pressure on extent and integrity of wetlands in general and tropical wetlands in specific (Junk, 2002; Tockner and Stanford, 2002), there are heavy deficits in knowledge of aquatic biodiversity, mostly in the tropics. Studies concentrate on few plant and animal groups only and often draw conclusions about biodiversity from rather incomplete species lists. Ecological information is dispersed in individual publications and there is a lack of a comprehensive analysis of the available data under conceptional considerations.

The Pantanal of Mato Grosso, a large wetland in the center of South America, is a good example for this situation. A comprehensive taxonomic inventory exists about fishes (Britski et al., 1999). A checklist of the flora was published by Pott and Pott (1996). Aquatic macrophytes have been well described including information on growth form and utility by Pott and Pott (2000). Regional inventories also exist of terrestrial grasses, herbs and trees (Prance and Schaller, 1982; Prado et al., 1992; Lemes do Prado et al., 1994; Schessl, 1999). Dispersed information is available about vertebrates, however at varying level of taxonomic and geographic scope, e.g., Schaller (1983) and Mauro and Campos (2000) on mammals from the municipality of Corumbá, Cintra and Yamashita (1990) and Strüssmann and Sazima (1993) on birds and snakes, respectively, from the region of Poconé, and Leite et al. (1998) on bats from Aquidauana and Nhecolândia. Gray literature from the Pantanal largely surpass indexed articles and there are many doubtful and not documented records. Inventories of aquatic and terrestrial invertebrates are incomplete or totally missing. First attempts have been made to relate general information on biodiversity with ecological concepts (da Silva et al., 2001).

In this paper we summarize data on species numbers of major plant and animal groups and classify them according to their distribution and life form under the theoretical framework of the Flood Pulse Concept (Junk et al., 1989; Junk, 2005; Junk and Wantzen, 2004). The description of the species categories reflects the differences in the amount of available information. References are given to the neighbouring Amazon River floodplain that shares many species with the Pantanal, but differs with respect to environmental variables, such as amount and distribution of rainfall, amplitude of the flood pulse, and nutrient status of water and sediments. The results are discussed in the light of the data about actual climate and paleoclimatic history, management policy and predictions about global climatic change.

Definition and classification of wetland species

The Pantanal belongs to the category of temporary wetlands subject to a predictable monomodal flood pulse (Junk et al., 1989). This wetland type is very common in the tropics and sub-tropics with a strongly seasonal rainfall pattern. Large parts of these wetlands become completely dry during the low water period and are colonized by terrestrial plant and animal species that may or may not be wetland specific. However, these species are integral parts of the wetlands because they contribute considerably to bioelement cycles, food webs, primary and secondary production, community structure and biodiversity.

These considerations have been taken into account by Gopal and Junk (2000) who define as wetland species "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". To be useful in practice, this comprehensive definition requires a subdivision in different categories according to distinct taxonomic units: (a) residents of the proper wetlands (specific to wetlands in general with a subgroup of endemics and residents not specific to wetlands), (b) regular migrants from deep water habitats, (c) regular migrants from terrestrial uplands, (d) regular migrants from other wetlands (for instance waterfowl), (e) occasional visitors, and (f) those dependent on wetland biota (for instance epiphytes, canopy invertebrates, and parasites).

This broad view and classification of species living in wetlands allows further sub-classification according to adaptations and life history traits that are driven by specific environmental variables. The level of complexity of reactions of the biota to the environmental conditions of a specific wetland is, in addition to the number of species and their singularity, an important parameter for environmental analyses. It allows the formulation of criteria for comparison of biodiversity between wetlands and the development of hypotheses about their role in speciation of organisms. A broad definition of wetland biodiversity is also essential for the management of biodiversity in a landscape perspective.

Ecological characterization of the Pantanal

The Pantanal is situated in the depression of the upper Paraguay River 16–20º S and 55–58º W that extends between the old crystalline shield of Central Brazil and its transition zone to the foothills of the geologically young Andes. The upper Paraguay River catchment area covers about 496,000 km^2, the Pantanal about 160,000 km^2, of which about 140,000 km^2 belong to Brazil, 15,000 km^2 to

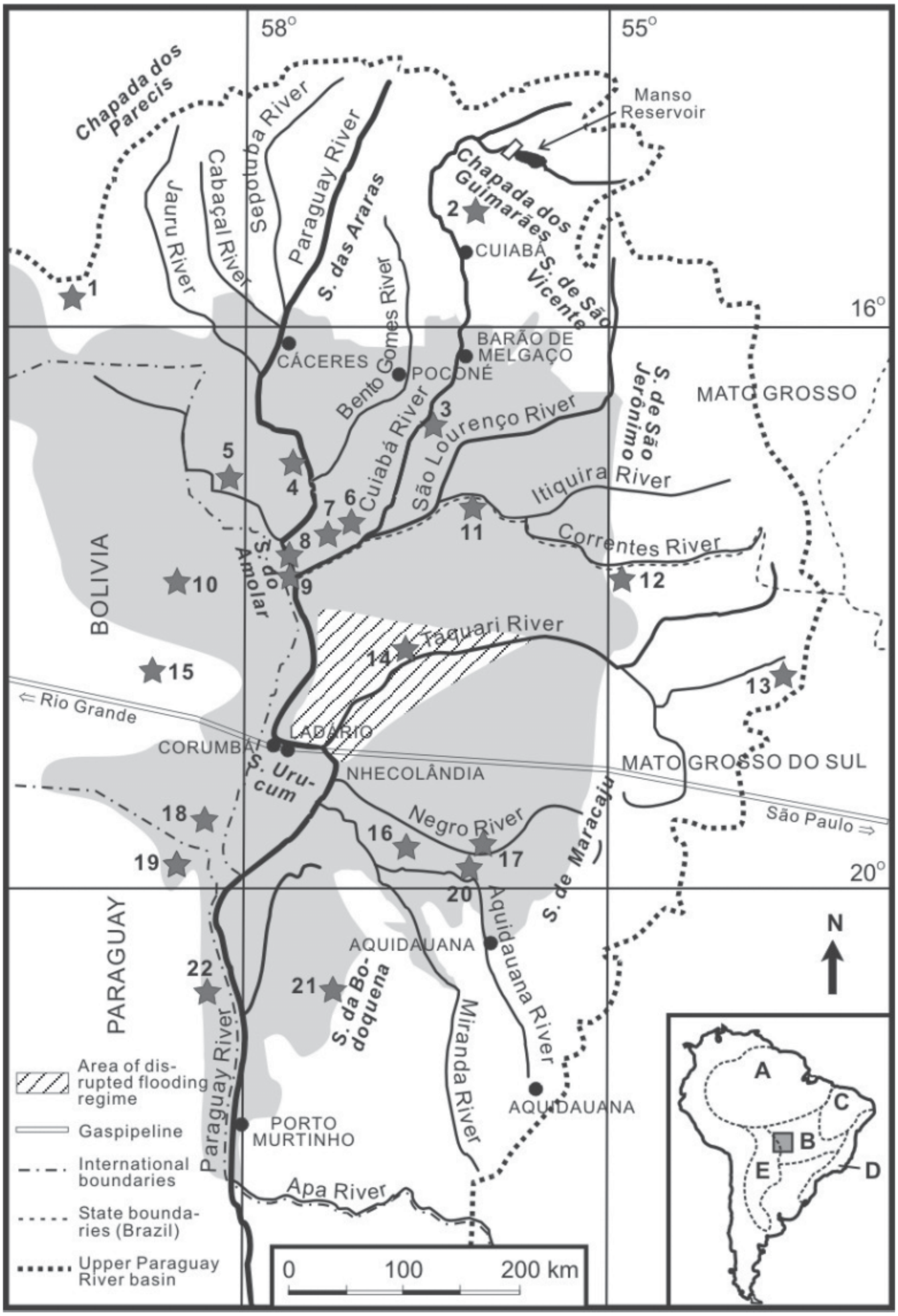

Figure 1. Map of the Pantanal and its catchment area and position of protected areas. 1 = Serra de Ricardo Franco State Park, 2 = Chapada dos Guimarães National Park, 3 = Serviço Social do Comércio Pantanal Private Reserve, 4 = Ecological Station Taiamã, 5 = Guira State Park, 6 = Private Reserve Dorochê, 7 = Pantanal National Park, 8 = Private Reserve Acurizal, 9 = Private Reserve Penha, 10 = National Reserve of Integrated Management San Matias, 11 = Fazenda Poleiro Grande Private Reserve, 12 = Serra de Sonora State Park, 13 = Nascentes do Rio Taquari State Park, 14 = Fazenda Nhumirim Private Reserve, 15 = Reserva Municipal del Valle de Tucavaca, 16 = Complex of the Pantanal do Rio Negro State Park and the Private Reserves Fazendinha and Santa Sofia, 17 = Fazenda Rio Negro Private Reserve, 18 = National Park and National Reserve of Integrated Management Otuquis, 19 = Rio Negro National Park, 20 = Dona Aracy Private Reserve, 21 = Serra da Bodoquena National Park, 22 = Fazenda Rancho Seguro and Tupaciara Private Reserves. For details see chapter 6. The hatched area around Nr. 14 indicates the area affected by the the hydrological changes at the lower Taquari River. The small map indicates the position of the Pantanal in South America and the biomes indicated in the text. A = Amazon forest, B = Cerrado, C = Caatinga, D = Atlantic forest, E = Chaco.

Bolivia and 5,000 km^2 to Paraguay (Fig. 1). The main period of subsidence resulting in the wetland depression is very likely related to the last compressional pulse of the Andes during the upper Plio- lower Pleistocene about 2.5 million years ago. The depression is surrounded by different geological formations which form the catchment area of the upper Paraguay River and its tributaries (Ussami et al., 1999). On the Brazilian side, eastwards, most common are sandstones of different age (Chapada dos Parecis, Chapada dos Guimarães, Serra de Maracaju, Serra de São Jeronimo). The Serra das Araras and Serra da Bodoquena are build by limestones (Fig. 1). There are also some minor granitic outcrops (Serra de São Vicente). In the western border Precambrian massifs of Urucum and Amolar establish abrupt ecotones with the seasonally flooded plains of the Brazilian Pantanal.

The major part of the depression is covered by leached Pliocene/Pleistocene sediments of fluvial and lacustric origin which are in part consolidated and lateritic. They are sandy and acidic with varying clay content and high aluminum content. 92 % are hydromorphic, 66 % are sandy and 70 % are of low fertility (Amaral Filho, 1986). In some areas soils have a high sodium content (RADAM-Brasil, 1982). Along the river courses deposits of recent sediments are found.

The Pantanal is situated in a circumglobal belt of climatic instability. Dramatic climatic changes during the Quaternary led to intermittent periods of large scale flooding and severe drought. During the last glacial period rainfall in the catchment area of the Paraguay River was much lower than today. Superficial but intense erosive processes in neighboring plateaus occurred, as well as continuous accumulation of sediments inside the depression, as indicated by studies on the alluvial fan of the Taquari River (Short and Blair, 1986; Ab'Saber, 1988). The Pantanal was almost dry and offered only scarce opportunities for wetland ecosystem development. During the Holocene, the Pantanal passed through different climatic episodes that are not fully understood yet (Assine and Soares, 2004). The following climatic episodes can be distinguished: 40,000–8,000 BP cool and dry, 8,000–3,500 BP warm and wet, 3,500–1,500 BP warm and dry and 1,500–Present warm and wet (Iriondo and Garcia, 1993, Stevaux, 2000).

Today, the climate in the Pantanal is hot with a pronounced dry season from May to September and a rainy season from October to April (Fig. 2). Annual rainfall decreases from 1,250 mm in the northern part near Cáceres to 1,089 mm in the southern part near Corumbá. Near Cuiabá, mean monthly temperature varies between 27.4 °C in December and 21.4 °C in July. Short-term ingressions of subpolar air masses can lead to a drop in air temperature to 0 °C. Pluriannual extreme dry and wet periods lead to extreme flood and drought events combined with large wild fires inside the Pantanal with dramatic consequences for fauna and flora (Fig. 3).

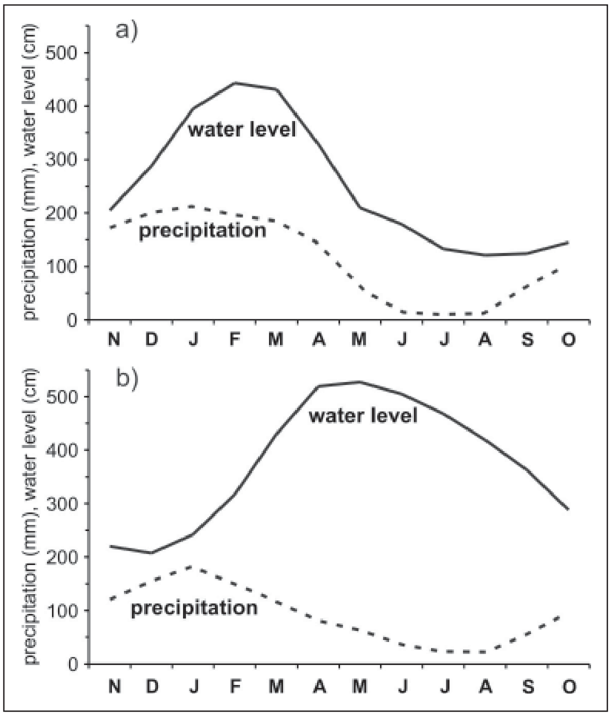

Figure 2. a) Mean monthly precipitation near Cuiabá (1933–1993) and mean water level of the Cuiabá River at Cuiabá (1971–1988), northern Pantanal, (according to Zeilhofer, 1996), and b) mean monthly precipitation near Corumbá (1912–1971) and mean water level of the Paraguay River at Ladário (1979–1987), southern Pantanal (according to Hamilton et al., 1999).

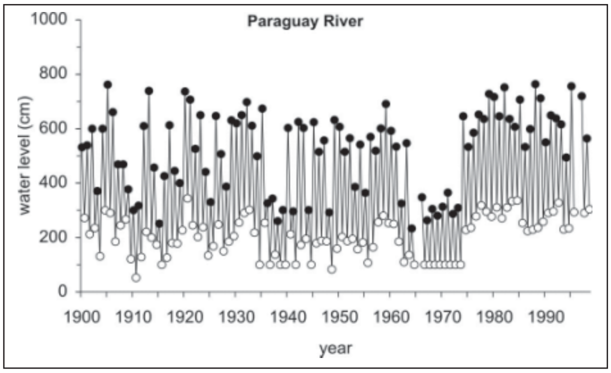

Figure 3. Annual water level fluctuations of the Paraguay River at Ladário from 1900 to 2000 (data according to DNAEE – Departamento Nacional de Águas e Energia Elétrica). ● = maxima; ○ = minima.

Flooding occurs by transbording rivers and local rainfall. Therefore the flood regime inside the Pantanal is variable and flow direction in the drainage system may change frequently from and to the river depending on the relationship of local rainfall and river stage. Because of the slight declivity of the terrain of 2–3 cm per kilometre in north to south and 5–25 cm in east to west direction flood waters require about 3–4 months to pass the Pantanal (Alvarenga et al., 1984). Therefore the flood pulse in the northern part coincides with the rainy season but there is a time lag of about 3 months between rainy season and flooding in the southern part (Fig. 2b).

Different discharge patterns of the Paraguay River and its tributaries during geological time periods resulted in a mosaic of geomorphologic formations and large habitat diversity inside the Pantanal (Jimenez-Rueda et al., 1998). Remnants of paleo-levees, for example, which rise one to two meters above the mean flood level, locally called *capão,* if circular, and *cordilheira*, when string-like, occur throughout the Pantanal and are important habitats for little flood adapted plants and refuges for terrestrial animals during floods. A characterization of the different habitats is given by Nunes da Cunha et al. (in press) and Wantzen et al. (2005).

Tributaries of the Paraguay River have individual flood patterns and sediment load. Therefore the Pantanal has been divided into 10 different subunits by Adámoli (1981), 12 subunits by Alvarenga et al. (1984), and 11 subunits by Silva and Abdon (1998). Flooding level and discharge of the sub-basins varies considerably according to regional rainfall (Hamilton et al., 1996).

Because of the large impact of local rainfall, the chemical composition of the water of the Paraguay River and its large tributaries can be traced only in areas near the river channels. Biogenic processes and evapotranspiration further modify the chemical characteristics of the water bodies inside the Pantanal. Depending on the position in the floodplain, lake water can be concentrated by evaporation, diluted by rainwater and enriched or diluted by the rivers. Mean electrolyte content of the upper Paraguay River is 47 µS cm^{-1} that of major tributaries varies between 32 µS cm^{-1} (Taquari River) and 159 µS cm^{-1} (Miranda River). Electric conductance of permanent lakes varies between 10 and 240 µS cm^{-1}. Isolated lakes (*salinas*) in the southern Pantanal have brackish water with electric conductance of up to 5,200 µS cm^{-1}. pH values in rivers and lakes vary between 5.5 and 7.5 but reach up to 9.8 in salinas (Hamilton et al., 1999). Algal blooms are frequently observed during low water period because of nutrient enrichment by decomposing organic material and animals that concentrate in and around remaining water bodies. Large differences in water chemistry and hydraulic conditions between catchment zone streams and floodplain water bodies inhibit a colonization of the Pantanal by rheophilic and oxygen-demanding aquatic organisms from the small tributaries, such as many fish species and Podostemaceae (Willink et al., 2000).

Biodiversity of different plant and animal groups

Algae

Algae occur in the Pantanal as periphyton on macrophyte roots and logs, as phytoplankton in lakes and rivers and – as an intermediate form of both types – as flakes of metaphyton, i.e. conglomerates of algae (mainly desmids and diatoms) and dead organic matter (Adler, 2002). The organic core of these flakes derives mostly from decomposing macrophytes (e.g., Fellerhoff et al., 2003). We believe that many of the algal species can occur in all three communities.

Table 1. Number of the algae species in the Pantanal according to De-Lamônica-Freire and Heckman (1996). The Desmidiaceae (numbers in parentheses) make up the largest part of the Chlorophyta. Some taxa occur during more than one phase of the flooding cycle.

		Water level			
	Sum	rising	high	falling	low
Cyanophyta	17	7	0	6	9
Euglenophyta	56	30	11	17	44
Pyrrophyta	2	1	0	0	2
Chlorophyta	226	127	124	82	77
Desmidiacea	(138)	(78)	(92)	(61)	(30)
Chrysophyta	7	3	1	3	7
Bacillariophyta	28	11	8	18	21
Charophyta	1	0	0	1	0
Total	337	179	144	127	160

Currently, 337 species have been identified from various floodplain habitats in the Pantanal, most of which are cosmopolitan or circumtropical (De-Lamônica-Freire and Heckman, 1996; Table 1). Following the floodpulse-induced change from dilution and concentration of the nutrients, the algae show a characteristic seasonal change. During the rising water period, diversity was reduced and tolerant species like *Scenedesmus quadricauda* and *Closterium ehrenbergi* prevailed. When the water level was highest, the water became crystal clear, as planktonic and benthic algal densities were strongly reduced in the open water and on open sediments, respectively. Differently from temperate lakes, algal grazing by cladoceran crustaceans plays a minor role as a cause for this clear-water stage in the Pantanal. When the water level dropped again, De-Lamônica-Freire and Heckman (1996) observed only few changes in the species assemblages, but a strong increase in the abundance of diatoms. In the water bodies remaining during the dry phase, the prevalence of desmid species from the former phases changed into an assemblage composed by larger proportions of euglenophyte, bacillariophyte and other chlorophyte species (De-Lamônica-Freire and Heckman, 1996). In puddles where caimans and large numbers of fish get crowded, the water becomes intensively colored by high concentrations of blue-green algae (especially *Microcystis*) including highly toxic strains (S. Azevedo, São Paulo, pers. comm. to KMW). These habitats show extremely high day to night oxygen variability (Nogueira et al., 2002).

In a quantitative study on the purely planktonic species of the Paraguay River and a floodplain lake near the City of Corumbá, Oliveira and Calheiros (2000) identified 82 taxa, dominated by chlorophytes (23 species). The river plankton was quantitatively dominated by cryptophytes (e.g., *Cryptomonas brasiliensis*) most of the year and showed high proportions of bacillariophytes (e.g., *Aulacoseira distans*) and cyanophytes (e.g., *Oscillatoria* sp.) during the falling water level. They also observed a seasonal change in the community composition but comparisons with the former study are difficult due to methodological differences. Oliveira and Calheiros (2000) measured a strong increase of the algal density in the floodplain during the flooding phase and an increase of phyto- and zooplankton abundance in the river when the water left the floodplains.

In the shallow flooded areas of the Pantanal, the sequential dominance of algae (at the beginning of the flooding) and aquatic macrophytes (at the peak of the flood) can be observed every year. These alternating stable states (Scheffer and Jeppesen, 1998) are probably caused by the fast numerical response of algae to increased nutrient availability and the accessibility of nutrients from the sediments during the high water phase to the roots of the macrophytes which also reduce the algal densities by shading (Adler, 2002). These spatiotemporal patterns in algal diversity and abundance underline the importance of the floodpulse as a driving agent in floodplain structure and productivity.

Higher Plants

The Pantanal belongs to the Cerrado biome, a vegetation complex that is composed by different savanna types. It borders in the south on the Chaco biome and in the north on the Amazon forest biome. According to Eiten (1982), the Pantanal is considered a "hyperseasonal savanna" that means a savanna subject to prolonged flooding. The floodplain is interspersed with small elevations of ancient and recent fluvial origin. Few decimeters change in elevation have dramatic importance for the environmental conditions in floodplain habitats because they influence length and depth of inundation and drought stress. Highest elevations in the Pantanal floodplain reach only about two meters above the mean flood level and are permanently dry or flooded for very short periods only during extreme flood events. They are covered by deciduous or semi-deciduous forests with trees shedding leaves during the dry season. Near the edges of the floodplain, there are some isolated outcrops from the surrounding mountains ("inselbergs") that are covered by deciduous forest and Cerrado vegetation. In lower areas along rivers and channels, evergreen floodplain forests are found, although they may shed part of their leaves during extreme drought or flood stress. At intermediate levels, different types of periodically flooded savannas occur, such as termite mound savannas, seasonally flooded woodland savannas and low tree-and-scrub woodland savannas (Eiten, 1982; Coutinho, 1982; Ratter et al., 1988; Nunes da Cunha et al., in press).

About 144 families of phanerophytes are estimated for the Pantanal (Pott and Pott, 1996; 1997): 104 families are exclusively terrestrial, 21 families exclusively aquatic and 19 families include terrestrial and aquatic species. The total number of species yet recorded amounts to 1,903, with 247 species considered aquatic macrophytes or hydrophytes and 1,656 species terrestrial (Pott and Pott, 2000). Of this number 900 species are grasses, herbs, vines, epiphytes, and parasites and 756 species are woody plants (shrubs, sub scrubs, trees, lianas and palms) (Fig. 4). Considering the fact that not all parts of the Pantanal have been sampled adequately, total species number may rise to about 2,000. The common occurrence of cacti (*Cereus kroenleinii, C. peruvianus, Harrisia bonplandii, Opuntia bergeriana, O. retrorsa, Aporocactus flagelliformis, Pereskia sacharosa*) and the low number

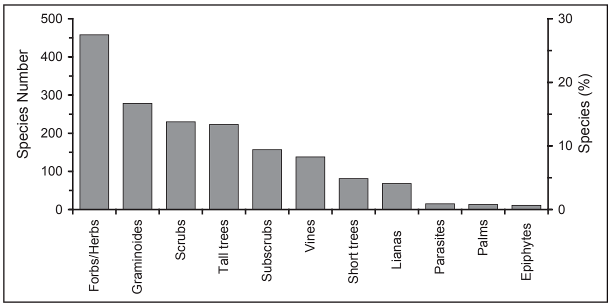

Figure 4. Species number and percentage of terrestrial herbaceous and woody plants in the Pantanal according to growth forms following species lists of Pott and Pott (2000). Total number 1,656.

Table 2. Number of families, genera and species of terrestrial graminoids, herbs, vines, epiphytes and parasites in the Pantanal of Mato Grosso (according to Pott and Pott, 1996).

Growth habit	Families (n)	Genera (n)	Species (n)	Cultivated	Ruderal
Forbs/herbs	62	226	458	15	60
Graminoides	2	84	278	4	33
Vines	25	60	138	8	6
Epiphytes	3	9	11		
Parasites	2	6	15		
Total	76	381	900	27	99

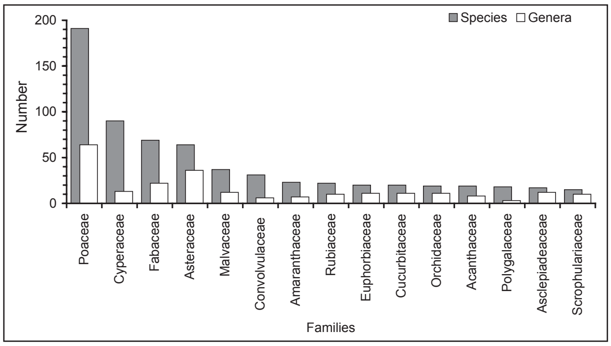

Figure 5. The most species-rich families of terrestrial herbaceous plants in the Pantanal (according Pott and Pott 1996).

of epiphytes point to the periodically pronounced dry climate.

Terrestrial herbaceous plants. The 900 terrestrial herbaceous plant species include grasses, herbs, vines, epiphytes and parasites. Herbaceous plants contribute with 51 % and graminoids with 31 % to the total. The number of vines is relatively high (15 %), the number of epiphytes (1.2 %) very low. Number of families, genera and species and the number of ruderal plants (introduced weeds) are indicated in Table 2, the most species-rich families are indicated in Fig. 5.

Herbaceous plants colonize the entire gradient from permanently dry to permanently wet conditions. Most of them are annual. There is one endemic species in the Santa Cruz Mountain near Corumbá, at the border of the Pantanal (*Aspilia grazielae*, Pott & Damasceno unpubl.) In the aquatic-terrestrial transition zone, terrestrial plants die when the water floods the area but seeds survive the flood period. There is a rich seed bank in the sediment that becomes partly activated when the sediments fall dry. The activation of only parts of the seed bank increases the resilience of the herbaceous plant community against irregular precipitation patterns or unpredicted short floods that may lead to losses of saplings. Germination and plant growth is highest at the beginning of the rainy season.

A similar strategy is used by many aquatic macrophytes, that start to grow from the seed bank with increasing soil moisture and continue growth after inundation thereby substituting the terrestrial plant community. Therefore aquatic and terrestrial herbaceous plant species are often found together (Fig. 6), however with larger biomass of terrestrial plants during the dry period and of aquatic plants during the water-logged and flood period, respectively. According to Pott and Pott (2000), *Arachis diogoi, Habranthus pantanensis, Stilpnopappus pantanalensis* and *Xanthosoma pottii* are endemic.

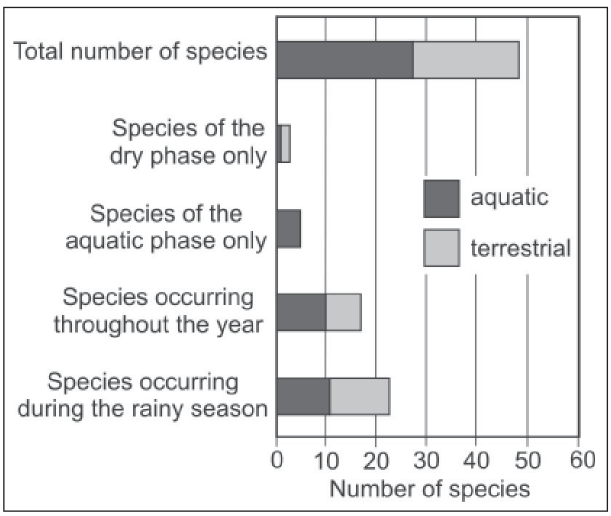

Figure 6. Distribution of 48 herbaceous plant species in a seasonally inundated savanna area according to the flood and drought pattern (Nunes da Cunha, unpubl. data).

Aquatic macrophytes. Hydrophytes or aquatic macrophytes are defined as "plants growing in water, in soil covered with water or in soil that is usually saturated" (Weaver and Clements, 1938). In the Pantanal this group consists of 248 species representing 108 genera and 57 families. Several genera are represented by a large number of species (Table 3; Pott and Pott, 2000). Many species have a large distribution area in Central and South America, some are pantropic as for instance *Ceratophyllum demersum, Eichhornia crassipes, Pistia stratiotes* and *Salvinia auriculata*, but there are no endemic species described for the Pantanal, yet.

Aquatic macrophytes can be classified according to their growth forms. However, many species show heterophylly and a large morphological and physiological plasticity and the attributes of several classes during their life cycle and under different environmental conditions. In this case, the species was located in the class corresponding to the quantitatively more important attributes. An analysis of the aquatic macrophytes according to their growth form is given in Table 4.

The analysis of life forms shows that most aquatic macrophytes in the Pantanal are rooted in the ground and belong to the submerged, floating-leaved and emergent sub-classes. These points to shallow water bodies, relatively small water level fluctuations and good light conditions in the water. Species diversity is very large and comprises all life forms. The annual set-back of the herbaceous plant communities by the flood pulse and a large habitat diversity reduce competitive exclusion of smaller species by vigorously growing ones.

These conditions strongly contrast to the Central Amazon River Floodplain. An analysis of a species list from Junk and Piedade (1993) of the growth conditions inside the floodplain shows that from a total number of

Table 3. The most species rich families and genera of aquatic macrophytes in the Pantanal (according Pott and Pott, 2000).

Family		Genera (n)	Species (n)
Poaceae		10	24
	Paspalum		6
	Luziola		5
	Panicum		5
Scrophulariaceae		7	20
	Bacopa		12
Cyperaceae		6	19
	Eleocharis		7
	Cyperus		6
Onagraceae		1	16
	Ludwigia		16
Leguminosae		5	13
	Aeschynomene		6
Alismataceae		2	13
	Echinodorus		10
Pontederiaceae		3	11
	Pontederia		5
Lemnaceae		4	9
Lentibulariaceae		1	9
	Utricularia		9
Nymphaeaceae		2	8
	Nymphaea		7
Polygonaceae		1	7
	Polygonum		7

Table 4. Classification of aquatic macrophytes of the Pantanal and the central Amazon floodplain according to growth forms, based on the species description of Pott and Pott (2000) and Junk and Piedade (1993). * = species growing on floating islands (*matupá*).

Life form	Number of species	
	Pantanal	Central Amazon
Free floating		
Emergent	12	11
Leaves at the surface	13	10
Submersed	10	7
Rooted in the sediment		
Emergent	175	17 + 9*
With floating leaves	15	2
Submersed	23	0

387 herbaceous species 47 can be considered aquatic or palustric, 28 are free floating and 19 rooted in the ground. Of the rooted species 4 become uprooted with rising water level and continue growing at least periodically free floating, 9 are rooted on free floating organic material, for instance some ferns and the orchid *Eulophia alta*. There are 7 free floating submerged species but no submerged rooted species.

However, a classification in aquatic, palustric and terrestrial species is difficult because of the large water level fluctuations. For instance, many Cyperaceae and Onagraceae occur outside the floodplain in moist conditions and have to be considered as palustric species**,** but inside the floodplain they grow during low water period on the dry sand and mud flats. These species are considered by Junk and Piedade (1993) as "terrestrial" species. A considerable number of "terrestrial" species grow on floating islands of organic debris, locally called *matupá*, but only the most typical species have been listed as palustric.

In comparison to the Pantanal, the growth of aquatic macrophytes in the Amazon River floodplain is strongly hindered by the large annual water level fluctuations of about 10m and the low transparency of the water of 1–2.5 m Secchi depth. Only few species with quick growth in length can accompany the rise in water level. There is a strong selection for a floating habit that allows the plants to maintain their position near the surface in suitable light conditions.

Woody plants. Pott and Pott (1996) list a total number of about 756 woody plant species in the Pantanal, corresponding to about 39.7 % of the higher plants. The most species-rich families are given in Fig. 7.

About 60 % of the woody plants belong to the category of scrubs and small trees up to 10m high, 29 % are tall trees and 9 % are lianas (Table 5). Palms make up a small portion of 0.2 %, however, one species, *Scheelea phalerata*, has to be considered a key-species because of its abundance and large fruit production that is of great importance for many mammals, birds and insects (e.g., Marques et al. 2001).

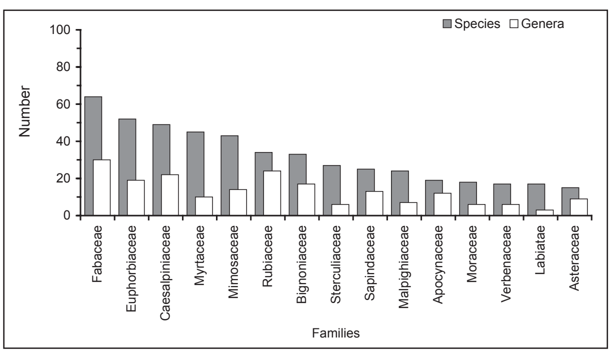

Figure 7. The most species-rich families and genera of terrestrial woody plants in the Pantanal (according to Pott and Pott, 1996).

Table 5. Number of families, genera and species of woody plants in the Pantanal of Mato Grosso according to growth habits (based on Pott and Pott, 1996). The total numbers of families and genera do not correspond to the sum of the numbers of the respective growth habit categories, because 37 families have representatives in several categories.

Growth habit	Families (n)	Genera (n)	Species (n)	Cultivated (n)	Ruderal (n)
Scrubs	43	96	223	3	7
Subscrubs	22	61	149	5	15
Small trees	27	63	83	4	2
Tall trees	43	148	220	12	2
Palms	1	11	13	1	
Lianas	14	36	68		1
Total	70	380	756	25	27

The characterization of the woody plants according to habitat preferences clearly shows the strong impact of the pronounced dry season on the vegetation. Despite an annual precipitation of 1,200 mm and an extended flood period, most trees and shrubs are drought resistant savanna species, with a tolerance to periodic flooding.

The number of species adapted to long-term flooding is small. A detailed analysis of the distribution of 85 tree species along the flood gradient in the northern part (Pantanal of Poconé) shows that 45 species are restricted to permanently dry areas and only 18 species show preference to habitats subject to extended annual flooding. 22 species tolerate a very broad spectrum of flood and dry conditions, a behavior that is favored by pluriannual extreme dry and wet periods. (Fig. 8; Nunes da Cunha and Junk, 1999). If we consider this relationship representative for the entire Pantanal, 355 species (47 %) would show flood tolerance however to different degrees.

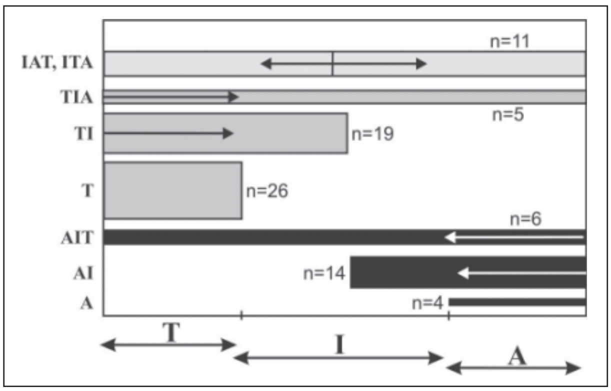

Figure 8. Distribution of 85 tree species in the Pantanal of Poconé according to their preference along the flood gradient. T = terrestrial habitats normally not subjected to inundation; I = habitats inundated during short periods (<two months), A = habitats with a pronounced aquatic phase (up to 6 month). Arrows indicate the supposed direction of expansion of the species from the center of maximum density (according to Nunes da Cunha and Junk, 1999).

There are no endemic tree species in the Pantanal. Most terrestrial species are immigrants from the adjacent savanna (Cerrado) biome. Species with a large tolerance to periodic dry and wet conditions are often found in gallery forests along Cerrado streams. Some of the very flood tolerant species are described from Amazonian river floodplains, such as *Licania parviflora, Triplaris americana, Vochysia divergens, Eugenia inundata,* and *Pouteria glomerata*. Some are immigrants from the Chaco biome, for instance, *Copernicia alba* in the periodically flooded areas, and *Schinopsis balansae, Calycophyllum multiflorum, Seguieria paraguayensis, Pterogyne nitens*, and *Perescia sacharosa* in the dry areas.

Estimates for Amazonian river floodplains show the existence of more than 1,000 flood resistant woody species. At the Mamirauá Reserve for Sustainable Development (Amazon River floodplain), 224 tree species were recorded on an area of 4 ha. 103 species were restricted to areas of high lying *várzea*, corresponding to mean flood levels <3 m and inundation periods of <45 days, and 94 species were restricted to areas of low lying *várzea*, corresponding to mean flood levels of up to 8 m and mean inundation periods up to 230 days per year. Only 27 species occurred in both areas. About 17 % of the species recorded in the floodplain were also found in the adjacent non flooded upland. All of them occurred in the high *várzea* and only 3.9 % occurred also in the low *várzea* (Wittmann et al., 2002). Amazonian floodplain forests are much more differentiated with respect to flood tolerance than Pantanal floodplain forests that are more drought tolerant.

Terrestrial arthropods

Knowledge on the taxonomy, geographical distribution and ecology of terrestrial arthropods of the Pantanal is poor, even on common representatives like ants and termites, and general statements on species number, origin and endemism cannot be given at this stage. However, pilot studies realized during the last five years revealed species numbers, survival strategies and seasonality in selected groups. In addition, data on the group spectrum and dominance of terrestrial arthropods are available from two monodominant floodplain forests. Data indicate that the flood pulse influences the community structure and ecology of terrestrial arthropods in Pantanal floodplains.

Soil fauna. In forest stands of *Vochysia divergens* (Vochysiaceae) (locally called *cambarazal*), Acari (70 %, 1,800 ind m^{-2}) and Collembola (11 %, 290 ind m^{-2}) dominated in the litter and upper soil layer (0–4 cm), followed by Formicidae (7 %, 175 ind m^{-2}) and Coleoptera

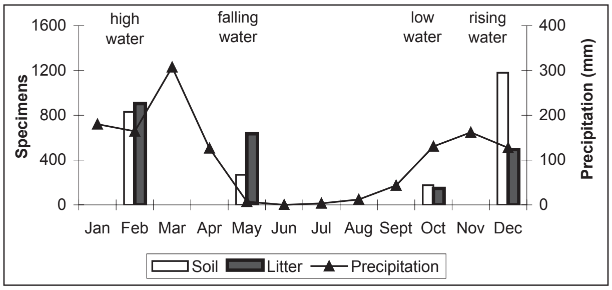

Figure 9. Coleoptera (larvae and adults) obtained from soil and litter during four characteristic water stages in the Pantanal floodplains of Poconé, Mato Grosso (Pinho et al., unpubl.).

(5 %, 120 ind m^{-2}). Adult Coleoptera represented 28 families and 357 morphospecies. Scarabaeidae (26.5 %), Staphylinidae (24.1 %) and Ptiliidae (19.0 %) dominated. Staphylinidae had the highest species richness (71 morphospecies), followed by Pselaphidae (32) and Ptiliidae (24). The dominant trophic groups were predators (35.0 %; mostly Staphylinidae & Scydmaenidae), herbivores (33.0 %; mostly Scarabaeidae & Curculionidae) and saprophages (23.5 %; mostly Ptiliidae), followed by fungivores (8.5 %; mostly Pselaphidae) (Fig. 10).

Highest abundance of arthropods (particularly of Acari, Collembola and Thysanoptera), was obtained during low water (October) when the amount of litter on the forest floor was highest. Other taxa like Araneae, Homoptera and Pseudoscorpiones were more abundant with the beginning rainy season during rising water (December). The highest density of Coleoptera during rising and high waters (Fig. 9) was due to the eclosion of adult beetles in litter and soil, while larvae dominated during falling water in the litter.

In forest stands of the palm *Attalea phalerata* (Arecaceae) (locally called *acurizal*), Acari (67 %, 858 ind m^{-2}) dominated in the litter and upper soil layer (0–4 cm), followed by Collembola (9 %, 122 ind m^{-2}) and Coleoptera (9 %, 121 ind m^{-2}). Adult Coleoptera represented 27 families and 195 morphospecies. Staphylinidae (36 %) and Ptiliidae (22 %) dominated. These two families accounted for the dominant trophic groups, i.e. predators (54.7 %) and saprophages (27.3 %), followed by herbivores (11.5 %; mostly Scarabaeidae) and fungivores (6.5 %; mostly Pselaphidae) (Fig. 10). Staphylinidae had the highest species richness (46 morphospecies).

Abundance of Acari in the upper soil was lowest during low water of the dry season. In Diptera and Hemi-

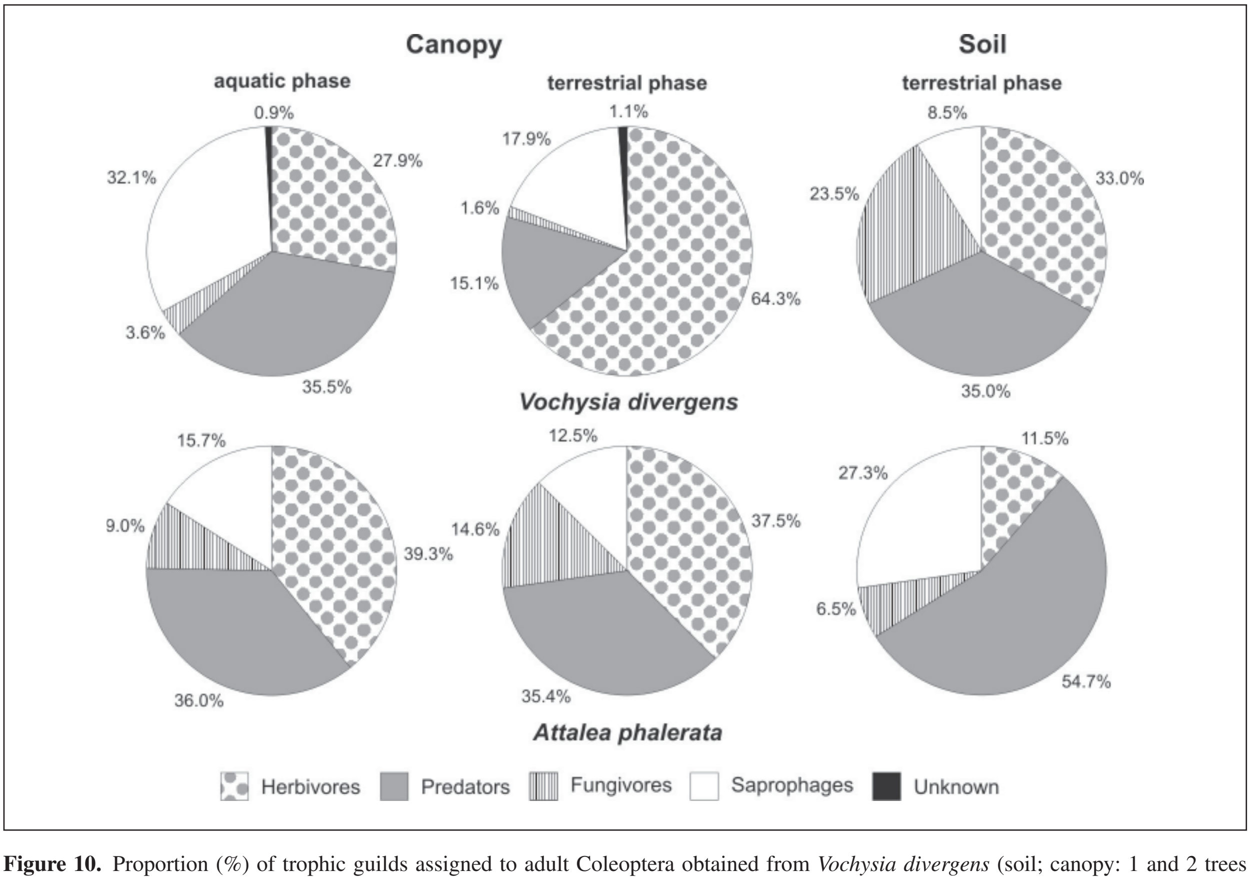

Figure 10. Proportion (%) of trophic guilds assigned to adult Coleoptera obtained from *Vochysia divergens* (soil; canopy: 1 and 2 trees during the aquatic and terrestrial phase, respectively) and *Attalea phalerata* (soil; canopy: 6 trees each during the aquatic and terrestrial phase) (Marques et al., unpubl.).

ptera abundance was highest during rising water at the beginning rainy season. About 69 % of all adult Coleoptera was obtained during high waters.

Soil living termites (*Cornitermes* spp.) play a key role as bioengineers in shallowly flooded areas of the Pantanal. Termite mounts, locally called *murunduns*, form non-flooded islands that are covered with terrestrial woody and herbaceous vegetation and are important refuges for terrestrial animals during flood periods, and possibly also during fire events. Samples taken during high water (February) showed an arthropod density two times higher compared to falling water (May).

Canopy fauna. In the canopy of *V. divergens*, arthropod abundance during the terrestrial phase (181 ± 65 ind m^{-2}) was comparable to that during the aquatic phase (188 ± 77 ind m^{-2}). Formicidae (30–50 % of the total catch) and Coleoptera (11–21 %) dominated independent of season, indicating that the canopy represents an important habitat. Some groups like Acari, Araneae, Coleoptera and Psocoptera showed greater abundances during the aquatic phase, while Thysanoptera, Homoptera and Collembola were more abundant during the terrestrial phase. Seasonality in Thysanoptera is attributed to flowering of the host plant during the terrestrial phase, and seasonality in Araneae to the temporary use of trees by terricolous species during the aquatic phase. More than 85 % of immature Blattodea, Homoptera and Heteroptera were obtained during the aquatic phase, indicating that the canopy is used by some groups for reproduction.

Coleoptera represented 37 families and 256 morphospecies. Nitidulidae (18 % of the total catch), Anobiidae (17 %), Meloidae (11 %) and Curculionidae (8 %) dominated. Rare species (102 (40 %) singletons, 47 (18 %) doubletons) caused the great diversity in adult Coleoptera. Distribution of species was even, however their abundance and richness was greater during the aquatic phase. The majority of morphospecies (46 %) was obtained exclusively during the terrestrial phase, 29 % only during the aquatic phase and 25 % during both phases. Five families were more abundant during the terrestrial phase (above all Nitidulidae), and nine families during the aquatic phase (above all Anobiidae). Herbivores and predators were the dominating trophic groups (Fig. 10). Predominance of predators during the aquatic phase is attributed to the flood pulse, that of herbivores during the terrestrial phase to seasonal phenological changes in the host plant (Marques et al., 2001; unpubl.).

In the canopy of *Attalea phalerata*, Coleoptera (27 % of the total catch) and Formicidae (19 %) dominated during the terrestrial phase (239 arthropods/m^2), Acari (40 %) and Coleoptera (12 %) during the aquatic phase (643 arthropods/m^2). Adult beetles represented 48 families and 326 morphospecies during the terrestrial phase. Tenebrionidae (23 %) and Curculionidae (22 %) were the most dominant families. Curculionidae (44 spp.) and Staphylinidae (40 spp.) had the highest number of morphospecies. During the aquatic phase, adult beetles represented 48 families and 467 morphospecies. Endomychidae (23 %) and Nitidulidae (16 %) were the most dominant families. Staphylinidae (89 spp.) and Curculionidae (56 spp.) had the highest number of morphospecies.

The aquatic phase showed a 2.6 times higher arthropod abundance and a greater diversity of adult beetles (141 more morphospecies) than the terrestrial phase. However, arthropod biomass was 2.2 times less during the aquatic phase (0.4 mg m^{-2}), indicating a higher amount of smaller-sized animals (e.g., Acari, Coleoptera: Ptiliidae) and a different structure of its canopy community. This also mirrors in the trophic guilds of Coleoptera, with fungivores being less dominant during the aquatic phase (Fig. 10). Differences may be attributed to restricted availability of habitats and their resources when wide areas are flooded. Data indicate, that the palm tree *A. phalerata* is used both as temporal refuge during flooding (e.g., Acari, Araneae, Isopoda, polydesmidan Diplopoda, Formicidae) and reproduction place by different arthropod taxa (Santos et al., 2003; Battirola et al., 2004; 2005).

A comparison of the Pantanal with Amazonian floodplains. In forest stands of *V. divergens*, total abundance of soil arthropods (≤2,600 ind m^{-2}) was much lower than in floodplain forests of Central Amazonia (whitewater region: ≤13,400 ind m^{-2}, blackwater region: ≤22,500 ind m^{-2}, Adis 1997). Compared to blackwater floodplain forests in Central Amazonia, several taxa common in the soil were lacking in the *cambarazal* (e.g., Pauropoda, Protura, Schizomida), others were less abundant (e.g., Chilopoda, polydesmidan Diplopoda, Isopoda, Opiliones, Pseudoscorpiones and Symphyla). Some of the reasons to be investigated include occasional strong fires, the island character of *cambarazal* forests and/or extreme dryness, low pH and a high aluminum content of sandy soils and litter.

The most common response of terricolous arthropods in Central Amazonian floodplain forests to the flood pulse is a temporal vertical migration to the trunk/canopy region were they pass inundation of 5–7 months duration (Adis, 1997; 2000). Similar survival strategies were observed in the Pantanal, at least in some species (Adis et al., 2001). In Central Amazonian floodplains, several arthropod species of different taxa survive under water (dormant and active stages) when being submerged (Adis, 1997; Adis and Junk, 2002). Up to now, this survival strategy has only been observed for Collembola (Symphypleona) in Pantanal floodplains (Adis, Marques and Battirola, unpublished).

Aquatic invertebrates

Due to inconsistencies in taxonomy and geographically isolated studies, the diversity of benthic invertebrates can only be partly assessed. Many taxa have remained undescribed. Some abundant groups, such as nematodes, have not been studied at all in the Pantanal. In a first attempt to summarize the known taxa, Heckman (1998a, 1998b) has listed the species from various habitat types (floodplain water bodies, root zones of macrophytes, river and stream benthos), indicating 55 ciliates, 97 amoeba, 151 rotifer species, 6 gastrotrichs, 6 oligochaetes, 5 gastropods and 5 bivalves among the non-arthropods. Species lists are continuously being updated, e.g., Wantzen, Callil & Butakka (unpublished manuscript) report 23 bivalve species, Marchese et al. (2005) 37 oligochaete species, and Brandorff, Pinto-Silva & Morini (unpublished manuscript) report planktonic species numbers of 81 cladocera, 33 copepoda, 16 ostracoda, 246 testacea and 285 rotifer. Until now, only one endemic copepod (*Argyrodiaptomus nhumirim*) has been described from the area (Reid, 1997).

Among studied sites, the precision of the taxonomic analysis differs greatly, therefore beta- and gamma-diversities can be reliably compared only within the dataset of individual studies. Seasonal occurrence of some species should also be taken into consideration. Morini-Lopes (1999) found 47 rotifers, 22 cladocerans, 7 copepods and 1 phantom-midge in the zooplancton community of the river-connected lake "Sinhá Mariana" near Barão de Melgaço, northern Pantanal. In the same lake, 24 genera of chironomids have been identified so far (Butakka, 1999).

The littoral stations were characterized by filter-feeders *(Caladomyia)*, gatherer-collectors *(Polypedilum*, *Aedokritus, Fissimentum)*, and predators *(Cryptochironomus* and *Ablabesmyia (Karelia)*. Some taxa occurred only during the low water period, including collectors like *Zavrelliela* and predators like *Larsia*. Others occurred only during the high water period, such as gatherer-collectors *(Chironomus* gr. *salinarius*, *Beardius*, *Chironomus* gr. *decorus*), filterer-collectors (*Rheotanytarsus*) and one predator *(Tanypus punctipennis)* (Butakka et al., in press).

Among the insects, chironomids are by far the most diverse group in the Pantanal and in the surrounding rivers and streams, e.g., the Bento Gomes river, where Stur (2000) identified 48 genera during a 3-year study. In the large Paraguay River, 20 genera were found in a survey by Marchese et al. (2005). The known chironomid diversity can be expected to increase manyfold as soon as adult chironomids are systematically identified to species level.

Because of the alternating inundations and harsh dryness, permanent rivers and lakes, and especially the connectivity between them, play important roles for the survival of aquatic biota. Benthic invertebrates show seasonal patterns and adaptations both to local changes (moving littoral) and hydraulic changes due to increased current and particulate organic and inorganic matter input. Lake centers and moving sand substrata are the least densely and less diversely colonized habitats whereas sites with high gradients (e.g., connection channels between lakes and rivers, large woody debris, gravel substrates) reveal high biodiversity and abundance.

Along floodplain rivers, as the Paraguay River, transversal habitat diversity is strongly increased compared with longitudinal dimensions (Wantzen et al., 2005) and species diversity accompanies this pattern (Marchese et

Table 6. Survival strategies of aquatic invertebrates in the Pantanal of Mato Grosso (from Wantzen, Callil and Butakka, unpublished manuscript, and several authors).

Strategy	Organism	Description
horizontal migration within the water body	*Campsurus* mayfly larvae	follow the adequate hydro-sedimentological conditions in floodplain lakes
estivation on trees	*Drulia* sponges	propagules (gemmulae) survive several months of drought
diapause in sediments (mature organisms)	ampullarid snails, some bivalves	avoidance of dessication by burrowing into the moist part of the sediments
diapause in sediments (resting eggs or cysts)	copepods and microzoobenthos	avoidance of dessication in hard-shelled propagules in the sediments
"pond-hopping"	small-bodied, winged insects, e.g., chironomids	performing short migrations between neighboring waterbodies
"long distance flyers"	large, winged insects, e.g., waterbugs and dragonflies	performing long-distance migrations between remote waterbodies
"drifting"	root fauna of aquatic macrophytes	dispersal on drifting macrophyte mats
r-strategy	most invertebrates	production of large numbers of small propagules, short life cycles
Parental care	trichodactylid crabs	carry offspring in brood-pouch to next water body during dry phase
short life cycles and badly synchronized emergence	most small-bodied insects, e.g., chironomids	avoidance of total population loss by presenting different life-cycle stages at the same time

al., 2005). Additional control on aquatic invertebrate diversity is caused by the periodical dryness of many habitats which can be recolonized from resistant eggs, diapause forms or by immigration (Table 6). Far-travelling insect taxa such as water bugs, beetles, mole-crickets and the *Campsurus* mayflies were observed to make dispersal migrations at the beginning of the freshet. Small taxa, such as the chironomid *Apedilum elachistum* which develops within less than one week (Nolte, 1995), have short life cycles enabling them to perform a kind of "pond-hopping" during the expansion or shrinkage of the floodplain water bodies. Consequently, long-lived, low-mobility species have the hardest stay in the Pantanal as they need to survive under severe drought conditions. The molluscs such as the large ampullariid snails (e.g., *Pomacea linata, P. scalaris* and *Marisa planogyra*) suffer high mortalities during the estivation in the sediments (Kretzschmar and Heckman, 1995), especially at the beginning of the wet season due to mass predation by birds (*Rosthramus sociabilis*, da Silva et al., 2001). The most endangered invertebrates, however, are the bivalves which suffer additional stress from heavy metal pollution (Callil and Junk, 2001) and by recently invading golden mussels (*Limnoperna fortunei*, Mytilidae) which settle on the shells and compete for plankton (Ezcurra de Drago and Wantzen, unpublished data).

Fishes

Fishes generally belong to the best studied animal groups in the Pantanal. However, there are still many gaps because many areas are not yet adequately sampled and life history traits are little known. Britski et al. (1999) list 263 fish species belonging to 161 genera and 36 families (Table 7). Characiformes with 65 genera and 129 species and Siluriformes with 61 genera and 105 species predominate, a pattern that is characteristic for neotropical freshwaters. The family Cichlidae that is very diverse in African fresh waters, is represented by only 11 genera and 16 species, less than 7 % of total number.

According to Junk et al. (1997) the impact of the flood pulse on the fish fauna of the Amazon River floodplain selects for r-strategies, great mobility, adaptations to varying water quality (hypoxia) and an explicit seasonality in an environment with weak climatic seasonality. This statement also holds true for the fish fauna of the Pantanal, however, knowledge about the biology and ecology of many species is limited (Resende and Palmeira, 1999; Machado, 2003). Feeding habits vary according to food availability between low water and high water period. The number of omnivorous species is large (Resende 2000). The changes in feeding habits between low and high water period are also reflected by their changing stable isotope ratios, pointing to the importance of flood plain resources during floods (Wantzen et al., 2002).

The fish fauna of river floodplain systems, including the Pantanal, can be divided into "white" fish, "black" fish and "gray" fish according to their migration and spawning behavior (Welcomme, 1985; Welcomme and Halls, 2001). White fish are more rheophilic species that move with receding water level from the floodplain into the river channels and perform large up-river spawning migrations. These species are one-shot spawners. Some white fish species are restricted to the river channel. Most white fish are of medium to large size to be able to perform the extended spawning migrations. Black fish are limnophilic species that retreat at low water level in the remaining water bodies inside the floodplain. Black fish often show parental care and extreme resistance to low oxygen concentration (Welcomme, 1985; Junk et al., 1997). Gray fish are eurytopic species that are intermediate between white and black fish in that they live in the main channel during the dry season, move on to the floodplain during floods and undertake short distance spawning and dispersal migrations. They are marginal spawners that deposit eggs in one or more batches on riparian vegetation and include one-shot spawners and species that produce several batches of eggs per year.

To the white and gray fish of the Pantanal belong *Pellona flavipinnis* (Pristigasterinae) and representatives of the families Characidae (mainly members of the subfamilies Bryconinae, Triporteinae, Salmininae, Myleinae, Serrasalminae, Cynodontinae), Prochilodontidae, Curimatidae, Anostomidae, Ageneiosidae, and Pimelodidae. Large upriver spawning migrations locally called *piracema*, are known for several species as for instance *Pseudoplatystoma corruscans, P. fasciatum, Paulicea luetkeni, Sorubim lima, Hemisorubim platyrhynchos, Piaractus mesopotamicus, Brycon microlepis*, *Leporinus macrocephalus* and *Prochilodus lineatus.* White and gray fish provide the bulk of the yield of the inland fishery in Amazonia and the Pantanal.

Most of the other species belong to the group of black fish. Typical black fish species are *Lepidosiren paradoxa* (Lepidosirenidae), *Synbranchus marmoratus* (Synbranchidae), and representatives of the families Characidae (Subfamily Tetragonopterinae and other subfamilies with small species,) Lebiasinidae, many Gymnotiformes, Callichthyidae, Loricariidae, Poecilidae, Rivulidae, Sciaenidae, Cichlidae. Parental care is known for Cichlidae, Scoloplacidae, Callichthyidae, Loricariidae, and *Pygocentrus nattereri* (Serrasalmidae). Some Ageneiosidae, Pimelodidae and Auchenipteridae have internal fertilization but parental care is only known for *Centromochlus perugiae* (Auchenipteridae) from the upper Amazon basin. Freshwater sting rays (Potamotrygonidae) are viviparous and *Pamphorichthys hasemani* (Poecilidae) is ovoviviparous. According to Resende and Palmeira (1999) of 101 species studied in 4 different environments along Miranda River, 15 % are white fish, 43 % black fish and 42 % gray fish.

Table 7. Families, genera and number of fish species in the Pantal of Mato Grosso according to Britski et al. (1999).

Order	Family	Genera (n)	Species (n)
Myliobatiformes	Potamotrygonidae	1	3
Clupeiformes	Pristigasteridae	1	1
Characiformes	Characidae	43	76
	Gasteropelecidae	1	1
	Cynodontidae	1	1
	Crenuchidae	1	3
	Parodontidae	2	2
	Hemiodontidae	2	3
	Prochilodontidae	1	1
	Curimatidae	6	8
	Anostomidae	4	10
	Lebiasinidae	1	1
	Erythrinidae	3	3
Gymnotiformes	Rhamphichthyidae	2	2
	Gymnotidae	1	1
	Sternopygidae	2	4
	Hypopomidae	1	3
	Apteronotidae	2	2
Siluriformes	Doradidae	8	8
	Auchenipteridae	6	8
	Ageneiosidae	1	3
	Pimelodidae	16	24
	Aspredinidae	2	3
	Cetopsidae	1	1
	Trichomycteridae	4	8
	Scoloplacidae	1	1
	Callichthyidae	4	13
	Loricariidae	18	36
Cyprinodontiformes	Poeciliidae	1	1
	Rivulidae	6	9
Beloniformes	Belonidae	2	2
Perciformes	Sciaenidae	2	2
	Cichlidae	11	16
Synbranchiformes	Synbranchidae	1	1
Pleuronectiformes	Achiridae	1	1
Lepidosireniformes	Lepidosirenidae	1	1
Total	36	161	263

In comparison with the fish fauna of the large Amazonian river floodplains, the fish fauna of the Pantanal is relatively species-poor. Bayley (1982) collected during a two-year period in the bay at the mouth of Camaleão Lake at the Amazon River near Manaus more than 226 species belonging to 132 genera and 40 families. Santos et al. (1984) found about 300 species in the lower Tapajos. Goulding et al. (1988) collected in a stretch of 1,200 km of the lower and middle Negro River between Manaus and Barcelos 450 species belonging to 202 genera and 39 families. Considering also literature data, the authors estimated a total of about 700 species in that area.

Fishery in the Pantanal is highly selective and concentrates mostly on carnivorous and frugivorous species that can be fished with hooks, for instance *Pseudoplatystoma corruscans, P. fasciatum, Paulicea luetkeni, Sorubim lima, Hemisorubim platyrhynchos, Serrasalmus nattereri, Hoplias malabaricus* (carnivorous) *Piaractus mesopotamicus* and *Brycon microlepis* (omnivorous). Of the iliophagous species only *Leporinus macrocephalus* and *Prochilodus lineatus* are of economic importance, but catch is low because fishing with nets is prohibited.

Fishery statistics indicate that in 1999 about 59,000 sport fisherman were registered in Mato Grosso do Sul (southern part of the Pantanal) that contributed about 75% of the total catch of about 1,400 tons (Catella, 2001). Similar numbers are expected for the northern part (Mato Grosso). Small fishes, mainly gymnotids and synbranchids, are used as living baits. Bait fishery is an economically important activity of the local population and is estimated to reach 17 million specimens per year. The demand is rising and ecologists are afraid of negative impacts of bait fishery on the stocks.

Amphibians and reptiles

First publications dealing with amphibians and reptiles from the Pantanal region base on material obtained by Captain Thomas J. Page, from the U.S. Navy, during fluvial exploration of tributaries of the River La Plata and adjacent countries in the years 1853, '54, '55, and '56 (Cope, 1863a, b; 1868). The first attempt to compile an herpetofaunal species list for the whole Upper Paraguay River Basin (UPRB), including the headwaters of all water courses flowing to the Pantanal, was presented by PCBAP (Brasil, 1997), a huge conservation plan undertaken by Brazilian government in the nineties. Among a total of 167 species of reptiles recorded for the whole basin, 83 were assigned as occurring in the floodplain. No similar indication was done regarding the 35 species of amphibians listed by the PCBAP (Brasil, 1997).

A recent examination of the material deposited in small regional collections, coming from different subregions of the Pantanal, allowed updating the UPRB herpetofaunal list (Strüssmann et al., in prep.). The herpetofauna presently known for the whole basin consists of 198 species of reptiles plus 72 species of amphibians. The herpetofauna of the Pantanal wetlands alone consists of at least 135 native species (40 anuran amphibians, three turtles, 25 lizards, two amphisbaenians, 63 snakes, and two crocodilians) (Table 8). The gekkonid lizard *Hemidactylus mabouia* is the only exotic species in the area. Both lists are by no means complete and undescribed species are being discovered after every field inventory (Strüssmann, 2003; Strüssmann et al., 2000; Strüssmann et al., in press).

In many hydrologic systems showing diverse aquatic habitats, great age and environmental stability lead to an explosive radiation of aquatic herpetofauna, which in some cases comprises strongly differentiated species (e.g., McCoy, 1984). In the Pantanal, however, in spite of the abundance and diversity of aquatic habitats, there are no strictly endemic amphibians or reptiles, indicating no long persistence of the environmental scenario, and a recent colonization by invading faunal elements. This invasion is still in progress, mainly from adjacent Cerrado, Gran Chaco and Amazonia domains, and apparently also from Atlantic and Chiquitan forests in a lesser extent. Therefore, species presently known only from peripheral elevated habitats may also be found in the Pantanal wetlands.

Additionally, some of the taxa in the list present taxonomic problems pending solution. Chelonia is certainly

Table 8. Higher taxa, families and numbers of genera and species of amphibians and reptiles in the Pantanal (in parenthesis, total number of genera and species presently known for the entire Upper Paraguay River Basin).

Higher taxa	Families	Genera (n)		Species (n)	
Amphibia	**Total 5**	**16**	**(21)**	**40**	**(71)**
Anura	Bufonidae	1	(2)	3	(6)
	Dendrobatidae	1	(2)	1	(3)
	Hylidae	6	(7)	16	(26)
	Leptodactylidae	5	(7)	16	(30)
	Microhylidae	3	(3)	4	(6)
Reptilia	**Total 17**	**63**	**(82)**	**96**	**(187)**
Chelonia	Testudinidae	1	(1)	2	(2)
	Chelidae	1	(2)	1	(3)
Sauria	Iguanidae	1	(1)	1	(1)
	Polychrotidae	2	(2)	2	(4)
	Tropiduridae	2	(2)	4	(7)
	Gekkonidae	4	(6)	4	(7)
	Gymnophthalmidae	4	(6)	4	(9)
	Teiidae	5	(6)	7	(13)
	Scincidae	1	(1)	3	(3)
	Anguidae	1	(1)	1	(1)
Amphisbaenia	Amphisbaenidae	1	(4)	2	(18)
Serpentes	Boidae	4	(4)	5	(6)
	Typhlopidae	1	(1)	1	(2)
	Colubridae	30	(39)	52	(92)
	Elapidae	1	(1)	2	(6)
	Viperidae	2	(3)	3	(9)
Crocodylia	Alligatoridae	2	(2)	2	(4)
Total	22 (27*)	79	(103)	136	(258)

* Families known exclusively from elevated areas of Upper Paraguay River Basin (number of genera/number of species): Amphibia – Gymnophiona: Caecilidae (1/1); Reptilia – Sauria: Hoplocercidae (1/1); Serpentes: Aniliidae (1/1); Leptotyphlopidae (1/6); Anomalepididae (1/2).

one of the poorest known reptile groups in the floodplain. Only three species are reliably recorded: *Geochelone* (*Chelonoidis*) *carbonaria*, *G. denticulata*, and *Acanthochelys macrocephala*. Nevertheless, the total number of vouchered records is incredibly low. The present analysis, then, must be considered provisional, as it is based on a still incomplete knowledge of a rich fauna.

The total number of species of the herpetofauna recorded for the Pantanal is roughly the same of that presently known for the entire Cerrado, the second largest biome in South America, with nearly two million square kilometers (Colli et al., 2002). Richness of the Pantanal herpetofauna is indeed increased by the position on major faunal boundaries that results in juxtaposition or interdigitation of Cerrado elements with those from adjacent biomes.

In a preliminary analysis of the zoogeographical relationships of reptiles from the Pantanal, Alho et al. (2001) found that at least 25 % of the species were ubiquitous, having an almost-continental distribution. These species were already recorded in at least five distinct biomes (Amazonian and Atlantic Forests, Cerrado, Caatinga and Gran Chaco), although local subspecies are occasionally recognized. Examples of these widely distributed species are the tortoise *Geochelone carbonaria*, the lizard *Iguana iguana,* the amphisbaenian *A. alba*, and the snakes *Boa constrictor*, *Liophis almadensis, Mastigodryas bifossatus*, and *Spilotes pullatus*. According to the same authors, species occurring in all extension of the "great diagonal belt of open formations" (which includes, from Northeast to Southwest, the Caatinga, the Cerrado, the Pantanal, and the Gran Chaco) represented 24 % of the reptiles from the Pantanal. This figure is elevated to more than 50 % when species occurring only in restricted parts of this "diagonal" are considered (Alho et al., 2001).

It is extremely difficult to generalize about ecology of amphibians and reptiles of the Pantanal, due to the lack of direct observations or published information on most of the taxa. Documented records in the literature and specimens in collections, however, seem sufficient to tentatively search for general patterns of distribution. The results of this analysis are presented below (Table 9).

Most of the herpetofauna of the Pantanal (including all aquatic species) are widely distributed in the floodplain. Among these "better-adapted" species, affinities with Amazonian taxa are more evident (although not taxonomically clear) among aquatic or semiaquatic species. The possibility that some related taxa occurring in the Pantanal and in Amazonia are in reality conspecific occasionally arise in the literature (Strüssmann et al., in press), corroborating the hypothesis of inexistence of a long-term abrupt boundary between aquatic herpetofaunas in the UPRB (Upper Paraguay River Basin) and in meridional Amazonia.

Although some of the aquatic reptiles in the Pantanal have been occasionally treated as endemic species (including the yellow-anaconda *Eunectes notaeus*, the paraguayan caiman lizard *Dracaena paraguayensis* and the freshwater turtle *Acanthochelys macrocephala*), their actual distributions are wide enough to not support this statement. *Eunectes notaeus*, as an example, is a common species also at Yaciretá Dam, on the Paraná River between Argentina and Paraguay, while *A. macrocephala* (originally described from Cáceres, UPRB) also occurs in aquatic habitats in the Mamoré river valley, a region belonging to the Amazonas River Basin.

According to their general distribution pattern in the Neotropical region, species already recorded in the Pan-

Table 9. Classification of amphibian and reptile species according to general patterns of distribution in the Upper Paraguay River Basin.

	Amphibians	Reptiles
a) Species widely distributed in the floodplain	31	65
b) Species peripheral or with restricted distribution in the floodplain	7	26
c) Species insufficiently known or rare, but reliably recorded from the floodplain	2	5
Total species in the floodplain (Pantanal wetlands)	40	96
d) Species widely distributed in the periphery of the floodplain	10	10
e) Species with restricted distribution in the periphery of the Pantanal, mainly Amazonian	6	27
f) Species with restricted distribution in the periphery of the Pantanal, mainly in Cerrado areas	13	34
g) Species with restricted distribution in the periphery of the Pantanal, mainly Chacoan	1	7
h) Species with restricted distribution in the periphery of the Pantanal, mainly Atlantic	0	3
i) Species with very limited distribution in the periphery of the Pantanal and/or uncertain zoogeographical affinities	2	21
Total species in the peripheric plateaus	32	102

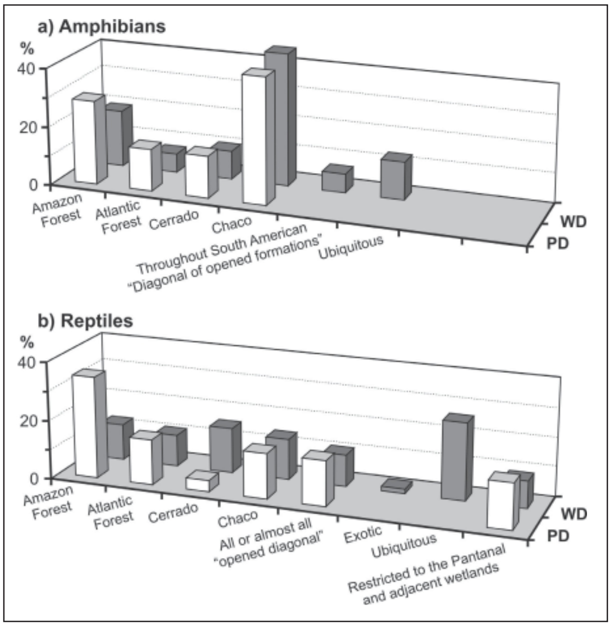

Figure 11. General patterns of distribution of the species already recorded in the Pantanal wetlands in other neotropical major formations; **a)** amphibians; **b)** reptiles. (Abbreviations: **PD** – species peripherally distributed in the floodplain; **WD** – species widely distributed in the floodplain).

tanal wetlands (those 40 amphibians and 96 reptiles included in the upper half of Table 9) can be subdivided in several categories (Fig. 11a, b). Among the amphibians widely distributed in the floodplain, and also among those with more limited distributions in the Pantanal, most species are considered Chacoan forms (Fig. 11a). "Amazonian" species are frequent among that subset of amphibian species occurring peripherally in the Pantanal, especially on its western border, a pattern that is also observed amongst Pantanal reptiles with limited distributions in the floodplain (Fig. 11b). Approximately one third of the widely distributed reptiles are also widely distributed in other opened formations, as well as in Amazon and Atlantic forests (Fig. 11b).

Ecologically 52 % of the reptile species of the Pantanal wetlands are terrestrial species, 21 are arboreal or semiarboreal (22 %), 12 are aquatic or semiaquatic (13 %), and 12 are fossorial, semi-fossorial or cryptozoic (13 %). When total herpetofauna of the floodplain is considered, figures are roughly the same: 52 % terrestrial (among anurans, all bufonids, leptodactylids, and the only dendrobatid), 26 % arboreal (nearly all hylid species), 12 % fossorial, and 10 % aquatic or semiaquatic (among anurans, only *Lysapsus limellus* and *Pseudis paradoxa* can be considered as such).

Although the overall herpetofauna of the Pantanal is comparatively poor in aquatic or semiaquatic species, local assemblages may harbor higher proportions of these specialized taxa than in other neotropical sites. In a snake assemblage studied in the northern part of the Pantanal, aquatic/semiaquatic species represented around 15 % of the total richness (Strüssmann and Sazima, 1993). In the same assemblage, another 15 % of the snake species were fossorial or semifossorial, an ecological category found to be fairly better represented at Acurizal reserve, Serra do Amolar, in the western border of the Pantanal. Fossorial and semifossorial snakes comprised 25 % of the species (43 in total) and 35 % of the individuals (308 in total) recorded in a recently-finished 1-year study at Acurizal, one of the private protected areas contiguous to the Pantanal National Park (Strüssmann, Ribeiro & Carvalho, unpublished data).

Data from both regional collections and unpublished field inventories indicate that around 30–35 species of anurans, 20–25 lizards, three to five amphisbaenians, and at least 40 snakes can be found in the same site, in the better-sampled localities within the Pantanal (e.g., Corumbá, Aquidauana, Cáceres, Serra do Amolar, Pantanal National Park). Some species have restricted distributions within the floodplain which results in distinct herpetofaunal assemblages on each of the distinct sub-regions recognized by different authors (Adamoli, 1981; Silva and Abdon, 1998). Additionally, among those species that are widely distributed in the floodplain, individual patterns of abundance may vary in every sub-region. These differences were not yet adequately evaluated.

Threatened species resume to those belonging to genera listed in Appendix II of CITES: *Geochelone carbonaria*, *G. denticulata*, *Caiman yacare*, *Paleosuchus palpebrosus*, *Iguana iguana*, *Dracaena paraguayensis*, *Tupinambis* spp., all boids, and *Hydrodynastes gigas*. Local status of these species, however, are better than in any other parts of their range, due to lower perspectives of habitat conversion in the Pantanal.

Birds

Birds are without doubt the best known faunistic group in the Pantanal. General knowledge about distribution and ecology of most species is now sufficiently advanced (e.g., del Hoyo et al., 1992–2003; Parker et al., 1996; Ridgely and Tudor, 1989, 1994) to give rather precise ideas about the bird species to be expected in the Pantanal.

The number of bird species of the "Pantanal region" is usually given as something between 600 and 700 species (e.g., Cintra and Antas, 1996; Heckman, 1998a; Por, 1995; Swarts, 2000), a number derived from a comprehensive review of Brown (1986). If all published species lists for the region of the Pantanal (Brown, 1986; loc. cit., Dubs, 1983a, 1992; Forrester, 1993; Mauro and Tomás, 1994; Heckman, 1998a; Tubelis and Tomás, 2001) are combined the total rises to 766 species. However, recently Tubelis and Tomás (2001) have estimated the number of species for the "Pantanal floodplain" only as 469 "confirmed" species plus 31 species not with certainty recorded inside the floodplain. Moreover, if the criteria for acceptable species records of the Brazilian Ornithological Records Committee (Comitê Brasileiro de Registros Ornitológicos, CBRO, 2000) are applied to this list, many of these 500 species also must be considered "unconfirmed", as there is no published evidence (specimens, photographs, voice recordings, etc.). Some species can even be shown to be included in error, as the record is not from the Pantanal region or identification of the species is dubious, at least. Apparently, the compilation of a bird species list of "the Pantanal" is not as straightforward as it would seem (da Silva et al., 2001).

Attempts to compile species lists have suffered from three main problems:

Spatial definition of the Pantanal. As there are surprisingly few species lists from the Pantanal floodplain, most comprehensive compilations have included records from adjacent regions. Obviously, the distinctiveness of the Pantanal avifauna will be obscured when tracts of the Cerrado, southern Amazonia, the Chaco and the Atlantic rainforest are all included in a vaguely delimited "region of the Pantanal".

Poor quality of records. The most reliable source of data is still Naumburg (1935), who critically reviewed the bird collections of the Roosevelt-Rondon Expedition together with previous collections from the Mato Grosso (Dubs, 1983a). In later decades, some collections have been obtained in the Pantanal, but the published lists (e.g., Aguirre and Aldrighi, 1983, 1987; Moojen, 1940) suffer from unreliable species identification, as apparently no comparison with major museum collections was possible. Many records are therefore not acceptable without a critical review of specimens (see Pacheco in Tubelis and Tomás, 2001). Additionally there are many published records of observations, which often lack even the most basic documentation (data, precise locality, description of species), let alone physical evidence (specimen, photographs, recordings).

Status of the species. For the evaluation of regional biodiversity, regularly occurring species (residents or migrants) should receive more attention than rare visitors. "Rarities" may gain some local economic importance, though, due to the rapidly growing birding tourism industry, estimated to move 25 billion Dollar per year in North America alone (source: Audubon Society Website, 2000). Due to its central geographic position, the Pantanal has a great potential to receive vagrants from neighboring biomes. The challenge is to distinguish these visitors from originally "rare" species with very low population density, that greatly contribute to the diversity of tropical ecosystems.

For this review, we critically re-evaluated the species lists, applying the criteria of CBRO where possible. However, this analysis should be seen as preliminary. Brazilian field ornithology is advancing fast (Alves et al., 2000; Pacheco, 2003), and excellent field guides combined to better means of documentation will soon greatly improve the available information on the Pantanal avifauna. In particular, one long-term study of bird communities in the northern Pantanal is close to conclusion (João Batista de Pinho, in prep.) and will greatly advance our knowledge.

Caution is also necessary as we still know very little about fluctuations in the distribution of neotropical bird species and in the composition of their communities. The Pantanal is subject to climatic fluctuations, which have repeatedly caused large-scale environmental changes. Anthropogenic landscape changes, and global climatic change are likely to have an impact. Responses of the regional avifauna must be expected, and should be carefully monitored.

How many bird species have been recorded from the Pantanal? Of 766 species mentioned for the "region of the Pantanal", 390 can be considered "confirmed". At least 58 of these species have so far been recorded only from peripheral areas in the extreme south or north of the Pantanal. 153 species have been mentioned without adequate documentation for the Pantanal, and many of these may probably be found in peripheral areas in the future, as some of them are common in adjacent regions. The remaining 223 species have been recorded from areas distant from the Pantanal, or may have been misidentified. The complete list with comments will be published elsewhere. A summary is given in Table 10.

Table 10. Bird species of the Pantanal according to the quality of data (Petermann unpubl.)

	All published records	Confirmed records	Confirmed, but occurring only peripherally	Unconfirmed, but occurrence possible	Not recorded in Pantanal, unlikely to occur
Species	766	390 (51 %)	58	153 (20 %)	223 (29 %)
Genera	431	282			
Families	68	61			

The biogeographical relationships of the Pantanal avifauna. To analyze the biogeographical relationships we excluded exotic species and nearctic migrants, and compared the list of the remaining 368 confirmed species with species lists of the surrounding biomes, Cerrado (Silva, 1995), Chaco (Hayes, 1995: Paraguayan provinces Alto Chaco and Matogrosense), Southern Amazonia and Mata Atlântica (Parker et al., 1996).

358 species of the Pantanal (97 %) have also been recorded in the Cerrado, and between 234 (64 %) and 277 (75 %) in each of the remaining three biomes. 151 species (39 %) have been found in all four biomes and the Pantanal. Both the Cerrado and Pantanal lists include an important group of Southern Amazonian species, which are generally found in gallery forests, and in geographical proximity to Amazonia (Silva, 1996). The avifauna of the Pantanal is thus basically a part of the Cerrado fauna.

There is, however, a small but remarkable influence of the Chaco. Though only a handful of typical Chaco species appear in the Pantanal, several of these are widespread and abundant (e.g., *Paroaria coronata*). On the other hand, no noteworthy influence of the avifauna of the Atlantic rainforest is apparent, though there are some unconfirmed records of typical Atlantic Rainforest species mostly from the southeastern periphery of the Pantanal. Obviously though, none of these is widespread in the Pantanal. Similarly we did not find any evidence that species of the Andes region have ever been recorded in the Pantanal (*contra* Eckstrom and Lanting, 1996).

There are no endemic bird species in the Pantanal (Tubelis and Tomás, 2001). Some species, though, have the center of the distribution in the Pantanal (Table 11), where they are generally common. All of them are weakly differentiated, and are replaced by closely related forms in adjacent regions.

Ecological differentiation of the avifauna: Wetland species vs. terrestrial species. To analyze the degree of dependence of bird species on wetland habitats, we define three categories: "Aquatic species" are those birds, that feed almost exclusively by diving, swimming or wading, or that feed on shores or mudflats in the vicinity of water.

"Wetland dependent species" are species inhabiting chiefly wetland specific habitats, like floodplain forests, palm swamps, marshes, reed beds, or open water (including the "aquatic species").

"Terrestrial species" are all other species, that don't show any preference for wetland habitats, though they may occur there as well.

Table 12 shows, that the vast majority of the species of the Pantanal are terrestrial birds. Among the 64 "aquatic species" the dominant groups are wading birds (Ciconiiformes: Egrets, Herons, Storks, Ibises, Spoonbills: 21 spp.), Shorebirds (Charadriiformes: Sandpipers, Stilts, Plovers and allies: 16 spp., among these 11 nearctic migrants), and Kingfishers (Alcedinidae: 5 spp.), while Waterfowl (Anseriformes: Screamers, Ducks and allies: 8 spp.) is relatively poorly represented.

For most species no breeding records from the Pantanal have ever been published. Most published information regards few conspicuous species (Yamashita and Valle, 1990; Antas and Nascimento, 1996; Guedes and Harper, 1995; Dubs, 1983a, b, 1988, 1992). The estimation of the numbers of breeding species in Table 13 is based on general information about migratory behavior (del Hoyo et al., 1992–2003; Ridgely and Tudor, 1989, 1994; Parker et al., 1996; Sick, 1997; Cintra and Yamashita, 1990; Forrester, 1993) and observations by Petermann (unpubl.).

Colonially breeding species. A number of aquatic and terrestrial species are social breeders. The number of colonial species among terrestrial birds is rather low, with the Monk Parakeet (*Myiopsitta monachus*), several species of Blackbirds (Icteridae) and Swallows (Hirundinidae) as most prominent examples. Of the aquatic birds of the Pantanal, 17 species (36 %) are breeding in colonies: three species of Kingfishers in river banks, and Terns and Skimmers on sandbars. Most conspicuous, however, are the large colonies of wading birds (Storks, Herons, Spoonbills).

In a part of the Pantanal of Poconé, approximately 10 % of the Pantanal, Yamashita and Valle (1990) calculated the total number of wading birds in 10 colonies (of

Table 11. Range-restricted species in the Pantanal (information about distribution from different sources).

Distribution pattern:	Pantanal and E-Bolivia	Pantanal, E-Bolivia, W- Paraguay, NW-Argentina	Pantanal and Bananal (Rio Araguaia)
Species:	n = 5 *Phaethornis subochraceus* *Pseudoseisura unirufa* *Cercomacra melanaria* *Thryothorus guarayanus* *Sporophila nigrorufa*	n = 6 *Ortalis canicollis* *Celeus lugubris* *Xiphocolaptes major* *Inezia inornata* *Cyanocorax cyanomelas* *Paroaria capitata*	n = 1 *Synallaxis albilora*

Table 12. Habitat requirements and status of bird species of the Pantanal (n=390 confirmed spp.).

Aquatic species?	yes	no	no	
Wetland dependent?	yes	yes	no	Total
Species	64	40	286	390
*Genera**	*51*	*36*	*208*	*282*
*Families**	*20*	*18*	*45*	*61*
Breeding	43–47	33–39	220–275	297–361

* some families and genera appear in more than one category

Table 13. Migratory status of bird species of the Pantanal.

Aquatic species?	yes	no	no	
Wetland dependent?	yes	yes	no	Total
Nearctic migrants	13	1	6	20
Austral migrants wintering	4	1	6	11
Other austral migrants	5	2	37	44
Nomadic	11	0	2	13

13 colonies found) as 40–50.000. The largest colonies had more than 10.000 birds. However, this number does not reflect the total population of colonial breeding waterbirds in this area. The timing of breeding activities depends on the water level and there are differences between the species, the regions, as well as between years (Yamashita and Valle, 1990; Willis, 1995). Diving species (*Phalacrocorax brasiliensis, Anhinga anhinga*) begin the breeding activity earlier, while the water level is still high. As these species are dark colored the respective colonies are locally called "*viveiros pretos*" ("black colonies"; Willis, 1995), in contrast to the "white colonies" of Egrets and Roseate Spoonbills, which become active during the dry season. "Black colonies" are more difficult to find (Yamashita and Valle, 1990), which is especially true for the nocturnal species Night Heron and Boat-billed Heron, which form well concealed colonies in riparian forest, sometimes together with Agami Herons or other species (Petermann, unpubl.).

Migrant species. The number and origin of migrant species in relationship to habitat is shown in Table 13. Migration is better known in nearctic species, as for neotropic species the exact limits of the breeding area are usually not well established, and an overlap of breeding and wintering areas is frequent. A few nearctic migrant species also have resident populations in South America, including the region of the Pantanal (*Elanoides forficatus, Gallinago* sp.*, Himantopus* sp.*, Vireo olivaceus*). However, nearctic migrants of those species apparently do not reach the Pantanal. "Other austral migrants" in Table 13 includes resident species of the Pantanal, which leave at least partially the Pantanal in the non-breeding season, as well as passing migrants.

Due to its geographic position the Pantanal has very limited importance for wintering migrant waterfowl (Anseriformes). Of some 20 nearctic migrants wintering in the Neotropics, only one (*Anas discors*, not known from the Pantanal) regularly migrates to the south of the equator (Rappole et al., 1995), while austral waterfowl species do not perform long-distance migrations (de la Peña and Rumboll, 1998), and only few species reach the Pantanal as rare visitors.

Very different is the situation among shorebirds. 25 nearctic species are known to winter in the southern Neotropics, mostly along the coasts. There is considerable migration through central South America (Antas, 1983; Stotz et al., 1992; Hayes et al., 1990) to important wintering areas in eastern Argentina. All of those species which take a continental migration route should be expected in the Pantanal. Until now, up to 22 species of nearctic shorebirds have been mentioned for the Pantanal (e.g., Dubs, 1992; Antas, 1994), though only 14 species are confirmed. There is a very limited number of austral migrant shorebirds in South America, and none of those migrate as far north as the Pantanal.

The Pantanal bird fauna in comparison to other neotropical wetlands. A comparison of the major neotropical wetlands clearly reveals the difference between temperate wetlands (e.g., in the High Andes; Fjeldså and Krabbe, 1990), with higher numbers of swimming species (Waterfowl, Grebes, Rails) and tropical wetlands which are characterized by a high number of wading birds (Storks, Herons, Ibises) and Kingfishers (see Reichholf, 1975). The Pantanal clearly classifies as tropical wetland, along with the Llanos of the Orinoco and the Amazonian floodplains. The composition of the group of aquatic species in these three large wetlands is extremely similar, indeed, with few exceptions all species can be encountered in all three regions. In Amazonia, several species are restricted to the more coastal areas.

As concerns wetland dependent terrestrial species, the biodiversity of Amazonia is much higher with some 100 species depending on floodplain habitats (Remsen and Parker, 1983). Remarkably, many of these species have also been found in the Llanos, but very few in the Pantanal.

The importance of the Pantanal for the conservation of avian biodiversity. As could be shown before, the Pantanal has little importance for endemic bird species, as all species have also been found in adjacent regions. The total species number of the Pantanal is high, but does not reach the extraordinary diversity of amazonian rainforest sites. This was to be expected, as only a limited portion of the Pantanal is forest. Further the notably more seasonal climate of the Pantanal as compared to Amazonia or the Llanos of the Orinoco must be expected to limit the southward expansion of Amazonian species.

Of all the species recorded from the Pantanal, very few are considered threatened on a global scale (Wege and Long, 1995). According to BirdLife International (2004) are critically endangered: *Numenius borealis*; endangered: *Anodorhynchus hyacinthinus, Harpyhaliaetus coronatus, Sporophila palustris*; vulnerable: *Penelope ochrogaster, Sporophila cinnamomea, S. nigrorufa, Alectrurus risora*; near threatened: *Rhea americana, Amazona xanthops, Neochen jubata, Polystictus pectoralis, Euscarthmus rufomarginatus*. However, this is a circular argument: due to the size and still excellent conservation of the Pantanal, any species with a healthy population in the Pantanal will not be considered endangered on a global scale. But this should no longer be taken as granted. The environmental impact studies concerning the improvement of the Paraguay River for navigation (Hidrovia Paraguay-Paraná-project, e.g., Huszar et al., 1999; EDF and CEBRAC, 1997) have shown, that even limited interventions could affect a great proportion of the gallery forests of the Pantanal, which in turn are a key resource for colonially breeding waterbirds (Schnack and Petermann, 1999), and other fauna (Lourival et al., 1999).

Though reliable numbers of population sizes are available for few species only, there is no doubt, that many bird species of the Pantanal, especially aquatic ones, have a major part of their global population in the Pantanal wetland. Among those are some very "charismatic" or endangered (Bird Life International, 2004) species, like the Jabiru stork, Hyacinth Macaw, Golden-collared Macaw, or Chestnut-bellied Guan (*Jabiru mycteria, Anodorhynchus hyacinthinus, Ara auricollis, Penelope ochrogaster*). It will depend on the conservation of the Pantanal, whether these and other species can be kept out of the "Red lists" of endangered species in the future.

Mammals

Similar to the birds, several species lists exist about the mammals of the Pantanal, however, a full record is still missing. Especially the small, species-rich taxa such as bats and small rodents require a thorough revision. Highest numbers of regional inventories are given by Schaller (1983) and PCBAP (Brasil, 1997) with 64 and 75 species, respectively. For the entire floodplain Rodrigues et al. (2002) indicate 93 species (Table 14). This is less than 50 % of the species number of the Cerrado (194 species, e.g. Marinho Filho et al. (2002). However, new records are reported frequently as, for instance, by a rapid assessment that was realized in 2001 in the National Park of the Pantanal of Mato Grosso and the Reservas Particulares do Patrimonio Natural (RPPN) Acurizal and Penha (Rossi et al., unpubl.). It lists 56 species belonging to 49 genera, 20 families and 8 orders and includes a couple of species not mentioned in the list of Rodrigues et al. (2002). An analysis of different inventories of mammals in and around the Pantanal and the extrapolation of distribution patterns of mammals in the Brazilian Cerrado and the Argentinean Chaco lead to an estimated number of 132 mammal species in the Pantanal (Alho and Lacher, 1991; Fonseca et al., 1996; Marinho Filho et al., 1998; Brasil, 1997). 91 % of the Pantanal-species also occur in the Cerrado, 85 % in Amazonia and 84 % in the Chaco. Total number of species in the Pantanal, the surrounding areas of Cerrado and Chaco and adjacent areas of Amazonia reaches 149 species, that should be the maximum number to be expected (Table 14). In all inventories, bats make up for about one third of the total species number.

Contrary to the African savannas, the Pantanal wetland is not characterized by large herbivorous mammals and its diversity and abundance of native ungulates is relatively low. Carrying capacity for large ungulates, however, is high as shown by the large number of cattle that maintain the "parkland" aspect in wide areas of the Pantanal for over 200 years. Schaller (1983) estimated a mammalian biomass of 380 kg km^2 for native species, mainly tapir, deer, peccary and capybara, and of 3,750 kg km^2 for cattle, thus a ratio of 1:10 between natural and introduced mammal biomass on the Acurizal ranch, now a private reserve, in the southern Pantanal. The most conspicuous native ungulates are the marsh deer *(Blastocerus dichotomus)* and the pampas deer (*Ozotocerus bezoarticus*) which are listed as endangered in Brazil and need efficient monitoring and conservation programs (Mourão et al., 2000). Tomas et al. (2001) report population densities of 0.382 ± 0.362 ind km^{-2} for the dry and 0.395 ± 0.144 ind km^{-2} for the wet season for the marsh deer.

The capybara (*Hydrochoerus hydrochaeris)* is a large rodent which is highly adapted to the changing environmental conditions in the Pantanal. Capybara live in organized families that forage on grasses and aquatic macrophytes along the borders of rivers and lakes where they can find water, feeding grounds and some woody vegetation as shelter (Schaller and Crawshaw, 1981; Schaller, 1983), therefore, proposals have been made to manage it as a protein source (e.g., Alho, 1986). Top predators of the Pantanal are the jaguar *(Panthera onca)* and the giant river otter *(Pteronura brasiliensis)* which are both well adapted to wetland conditions. Also well adapted is the crab-eating raccoon *(Procyon cancrivorus)*.

Apart from these flood adapted species, the Pantanal also harbors a relatively large numbers of more terrestrial

Table 14. Orders, families, and number of genera and species of mammals in the Pantanal of Mato Grosso, in the Pantanal and surroundings (*), and in adjacent areas of Amazonia, *Cerrado* and *Chaco* (in parentheses), according to Rodrigues et al. (2002) and Brasil (1997). (Differences in the number of genera in some families, e.g., in the Felidae and Tayassuidae are the result of different taxonomic systems. The listed species are identical.)

Order	Family	Genera (n)	Species (n)
Didelphimorpha	Didelphidae	7 (11) 11*	7 (15) 14*
Xenarthra	Dasypodidae	4 (5) 5*	4 (7) 7*
	Myrmecophagidae	2 (2) 2*	2 (2) 2*
Chiroptera	Emballonuridae	4 (4) 4*	4 (4) 4*
	Noctilionidae	1 (1) 1*	2 (2) 2*
	Mormoopidae	0 (1) 1*	0 (1) 1*
	Phyllostomidae	15 (18) 16*	19 (30) 21*
	Vespertilionidae	2 (3) 3*	3 (4) 4*
	Molossidae	5 (5) 5*	8 (9) 8*
Primates	Callitrichidae	1 (1) 1*	1 (1) 1*
	Cebidae	3 (5) 5*	3 (5) 5*
Carnivora	Felidae	5 (6) 6*	6 (8) 8*
	Canidae	4 (5) 5*	4 (5) 5*
	Procyonidae	2 (3) 3*	2 (3) 3*
	Mustelidae	5 (5) 5*	5 (5) 5*
Perissodactyla	Tapiridae	1 (1) 1*	1 (1) 1*
Artyodactyla	Tayassuidae	2 (2) 1*	2 (2) 2*
	Cervidae	3 (3) 3*	4 (4) 4*
Rodentia	Sciuridae	1 (1) 1*	1 (2) 2*
	Muridae (Cricetidae*)	7 (13) 11	7 (23) 18*
	Erethiozontidae	1 (1) 1*	1 (1) 1*
	Caviidae	1 (2) 1*	1 (2) 1*
	Hydrochoeridae	1 (1) 1*	1 (1) 1*
	Agoutidae	1 (1) 1*	1 (1) 1*
	Dasyproctidae	1 (1) 1*	1 (2) 2*
	Ctenomyidae	0 (1) 1*	0 (1) 1*
	Echimyidae	2 (6) 6*	2 (7) 7*
	Leporidae	1 (1) 1*	1 (1) 1*
Total	28	82 (109) 103*	93 (149) 132*

mammals, like the coati *(Nasua nasua),* the puma *(Felis concolor)*, ocelot *(Felis pardalis)*, jaguarundi *(Felis yagouarundi)*, and the giant anteater *(Myrmecophaga tridactyla)*. Traces of the extremely rare giant armadillo *(Priodontes maximus)* are regularly reported however its current status in the Pantanal is uncertain. Non flooded *terra firme* islands and levees are indispensable for their occurrence during the flooding period. Some species such as the maned wolf *(Chrysocyon brachyurus)* seem to migrate between the Pantanal and the surrounding Cerrado habitats. The rareness of contiguous dense forests seems to be the reason for the low numbers of rodents and monkeys.

The role of exotic species

The physiological stress related with the change between pronounced terrestrial and aquatic conditions make floodplains a difficult place for exotic species. But there are exceptions, such as flood-tolerant species from other floodplain areas or ruderal plants with short life cycles, high reproduction rates and flood resistant propagules. Rivers serve as natural dispersal and migrating routes for plant and animal species of the entire catchment area and from abroad. Seidenschwarz (1986), studying the vegetation of the upper Amazon River floodplain points to the importance of river floodplains in the distribution of ruderal plants. Frequent disturbance by floods and droughts reduces competition with native species and favors colonization of strongly disturbed erosion and deposition areas along the main river channels.

Major scale introduction of exotic plants and animals into South America started with the arrival of the Europeans. A few exotic bird species established themselves in Brazil, such as Feral Rock Dove and the House Sparrow from Europe, or the African Common Waxbill (*Columba livia, Passer domesticus, Estrilda astrild*). However, in the region of the Pantanal these species are still restricted to urban centers at the periphery, but have not established inside the Pantanal. The only colonization of near-natural habitats by a non-native bird species is the paleotropic Cattle Egret (*Bubulcus ibis*), which has invaded the Americas at the turn of the 19th century, following the spread of domestic cattle throughout the Neotropics. In the Pantanal it must have arrived in the middle of the 20th century, but when it was first recorded in the 1960s it was already common. The gekkonid lizard *Hemidactylus mabouia* that possibly arrived together with the slaves from Africa, is well established in almost every periantropic habitat in farms and settlements throughout the Pantanal, as it is elsewhere in Brazil (Avila-Pires, 1995). The grasses *Cynodon dactylon* (Africa or Indo-Malaysia), *Eleusine indica* (probably S.E. Asia), *Dactylotenium aegyptium* (trop. Africa), *Panicum repens* (Australia), the herb *Sphenoclea zeylanica* (trop. Africa), and the tree *Acacia lebbeck* (S.E. Asia) are common but they do not create problems for the native fauna and flora. Two African grasses, *Hyparrhenia rufa* and *Panicum maximum*, have been introduced in high lying areas to improve pasture, but both species are little flood tolerant. There is rising concern about *Brachiaria subquadripara* (tanner grass), an aggressive old world wetland grass, that was introduced some years ago and is spreading now in some parts of the Pantanal near the Pantanal National Park (Pott et al., 2001).

Cattle and horses were introduced about 300 years ago in the Pantanal and developed specific wetland races (*tucura,* and *cavalo pantaneiro*). During the last decades, the *tucura* became substituted by nelore that is more productive (Mazza et al., 1994). Aerial surveys (with correction of visibility), indicate 4.5 million cattle in the Brazilian part of the Pantanal, densities being higher in less inundated areas and lower in deeply inundated or forested areas (Mourão et al., 2002). Cattle play an important role in maintenance of the parkland aspect of the Pantanal and low density cattle ranching is considered an ecologically sound and sustainable management method. Major risks arise from high stocking rates and increasing deforestation of forested areas to increase pasture area. About 49,000 horses exist in the Pantanal being used mainly for the management of the cattle population.

Probably during the Paraguay War (1864–1870), pigs developed a feral population (*porco-monteiro*) that is managed by the local population. Aerial surveys indicate about 9,800 groups. A few decades ago, water buffaloes (*Bubalus bubalis*) were introduced, reaching now a population of about 5,100 specimen (numbers not corrected for visibility, Mourão et al., 2002). Feral pigs and water buffaloes can create major problems to the ecosystem, however, there are no studies about their impact on the Pantanal.

Of major importance are some animal diseases that were introduced with cattle and horses. Mal-de-cadeiras (*Trypanosoma evansi*) was probably introduced by Spanish settlers in the sixteenth century and affected also the populations of the capybara (*Hydrochoerus hydrochaeris*) (Franke et al., 1994, Silva et al., 1995). The parasite has also been found in coatis (*Nasua nasua*) and dogs (Nunes and Oshiro, 1990). Since the 1930s the viral Foot- and Mouth-Disease is observed and severely affected the populations of deers (Wilcox, 1992). To what extent recently introduced diseases and parasites, such as the hornfly (*Haematobia irritans*) observed since 1991, (Barros et al., 2002), the equine infectious anaemia (swamp fever) created by a retrovirus and transmitted by horseflies (tabanids), observed since 1974 (Silva et al., 2001), and the bovine trypanosomiasis (*Trypanosoma vivax*), also transmitted by tabanids and observed since 1996 (Silva et al., 1997) can affect the populations of wild animals is not known.

Several exotic fish species are created in fish culture facilities in the catchment area of the Pantanal, such as tilapia (*Tilapia mossambica*) and the African catfish (*Clarias* sp.). Certainly, specimens have escaped into the river system, but there is no information about the establishment of these species inside the Pantanal. The Amazonian Tucunaré (*Cichla ocellaris*), a voracious predator, was introduced for sport fishing and is now abundant in the Piquirí River, left hand tributary of the São Lourenço River (F. A. Machado, Federal University of Mato Grosso, pers. comm.) and spreading in the Taquarí River system (W. J. Junk, pers. observ.).

27 foreign useful herbaceous plant species and 17 tree species are planted by local farmers without major effects on the natural vegetation. Roads constructed on dikes serve as immigration routes of strictly terrestrial plants from the uplands into the Pantanal, as can be shown by the plant communities along the roadsides. 99 species are listed but, there is no evidence that these species become permanently established in the floodplain, and create problems for the native vegetation.

Impressive examples for quick dispersal of exotic species are the African bee and the Asian golden mussel. African bees (*Apis mellifera adansoni*, *A. mellifera capensis, A. mellifera scutelata*) were introduced in 1956 to São Paulo State, where they escaped and formed hybrids with local bees introduced from Europe decades ago, such as *Apis mellifera ligustica*. These hybrids extended theire range with a mean velocity of about 110 km yr^{-1}. The very aggressive bees (*Apis mellifera* hybrid de *ligustica* with *scutelata*) also occur in the Pantanal. In March 2004, they attacked scientists of the University of Mato Grosso and killed our collegue Vangil Pinto da Silva.

The Asian golden mussel (*Limnoperna fortunei,* Mytilidae), about one centimetre long, was introduced in 1993 probably with ballast water by ships from Asia to the La Plata system. In 1995 it reached Santo Tomé on the middle Paraná River about 400 km upstream (Darrigran and Ezcurra de Drago, 2000) and was recorded in 2001 in the Pantanal, about 2000 km from the mouth (C. T. Callil, Federal University of Mato Grosso, pers. comm.). The mussel fixes with byssus on hard substrates and creates serious problems for instance on water supply plants by clogging water intake pipes. Its impacts on the ecosystem are not studied yet. Several fish species heavily feed on it without affecting its spread. The mussel will probably negatively affect native mussel populations in the river channels and permanent water bodies by growing on their shells and hindering filtration. To what extent the species is able to colonize the floodplain proper is still unknown, but its low resistance against periodic drought will probably limit its spread.

A major point of preoccupation of the local ranchers is the undesired spread of native plants into pastures, such as the herb *Ipomoea fistulosa (algodão bravo)*, and the trees *Vochysia divergens* (*cambará*), *Combretum lanceolatum, C. laxum, Vernonia brasiliensis, Sphinctanthus hasslerianus, Mimosa pellita (M. pigra), Byrsonima orbygniana, Licania parvifolia* and *Couepia uiti*. Several authors speculate about reasons for the spread of these species, such as overgrazing by cattle, large scale changes in environmental conditions or change in global climate, however, without any data. A detailed study of Nunes da Cunha and Junk (2004) about the spread of *Vochysia divergens* points to multiannual natural dry and wet periods as determining factor. *V. divergens* is a flood adapted tree that is spreading during wet periods and restricted during multiannual droughts because it does not tolerate the impact of wild fires.

Threats and protection

Because of its long distance from major urban centers and its difficult access, the Pantanal has been on the sidelines of the economic development in South America. The European immigrants used the area mostly by low density cattle ranching on natural pastures. Pasture areas were slowly increased by cleaning parts of periodically flooded shrub-savannas (*campo sujo*) from shrubs and trees, but maintaining forested islands on elevations (*capões* and *cordilheiras*), in depressions (*landis*) and on levees along river courses and around lakes. Grazing cattle controlled the re-growth of shrubs and trees and maintained a "park-landscape" of scenic beauty with high habitat and species diversity. Most wildlife was rather well protected because of the availability of cheap beef. Travelers report on herds of 300 to 400 deer and huge numbers of peccaries, tapirs and jaguars (Ulrich, 1936). In the second half of the last century, poaching for hides strongly reduced the abundance of most species and threatened jaguars, otters, and deer, a problem that is not yet completely under control.

At the beginning of the 1970s, the Brazilian government established large development programs to stimulate economic productivity of the entire Paraguay River catchment area, including the Pantanal. Large scale soybean production in the catchment resulted in increased erosion and sediment deposition inside the Pantanal with dramatic consequences. For instance, the sediment load rose the river bed of the Taquarí River and because of the low declivity, the river left the former channel and floods, since a couple of years, an area of about 11,000 km^2 for much longer periods than before (Fig. 1).

Several hydroelectric power plants are planned or under construction on large tributaries of the upper Paraguay River. In November of 1999, a huge reservoir (428 km^2) at the Manso River near Cuiabá was closed interrupting the migration route of many fish species from the Pantanal to their upstream spawning grounds and also altering the flood regime of the Cuiabá River inside the Pantanal. The immediate effects of the lake filling on terrestrial and volant vertebrates have been monitored in detail by Alho et al. (2003), but the long term consequences of the hydrological changes on the low-lying plains are not yet understood. Some negative effects have already been observed, e.g., on shorebirds that lost their nesting areas on exposed sand beaches due to a higher discharge from the reservoir at low water period. The vegetation will require decades to readjust to the new hydrological conditions.

A major threat is the plan to rectify and deepen the sinuous channel of the Paraguay River to facilitate ship transport through the Pantanal (*hidrovia* project). This would dramatically affect the hydrology of the entire Pantanal with far reaching negative consequences for flora, fauna and the local human population (Ponce, 1995; Hamilton, 1999). In 2000, the Brazilian government stepped back from this plan, however private enterprises continue with the construction of infrastructure against heavy resistance of NGO's.

The increasing competition with the cattle ranches on artificial pastures of the surrounding upland are forcing ranchers inside the Pantanal to increase the number of animals and accelerate deforestation of forested high lying areas to provide additional pasture areas. The destruction of these key habitats will on the long term severely affect species diversity.

Conservation plans should consider the wide home range of large "flagship species" and the necessity of contiguous adequate migration corridors between the conservation units. Telemetry studies have shown territory sizes of 25 to 38 km^2 in jaguar females and 90 km^2 in males (Schaller and Crawshaw, 1980) in the Pantanal. Quigley and Crawshaw (1992) developed a comprehensive conservation plan for the species in the region in which they recommend the establishment of large reserves and the maintenance of gallery forests as corridors for inter-refugia movement. Mammals are especially sensitive to fire, and even large mobile species such as marsh deer and jaguar can become killed (Wantzen, pers. obs.).

Presence of human settlers always implies environmental problems, however, traditional farmers generally hunt moderately on more common species as the paca (*Agouti paca*), brocket deer (*Mazama* spp.), and nine-banded armadillos (*Dasypus novemcinctus).* There is also heavy pressure on predators, e.g., jaguar, puma and eagles. Large raptors are usually not tolerated near fazendas because they frequently attack free-living domestic fowl. Cats and dogs often hunt in the surroundings of the settlements, but are not able to survive in the wilderness. Increasing ecotourism is beginning to stimulate the local economy, however, it is also bringing many environmental and socio-cultural problems to the area, mainly by little controlled sport fishers (more than 100,000 sport fishers in the Brazilian Pantanal) and little adapted tourist facilities (about 20,000 eco-tourists per year in the northern Pantanal; Köhnlein, 1995).

Rising concern about the future of the Pantanal led to a variety of activities by universities, state- and government agencies, and national and international NGO's (Harris et al., 2005). According to a conservation assessment of the WWF and the Biodiversity Support Program, the Pantanal was considered "globally outstanding" (rank 1 of 4), in terms of biological distinctiveness, "vulnerable" (rank 3 of 5) in terms of conservation, and has "highest priority" (rank 1 of 4) in regional priorities for conservation action (Olson et al., 1998). In 1988, the Pantanal was proclaimed by the Brazilian Constitution as National Heritage, in 1993 by UNESCO as Ramsar Site, and in 2000 as World Biosphere Reserve. In the same year, UNESCO also granted the Pantanal the Natural World Heritage certificate, and in 2002 the Pantanal Regional Environmental Program related to the United Nations University (UNU/PREP) was founded at the University of Mato Grosso, Cuiabá. UNU/PREP pretends to establish a network of national and foreign institutions interested in sustainable management and protection of the Pantanal.

Actually, there are two national parks and one ecological station under federal administration in the Brazilian part of the Pantanal, some state parks and an increasing number of private protected sites (e.g., Reservas Particulares do Patrimonio Natural – RPPN, administrated by the NGO ECOTROPICA and the by Social Service of Commerce – SESC). Total protected area corresponds to 360,000 ha (2.6 % of the Brazilian Pantanal) (http://www.ibama.gov.br/). In Paraguay, the National Park Rio Negro was recently expanded to 123,786 ha. In Bolivia there are the Natural Area of Integrated Management San Matías (ANMI San Matías) of 2,918,500 ha, the National Park and Area of Integrated Management Otuquis (PN-ANMI Otuquis) of 1,005,950 ha and the Municipality Reserve of Tucavaca of 262,305 ha. These areas include flooded areas but also uplands in different proportions (http://www.fobomade.org.bo/pantanal_bolivia/conociendo.php) (Fig. 1).

Discussion and conclusions

The geographic isolation and the very slow economic growth of the Pantanal led to the maintenance of rather pristine conditions of the area, but also to a dramatic lack of knowledge about structures and functions including species diversity. With the beginning of large scale development plans for the Pantanal and its catchment area, the Brazilian government also stimulated research projects. However, lack of infrastructure and a low number of qualified local scientists retards until today the elaboration of a sound data base that is required for of the already ongoing or planned large development projects.

A good example for this statement is the state of knowledge about species diversity, and the natural and anthropogenic factors affecting it. Species lists even on well known groups such as trees, herbaceous plants, mammals, fish and birds are incomplete and do not consider distribution pattern inside the Pantanal. Authors often include upland species of the catchment area in their species lists that have not been confirmed for the Pantanal lowland. Life history traits, ecological requirements, and migration pattern of most species are unknown. Major gaps exist about terrestrial and aquatic invertebrates (Table 15). This hinders detailed environmental impact analyses of large ongoing development projects and makes predictions about the impact of planned projects very difficult.

Species composition and diversity of the Pantanal is the result of paleoclimatic history and recent climatic and hydrological conditions. During and after the last ice age and probably also in earlier glacial periods, the Pantanal passed through periods of heavy drought. Wetland organisms were extinct or survived in refuges along the lower Paraguay River, and in moist areas of the surrounding Cerrado, the adjacent Argentinean Chaco and Amazonia. When the climate became wetter, wetland areas in the Pantanal expanded and wetland organisms immigrated from the refugia of the surroundings. Highly mobile spe-

Table 15. Number of families, genera and species of different plant and animal taxonomic categories, confirmed for the Pantanal of Mato Grosso. Species lists of higher plants and vertebrates cover about 80 to 90 % of the total. The numbers of most aquatic and all terrestrial invertebrate groups is not known. For data sources see this paper.

Taxonomic category	Families (n)	Genera (n)	Species (n)
Algae	30	63	337
Herb. terr. Plants	76	381	900
Herb. aquat. Plants	57	108	248
Woody plants	70	380	756
Aquatic Invertebrates			
Testacea	10	34	246
Ciliata	32	40	55
Rotifera	24	57	285
Cladocera	7	35	117
Copepoda	2	13	33
Ostracoda			15
Bivalves	5	10	23
Aquatic snails	3	4	5
Oligochaetes	8	20	37
Terr. Invertebrates	?	?	?
Fishes	36	161	263
Reptiles	17	63	96
Amphibians	5	16	40
Birds	61	282	390
Mammals	28	94	130

cies were more efficient in comparison to less mobile species as shown by the large number of aquatic birds.

Drought tolerant species lost part of their habitats but found refuges on high lying areas. Most mammals, 50 % of the reptiles and 73 % of the birds are terrestrial species that have a wide distribution in the dry areas of the Cerrado, Chaco and Amazonia. About 78 % of the 1,148 grasses and herbs are terrestrial. From 85 analyzed tree species 26 are terrestrial, 4 occur only in habitats subjected to long term inundation, and the other 55 species show a wide range of periodical flood and drought tolerance. An impressive morphological and physiological plasticity allows the co-occurrence of many terrestrial and wetland grasses and herbaceous plants on moist ground during the rainy season. A large seed bank in the sediments that is activated only in small portions at a time, allows the recolonization of the floodplain by terrestrial and aquatic species after floods and droughts and gives the system a high resilience against unpredictable hydrological events that frequently occur in the Pantanal. The large habitat diversity that includes permanent aquatic, periodically flooded and permanently dry habitats is the ecological basis for the species diversity.

Our knowledge about terrestrial invertebrates and their adaptations to periodic flooding is not sufficient yet to make general statements about species diversity and to build hypotheses about the impact of environmental factors. Several taxa common in Amazonian black water inundation forests were missing or less abundant in the *Vochysia divergens* forest studied in the Pantanal. Environmental factors such as fire, sandy soils, the pronounced dry periods or the island character of the study site may be the reasons. Also some adaptations to flooding, frequently found in terrestrial invertebrates of Amazonian floodplains were not yet detected in the Pantanal. These findings may point to a lower level of adaptation of terrestrial invertebrates to prolonged flooding, as already shown by the woody vegetation.

Important environmental factors for species composition are the rather predictable low flood amplitude and the pronounced seasonality in rainfall. The shallow flooding of large areas with transparent water during several months favors the development of luxuriant and species-rich submerged and emergent herbaceous plant communities. Shadowing by a flood tolerant forest is hindered by the pronounced dry periods, accompanied by frequent wild fires that restrict tree growth. This explains the very large diversity of aquatic macrophytes, but also the high number of terrestrial grasses and herbs. Wading birds find excellent living conditions in the shallowly flooded savannas and occur in large species numbers and great abundance.

Interpretation of the importance of the specific environmental conditions of the Pantanal on species diversity is facilitated when comparing them with the neighbouring Amazon River floodplains that are quite different. There, the mean flood amplitude reaches about 10 m and soil moisture allows tree growth in all habitats inundated less than about 240 d yr^{-1} and up to a water depth of about 8m. Aquatic macrophyte diversity is strongly reduced and free floating submersed and emergent plants that can accompany the fluctuating water level prevail. Submersed plants rooted in the ground are missing. Terrestrial herbaceous plants colonize very low lying areas without forest cover that fall dry during few months only or have to live under very poor light conditions in a dense floodplain forest. Large wading birds find good living conditions only during low water period. Only species that are able to fish from tree branches near the surface or from floating macrophytes such as most herons and egrets (e.g., *Ardea cocoi, Casmerodius albus*, *Egretta thula)* occur throughout the year.

There are very few endemic species described for the Pantanal. A time span of a few thousand years after the last heavy dry period was obviously not long enough to produce endemic species. This seems to be strange, because studies on the fish fauna in the large East African lakes show, that speciation in the tropics can happen in a few thousand years period (Kaufmann et al., 1997). This process was certainly hindered in the Pantanal by the flood pulse that forces mobile species to move from the floodplain to the rivers and back, and passively transports propagules or less mobile species by water current. This active and passive mobility leads to a permanent genetic exchange in the entire area and hinders speciation by spacial segregation of populations.

The Pantanal is subject to strong multi-annual variations of flood and dry periods. These periods strongly affect aquatic and terrestrial organisms. During the very high floods in the early 1970s, about 30 % of the cattle population and an undescribed number of native terrestrial animals died (Cadavid García, 1981). Fire is an additional stress factor of the system that becomes critical in multi-annual dry periods. Populations of long living plants and animals require more time to re-establish after such periods as shown for *Vochysia divergens* (Nunes da Cunha and Junk, 2004). Climate models predicting changes in global climate indicate a rise of 1.4–5.8 °C, the larger temperature increase being in higher latitudes than in the tropics. By the second half of the 21th century, at low latitudes, both regional temperature increases and decreases are expected over land areas, with larger year-to-year variations in precipitation and associated heavy droughts and floods (Intergovernamental Panel on Climate Change; IPCC, 2001). This increase in extreme droughts and floods will heavily stress the organisms in the Pantanal and add to human induced stress factors.

Since the formation of large wetland areas inside the Pantanal, the area experienced the invasion of many plant and animal species from the surrounding biomes, a process that probably continues until today. Large habitat diversity and natural and man-induced disturbances make the Pantanal susceptible for species invasion. This also holds true for exotic species. Their number and related problems are still small, but strong efforts should be undertaken to avoid their import because negative side effects could be dramatic and their control extremely costly, or even impossible.

The Pantanal is one of the outstanding large wetlands of the world and requires highest priority in environmental protection, as indicated by all national and international environmental agencies. However, efficient protection will be reached only, when an integrated management plan for the entire upper Paraguay River basin is elaborated and implemented that considers the environmental impact on the Pantanal. Considering the overwhelming importance of the flood pulse for structures and functions and the maintenance of biodiversity of floodplain systems, development projects that modify the natural hydrological regime in large scale, such as reservoirs, dikes and channels should be avoided. Strong efforts are required to reduce the input of sediments and pollutants (agrotoxics, mercury, industrial and domestic wastes from mayor cities, etc.) into the rivers that deposit the material inside the Pantanal.

Furthermore, species diversity of the Pantanal is closely linked to habitat diversity. The maintenance and protection of key habitats, such as different types of forests, lakes and channels in areas used for cattle ranching should be given top priority. The different types of forests are key habitats for the maintenance of mammal and bird diversity, whereas permanent lakes and channels are crucial for the survival of aquatic plants and animals. More than this, connectivity of these divergent habitats must be guaranteed, as well as connectivity between rather protected areas in the core of the Pantanal and in adjacent biomes. This is the basic requirement to maintain genetic flow and survival of large, vagrant "umbrella species". In this sense, ecological corridors must be implemented and their structure and function monitored over time.

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